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THE ECOLOGY OF INTERFACES—Riparian Zones

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ABSTRACT

Riparian zones possess an unusually diverse array of species and environmental processes. The ecological diversity is related to variable flood regimes, geographic channel processes, altitudinal climate shifts, and upland influences of the fluvial corridor. The resulting dynamic environment supports a variety of life history strategies, biogeochemical cycles and rates, and organisms adapted to disturbance regimes over broad spatial and temporal scales. Riparian zone management has been effective in ameliorating many ecological issues related to land use and environmental quality. Riparian zones continue to play essential roles in water and landscape planning, in restoration of aquatic systems, and in catalyzing institutional and societal cooperation for these efforts.

INTRODUCTION

Natural and managed ecosystems are mosaics of environmental systems or patches (Wiens 1992, Forman 1995). These patches are defined by their boundaries, with the transition zone between adjacent patches recognized as an interface. First described nearly a century ago (Clements 1905), interfaces occur when structural or functional properties of ecological systems change discontinuously in space or time. Interfaces are characterized by (a) the rate of change in variables in space or time, (b) the contrast between the states of the patches on either side of the interface, and © the homogeneity (or variance) of variables within the interface.

Several terms have been used to describe interfaces, and these are used synonymously in this review: transition zone, ecotone, and boundary (Holland et al. 1991, Naiman and Decamps 1990, Hansen and di Castri 1992). Each term can be defined as a zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of interactions between adjacent ecological systems (Holland et al. 1991).

The phrase "ecological system" usually includes such commonly described biological assemblages as communities, ecosystems, and biomass. Thus, an interface can be described as a type of transition zone which, like

ecosystems and biomass, possesses specific physical and chemical attributes, biotic properties, and energy and material flow processes but is unique in its interactions with adjacent ecological systems (Naiman et al. 1988, Risser 1993). The strength of these interactions, which vary over wide temporal and spatial scales, appears to be controlled by the contrast between adjacent resource patches or ecological units. In general, an interface may be thought of as being analogous to a semipermeable membrane regulating the flow of energy and material between adjacent resource patches (Naiman et al. 1988). Even though research on interfaces has expanded significantly in the last decade, understanding boundary characteristics and how they relate to ecosystem and regional-scale patterns and processes remains in the formative stage. Nevertheless, interfaces are widely recognized as having some interesting characteristics: elevated abundance of resources; important control points for energy and material flux; potentially sensitive sites for studying interactions between biological populations and their controlling variables; support of relatively high biodiversity; maintenance of critical habitat for rare and threatened species, and refuge and source areas for pests and predators (Naiman et al. 1988, Holland et al. 1991, Hansen and di Castri 1992, Risser 1993). Other characteristics that may be specific to a particular type of interface include: sites for longitudinal migration (i.e., along windbreaks or riparian zones), influence on the climatic regime of the surrounding area or on the development of soil conditions (i.e., forest/grassland interfaces), and as genetic pools or sites for active microevolution (i.e., forest/agricultural interface; Forman 1995). It is well known that interfaces between terrestrial and freshwater ecosystems are particularly sensitive to environmental change (Naiman and Decamps 1990, Malanson 1993). Examples include riparian forests, marginal wetlands, littoral lake zones, floodplain lakes and forests, and areas with groundwater-surface water exchanges.

In this article we specifically consider riparian zones associated with streams and rivers because of their ability to encompass most of the characteristics considered to be important for interfaces. In general, natural riparian zones are some of the most diverse, dynamic, and complex biophysical habitats on the terrestrial portion of the Earth (Naiman et al. 1993). The specific emphasis on riparian zones in this article provides an overview of important characteristics, describes the physical effects on adjacent

environments, summarizes the ecological characteristics, and discusses the consequences of environmental alterations on form and function.

THE RIPARIAN ZONE

Riparius is a Latin word meaning "of or belonging to the bank of a river (Webster's New Universal Unabridged Dictionary). The term riparian has generally replaced the Latin and refers to biotic communities living on the shores of streams and lakes. Riparian zones, as interfaces between terrestrial and aquatic systems, encompass sharp environmental gradients, ecological processes and communities (Naiman et al. 1993). Riparian zones are an unusually diverse mosaic of landforms, communities, and environments within the larger landscape, and serve as a framework for understanding the organization, diversity, and dynamics of communities associated with fluvial ecosystems (Naiman et al. 1988, Gregory et al. 1991, Decamps 1997). Often it is difficult to precisely delineate the spatial extent of the riparian zone because the heterogeneity is expressed in an array of life history strategies and successional patterns while the functional attributes depend not only on community composition but also the environmental setting.

Defining and Delineating Riparian Zones

The riparian zone encompasses the stream channel and that portion of the terrestrial landscape from the high water mark toward the uplands where vegetation may be influenced by elevated water tables or flooding, and by the ability of the soils to hold water (Naiman et al. 1993). [COMMENT ABOUT ADDING JUNK ET AL. 1989 ON FAX THAT I COULD NOT READ] The width of the riparian zone, the level of control that the streambed vegetation has on the stream environment, and the diversity of functional attributes (e.g., information flow, biogeochemical cycles) are related to the size of the stream, the position of the stream within the drainage network, the hydrologic regime, and the local geomorphology (Salo and Cundy 1987, Naiman and Decamps 1990, Decamps 1997, Rot et al. 1997). For example, the riparian zone is often small in the numerous headwater streams that are almost completely embedded in the forest. In mid-sized streams the

riparian zone is larger, being represented by a distinct band of vegetation whose width is determined by long-term (>50yr) channel dynamics and the annual discharge regime. Riparian zones on large streams are characterized by well-developed but physically complex floodplains with long periods of seasonal flooding, lateral channel migration, oxbow lakes in old river channels, a diverse vegetative community, and moist soils (Salo et al. 1986, Malanson 1993). Vegetation outside of the zone not directly influenced by hydrologic conditions but contributing organic matter (e.g., leaves, wood, dissolved materials) to the floodplain or channel, or which influences the physical regime of the floodplain or channel by shading, is often included in the delineation or definition of riparian zones (Gregory et al. 1991, Brosofske et al. 1997).

Defining and delineating riparian zones is not only important for ecological reasons but also for management applications. Riparian buffer zones, a defined distance from a stream in which land use activities are restricted for stream protection purposes, are becoming an increasingly common management tool (Fry et al. 1994, Kovalchik and Chitwood 1990, Scatena 1990, Bren 1995). Methods for delineating the riparian zone and eventually the effective buffer width are being continuously refined but generally incorporate ecological characteristics such as the spatial extent of herbaceous plants adapted to wet soil conditions, production of nutritional resources for aquatic systems, local geomorphology, and area of sediment generation (Scatena 1990, Gregory et al. 1991, Kovalchik and Chitwood 1990). Increasingly, Geographic Information Systems (GIS) and Digital Elevation Models (DEM) are being used to provide an initial estimate of riparian zone area and its distribution throughout the drainage network (Belknap and Naiman 1997, Xiang 1993). In areas where the riparian vegetation has been removed, additional methods are being developed to assist in determining the spatial potential for riparian vegetation regeneration (Petersen 1992, Kovalchik and Chitwood 1990).

Life History Strategies

Streams are non-equilibrium systems having strong effects on the biotic characteristics of riparian communities. The active channel and floodplain are harsh environments for the colonization and establishment of both plants and animals

(Fetherston et al. 1997). In this section we focus on the morphological, physiological, and reproductive strategies of the vegetation even though an equally informative review could be made for the animal community (see Raedeke 1988).

Seasonal variations in discharge and wetted area create a multitude of environmental conditions which challenge even the most tolerant species. For example, in the first year of life, most riparian plants will be subjected to floods, erosion, abrasion, drought, freezing, and occasionally toxic concentrations of ammonia in addition to the normal biotic challenges. Fortunately, the life history strategies of most riparian plants are such that extreme conditions are either endured, resisted or avoided (Grime 1979, Noble and Slayter 1980, Agee 1993).

In general, riparian plant communities are composed of specialized and disturbance-adapted species within a matrix of less specialized and less frequently disturbed upland forest (Fetherston et al. 1997). The classification of plants into suites of similar life history strategies is useful for understanding processes leading to riparian forest succession and distributional patterns. Functional adaptations of plants fall into four broad categories:

Invader—Produces large numbers of wind-disseminated propagules that colonize alluvial mineral substrata.

Endurer—Resprouts after breakage of either the stem or roots.

Resister—Can withstand flooding or desiccation for long periods.

Avoider—Lacks an adaptation to specific disturbances.

Functional classification of some widely distributed species illustrates the variety of life history strategies. For example, Sitka willow (*Salix sitchensis*) and Scouler's willow (*Salix scouleriana*) are pioneer plants well adapted to living under a number of disturbance regimes. In response to fire these species can invade the post-fire landscape as well as resprout following low intensity fires that have not destroyed the root system (Fetherston et al. 1997). Their adaptive characters make them well suited as invaders, endurers, or resisters depending upon local

environmental conditions. In contrast, Sitka spruce (g. sp.) is more restricted, colonizing woody debris and mineral substrata on the floodplain (Harmon and Franklin 1989, McKee et al. 1982). Sitka spruce is resistant to both flooding and sediment deposition but it is sensitive to fire, avoiding sites where fire is a regular occurrence.

Morphological and Physiological Adaptations. Flood tolerance strategies developed by trees employ both morphological and physiological adaptations. In general, the variety of morphological adaptations (e.g., adventitious roots, stem buttressing) seen in riparian plants are in response to either soil ammonia or unstable substrata conditions. Vascular plants in periodically flooded areas have several morphological adaptations to ammonia including: a) air spaces (aerenchyma) in the roots and stems which allow for the diffusion of oxygen from aerial portions of the plant to the roots and b) adventitious roots that grow above the anaerobic zone enabling oxygen absorption by the plant. The development of these structures is mediated by increased levels of the hormone ethylene initiated by the anaerobic soil conditions (Kozlowski et al. 1991, Mitsch and Gosselink 1993). Root and stem aerenchyma are common species of the plant subfamilies Cyperaceae and Juncaceae which are normally found on poorly drained floodplains. Adventitious roots occur in a variety of tree genera (e.g., Populus, Salix, Alnus, coast redwood) living in riparian environments where regular sediment deposition and wetted soils are common (Sigafos 1964, Stone and Vasey 1968, Blom and Voeseck 1996).

Flooding also mechanically disturbs plants by eroding substrata and by abrasion. Stem flexibility among woody genera (i.e., Populus, Salix, Lanes) imparts endurance and resistance to potentially high levels of shear stress accompanying seasonal floods. Floods often occur during periods when the vegetation is without leaves, further reducing potential damage (Featherston 1997).

In addition to the examples cited previously, anoxic conditions are challenging to plants not only because of the need to acquire oxygen but also because anoxic conditions mobilize soluble reduced ions (such as manganese) which are toxic (Mitsch and Gosselink 1993). Rhizosphere oxygenation reduces this threat by moving oxygen from the root to the adjacent soil to form a very small but effective oxidized zone. However, riparian species show a large variety of responses to flooding. For example, in the tropical gallery forests of Brazil, *Sebastiania klotchyana* [CHECK SPELLING]

accelerated glycolysis with ethanol as the major end product of anaerobic metabolism but without detectable oxygen diffusion to the root system (Joly 1991). Whereas, a second species, *Hymenaea courbaril* [CHECK SPELLING], kept its root metabolism aerobic (with a 50% decrease in metabolism) through oxygen diffusion from the aerial[???] system. Third species, *Choriste speciosa* [CHECK SPELLING] developed hypertrophic lenticels to improve the aeration of the root system, although not reaching full metabolism. A fourth species, *Schyzolobium para* [CHECK SPELLING] did not accelerate glycolysis enough to maintain the rate of energy production required by the roots, and did not grow.

Reproductive Adaptations. Plant life history strategies also include a suite of co-adapted characters whose functions enhance reproductive success in specific environmental settings (Barbour et al. 1987). The primary reproductive characteristics of riparian plants are tradeoffs between sexual and asexual reproduction, seed size, timing of dormancy, timing of seed dispersal, seed dispersal mechanisms, and longevity. For example, several plants (e.g., *Populus*, *Salix*) disperse seeds in phase with the seasonal retreat of floodwaters, insuring moist seedbeds for successful germination and plant colonization (Sigafos 1964, Johnson 1994). Seeds, as well as vegetative fragments, are ubiquitous in river networks with many species using transport by flowing water, a phenomenon known as hydrochory, for dispersal to new sites (Nilsson et al. 1991, Johansson et al. 1996). Schneider and Sharitz (1988), working in a South Carolina swamp forest, found that bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) rely on water more than wind to disperse seeds away from parental trees. Furthermore, they found that small pulses of increased water levels tended to introduce seeds from adjacent plant communities. Nevertheless, hydrochory is only one means for dispersal. Dispersal by animals (**zoochory**) and by wind (anemochory[SPELLING]) may be even more important but little empirical data exist for comparison.

How propagules are dispersed also has a certain role in structuring the riparian flora and may provide a basis for explaining species distribution patterns (Johansson et al. 1996). In Sweden, Johansson et al. (1996) found a positive relationship between floating capacity of the diaspores and the frequency of species in the riparian vegetation. A comparison of floating capacity between species with and

without certain dispersal devices showed that seeds of vegetatively dispersed species had better floating capacities than other seeds. For other types of dispersal, such as by animals or wind, floating time did not differ between groups.

In addition to reproduction by means of seeds, many riparian plants reproduce vegetatively (e.g., asexually). Poplars (i.e., cottonwood), for example, exhibit the trait of branch abscission, or cladoptosis, in which otherwise healthy branch tips are shed (Galloway and Worrall 1979, Dewit and Reid 1992). Shed branches, like other live fragments, frequently develop adventitious roots and grow into new, genetically identical trees (McKay 1996).

Successional and Vegetative Patterns

Physical Controls. Interactions between hydrology, geomorphology, light, temperature, and fire exert considerable influence on the structure, dynamics, and composition of riparian zones (Brinson 1990, Malanson 1993). Depending on the setting, there are variable and complex interactions between these factors, making it especially difficult to develop a model for broad applications. In general, however, the literature suggests that hydrology (and how it interacts with local geology) is hierarchically the most important factor, setting the stage for other physical controls on the vegetation. For example, in riparian floodplains having a ridge-and-swale topography, the internal vegetative patch types alternate between topographic lows adapted to long hydroperiods and topographic highs supporting species also found in mesic uplands (Salo et al. 1986, Brinson 1990, Mertes et al. 1995).

Brinson (1990) provides a conceptual model that is useful in understanding the complex interactions between hydrology, other physical factors and vegetation. Flood power and frequency of inundation are inversely proportional and exist in a continuum from high-power, low-frequency floods that affect the whole floodplain to low-power, high-frequency floods that influence only the area adjacent to the wetted channel. It is the high-power, low-frequency flood type that determines patterns of the large geographic features that persist for hundreds to thousands of years (e.g., oxbow lakes, relic levees). Medium-power, intermediate frequency floods determine patterns of ecosystem structure that have lifetimes of tens to hundreds of years. Tree community

zonation is influenced at this scale because of the similar generation times of many tree species (Baker 1990, Harris 1987, Hupp and Osterkamp 1985). The low-power, high-frequency floods that occur annually determine short-term patterns such as seed germination and seedling survival (Baker 1990, Langlade and Decamps 1994, 1995). For example, in cottonwood (*Populus angustifolia*) in southwestern Colorado, seedlings are most abundant in years with cool winters, wet springs and cool, wet autumns. Both good seedling years and stand-origin years are associated with winter blocking of storms in the North Pacific and a persistent late-summer Arizona monsoon (Baker 1990). Good seedling years occur more frequently (about every 3.4 years) than stand origin years (about every 10-15 years); both are heavily dependent on the hydrology.

The ability of soils and sediments to hold water, and the existence of tributary and groundwater flows, are equally important in determining vegetative distribution (Brinson 1990, Hupp and Osterkamp 1985, Keller et al. 1990, Thorburn et al. 1994, Dawson and Ehleringer 1991). Distance from the river and microtopographic variations determine lagtimes between increasing discharge in the main channel and arrival of water on site. Once the water has arrived the composition of the soil and the alluvium (as well as the rate of evapotranspiration) determine how long the substrata remains saturated. Finally, the existence of external water sources can create conditions which allow vegetation to persist largely independent of the flood regime (Bell and Johnson 1974, Keller et al. 1990, Thorburn et al. 1994, Dawson and Ehleringer 1991). Indeed, older cottonwood (*Populus*), river red gum (*Eucalyptus camaldulensis*), and host mature riparian trees make use of groundwater rather than nearby creek water, presumably because groundwater is a more reliable source during droughts (Malanson 1993).

[THIS PARAGRAPH MAY BE REDUNDANT; SEE LATER] Even though these studies demonstrate that hydrologic factors are important influences on riparian vegetation, the vegetation also can influence base flows, especially in drier climates. Numerous studies have demonstrated that evapotranspiration by riparian vegetation can significantly alter discharge producing diel fluctuations in flow (Smith 1992, Weisman 1977).

The geomorphic template upon which the riparian forest develops is constantly undergoing change induced by the discharge regime (Naiman et al. 1992, Brinson 1990). The drainage network, from headwaters to the estuary, represents

a mosaic of sites which may be aggrading, degrading, or maintaining a steady state. Even sites in a steady state, where the downstream movement of deposited materials is balanced by the transport of alluvium from upstream, the stream channels will continue to meander laterally and downvalley so that the physical features of the riparian zone continue to change (Dunne and Leopold 1979). These changes include (a) formation of natural levees adjacent to the channel which contain coarser material deposited during flood overflow; (b) meander scrolls and ridge-and-swale topography created by abandoned point bar deposits as the channel migrates laterally and downslope; © oxbow lakes which are relict meander bend that have been cut off; and (d) point bars on the inside curve of river bends where deposition is rapid (Dunne and Leopold 1979, Brinson 1990). Levees support riparian gallery forests that may flood frequently but the coarse deposits normally result in rapid drainage when water levels drop. Oxbow lakes are the most hydric of the riparian habitats, supporting species adapted to constant flooding and anaerobic soils.

There is rich and comprehensive literature on fluvial geomorphology (Dunne and Leopold 1979). However, two aspects are particularly important for understanding patterns and processes in riparian vegetation: site specific erosion and deposition and lateral channel migration. Over **time**, all streams undergo periods of erosion and deposition in response to interactions between the hydrology and the sediment supply. The sediment supply is variable depending upon land use, climate change, and tectonic activity. Rates of erosion and deposition vary widely in space and time ranging from a few millimeters to several meters annually. For example, erosion (or incision) often occurs in small streams in tectonically active areas of uplift which increases sediment yield to downstream reaches, and this is expressed in the development of locally braided channels in the new floodplain. This process has been occurring in the Andes Mountains for millennia and appears to be a central speciation mechanism for riparian forest communities in the floristically rich upper Amazonian basin (Rasanen et al. 1987, Salo 1990). Further, lateral channel migration may be slow (centimeters/year) to fast (tens of meters per year), depending on the type of stream and channel hydraulics (Brinson 1990, Salo 1990, Begin and Lavoie 1988), having substantial influences on the composition and demography of the vegetative communities (Ishikawa 1991, Kalliola and Puhakka 1988, Hupp and Simon 1986).

The physical influences of light and temperature on the vegetative community are less well investigated than either hydrology or geomorphology. The understory light regime tends to be highest at the riparian forest edge but rapidly declines toward the forest interior (unless gaps have been created by fallen trees). One would expect that light might be limiting in the interior where levels are often <2% of full sunlight. However, seedling densities and diversity are not correlated with variations in understory light intensity, suggesting that other factors are more important in germination and establishment (MacDougall and Kellman 1992, Pollock et al. 1997 1994). The temperature regime is markedly different from upland forests but no studies have attempted to link this difference to the vegetation (Brosofske et al. 1997). Nevertheless, the compass orientation of the riparian zone does influence the light and temperature regimes, and there are significant floristic differences between riparian zones on north-facing and south-facing slopes (Szaro 1990).

Fire occurs rarely in the riparian zones of humid regions but plays a significant role in dryer climates (Agee 1993). In seasonally or perennially dry regions, fire may be relatively common in riparian zones. For example, in the lower Colorado River nearly 40% of the riparian vegetation burned in 12 years with halophytic shrubs recovering faster than mesophytic trees (Busch 1995). The long-lived coast redwood (*G. sp*) experiences many fires in a lifetime and is well adapted to all but the most extreme ones by virtue of its stature and thick, fire resistant bark. In humid regions, most riparian vegetation cannot withstand even mild fires (Fetherston et al. 1997).

Biotic Patterns. As corridors within watersheds, riparian zones have a unique longitudinal pattern which exerts substantial controls on the movements of water, nutrients, sediment, and species (Malanson 1993, Forman 1995). Shape and network configuration are particularly important in this regard. Forman (1995) recognizes eight common shapes for riparian corridors, ranging from strictly linear (mostly uplands) to highly variable (low elevation valley bottoms). In addition, cross sectional profiles provide an important third dimension. Large variations in height and depth are present as one crosses apparently flat terrain. Depending upon the local geographic setting, cross sectional profiles offer a bewildering array of variation in width and microtopography with the simplest cross-sectional profiles

tending to be upstream and the more complex ones downstream (Rosgen 1994, Forman 1995). The usual dendritic pattern of riparian zones within watersheds, combined with variations in channel density and topography, provide for complex network configurations.

Even though hydrologic and geographic influences on riparian vegetation are strong, ecological influences (such as competition, herbivory, soils, and disease) are increasingly recognized as being significant in shaping community characteristics. Consider competition. Even though competition is probably reduced in riparian systems because of the frequency of disturbance a competitive hierarchy does exist. There is some evidence that several species could exist in environments beyond their present range, specifically in the direction of less stress, except for the presence of competitors (Keddy 1989).

In regions with reasonably intact animal populations, herbivory exerts strong influences on vegetative characteristics (Butler 1995, Naiman and Rogers 1997). Physical processes structuring the riparian zone create habitat for plants and animals. The habitat, however, is further modified by the activities of larger animals (such as birds and mammals) as they selectively eat vegetation, burrow and wallow in soils, and build dams on streams, among other activities. The net result is that the variety of riparian habitats (or resource patches) is increased with the vegetation and microorganisms living on the increased variety of habitat patches largely determining the eventual distribution and cycling rates of elements (such as N and P). The physical and trophic activities associated with herbivory have ecosystem-level consequences that go far beyond the requirements of individuals for food and habitat (Naiman 1988, Jones and Lawton 1995, Johnston 1995).

Soil conditions (especially the degree of saturation) coincides with patterns sediment grain size and microtopography, affecting plant distribution from the river to the uplands (Sollers 1973), and is discussed later in this review. On the other hand, disease as an agent influencing biotic patterns is little studied, although pests (such as budworm caterpillar, *Choristoneura fumiferana*) are known to spread rapidly along riparian corridors in quest of food (Forman 1995).

Vegetative density, biomass, production, and species distributions also exhibit patterns within sites, among sites, within regions and between regions (Brinson 1990, Malanson 1995, Naiman and Decamps 1990). Available data

suggest that riparian forests in the southeastern United States and the humid tropics tend toward greater stem density and basal area than those in more arid regions and more northern latitudes. Although values vary widely within regions, largely due to stand age, the variation is usually less than an order of magnitude. In general, the basal area of riparian forests is as great or greater than that of upland forests (Brinson 1990).

The aboveground biomass of riparian forests ranges between 100 and 300 t/ha with few exceptions (Brinson 1990). Leaves represent 1-10 % of the total. Belowground biomass varies from 12 to 190 t/ha, but much of this variation may be due to sampling methods and site-specific conditions. In general, however, belowground biomass tends to be less than aboveground biomass but will range from 5-120 %. Published values for aboveground riparian production ranges from 6.5 to 21.4 t/ha/yr; litter fall averages 47 % of the annual production. The limited data does not reveal latitudinal or successional gradients. Rates of belowground production have received virtually no attention in riparian forests. Overall, most evidence supports the concept that riparian forests have relatively high rates of production in comparison with upland forests. The data suggest that there are no strong limiting factors associated with water or nutrients that would result in unusually low production estimates.

If the arrangement of vegetative communities in riparian zones is heterogeneous, so are the successional processes. Spatial zonation often exists as a transverse gradient perpendicular to the wetted channel, that is often made very complex by vegetative responses to local variations in topography and susceptibility to flood (Rot 1995). In general, vegetative patterns follow predictable patterns in physical features (Welcomme 1979) and disturbance patterns (Fetherston et al. 1997). Decamps et al. (1988) present a model of riparian forest succession for the Garonne River in France where cyclical successional processes occur within the floodplain where flood-induced erosion and deposition are common. However, on the higher terraces without repeated flooding the successional dynamics are no longer reversible and internal autogenic forces dominate.

The earliest studies of vegetation dynamics in riparian zones did not refer to the concept of succession (Fitzpatrick and Fitzpatrick 1902) but nevertheless illustrated the process. Many of the successional patterns in riparian areas are primary succession: the development of

a new plant community in an area without the effects of a previous plant community (Malanson 1993). However, an equal number of successional patterns begin with plant fragments, propagules or biomass remaining from previous communities. Avalanche, flood, wind, fire, drought, disease, herbivory, and other physical influences on the vegetation each leave unique biotic legacies that are displayed in a wide variety of successional patterns (Nilsson et al. 1993, Fetherston et al. 1997). Many riparian plants possess adaptations allowing them to recover and reproduce by root suckering, adventitious root development on plant fragments, and stem flexibility. The amount of biotic material remaining to initiate succession, and its viability, depends of the type, intensity, frequency, and duration of the disturbance (Decamps 1997). These same disturbances also prepare the site for invasion by additional species favored by the new conditions.

Functions of the Riparian Vegetation

The ecological functions performed by riparian communities are as diverse as the communities themselves. Riparian vegetation affects the flow of water, nutrients, and other materials from uplands into streams as well as transfers within the riverine corridor (Pinay et al. 1990). Additionally, riparian communities (a) produce organic matter which may arrive in the stream as direct litter fall or move laterally as partially decomposed litter or be leached from soils, (b) provide habitat for a broad assortment of fauna in both the aquatic and terrestrial portions of the system, modify the microclimate of the surrounding area, (d) maintain enhanced levels of biodiversity, (e) act as corridors for movements, including exotic invasions, and (f) provide sites for active microevolution (Naiman et al. 1988, Risser 1990). These subjects are addressed in the following sections.

PHYSICAL FUNCTIONS OF RIPARIAN ZONES

Mass Movements of Materials and Channel Morphology

Riparian vegetation affects the downslope movement of materials by influencing the supply rate to the stream channel and the transporting processes. The material supply

rate is closely related to the physical stability of the riparian vegetation. Much of the material supplied to streams comes from erosion of stream banks, which is influenced by root strength and resilience (Griffiths 1980), as well as from the uplands (Myers and Swanson 1992). Stream banks largely devoid of riparian vegetation are often highly unstable and subject to mass wasting, widening channels by several to tens of meters annually (Hupp and Simon 1986, Salo 1990). Major bank erosion has been found to be 30 times more prevalent on non-vegetated banks exposed currents as on vegetated banks (Beeson and Doyle 1995). Once the material enters the stream it is subject to transport processes which are further modified by the riparian vegetation.

Riparian vegetation modifies transport processes by either physical entrapment or by altering channel hydraulics. Physical entrapment of materials appears to be most important in relatively low gradient environments. In experimental channels Kentucky bluegrass (*G. sp*) entrains sediment at the base of the vegetation, with the 30-70% retained dependent on blade length (Abt et al. 1994). In field measurements, accretion of sediment and organic matter by the vegetation can be substantial, especially during floods (Hubbard et al. 1990, Lowrance et al. 1986). Over a century (1880 - 1979) sediment deposition on a coastal plain river in the southeastern United States averaged 35-52 Mg/ha/yr (Lowrance et al. 1986). Alteration of channel hydraulics is accomplished either by roots or by large woody debris in the channel at low flows and, additionally, by stems at high flows. All provide physical structure that slows water velocity, decreases stream power, and provides retention structures to hold materials in place. Experimental **manipulations** involving the removal of large woody debris have resulted in dramatically increased erosion rates (Bilby 1981, Nakamura and Swanson 1993, Macdonald and Keller 1987).

Erosional and depositional events shaping channel morphology are the subject of a large literature addressing fluvial geomorphology (Dunne and Leopold 1979). The extent to which riparian vegetation influences these events is a topic of much current interest. In general, the spatial heterogeneity introduced into the channel by either the vegetation or the large woody debris produced by the vegetation acts to shape channel morphology by redirecting flows of water and sediment, sorting sediments, and either

retaining or moving materials (Hupp et al. 1995). Large woody debris is especially important in this regard.

Wood in Streams and Riparian Zones

It is well known that woody debris produced by riparian vegetation plays important biophysical roles at the land-water interface (Harmon et al. 1986, Maser and Sedell 1994). In the riparian forest, on exposed alluvial substrates and in streams, woody debris often accumulates during floods in discrete and conspicuous piles. The architecture of the piles usually includes at least one large piece of dimensionally complex wood (i.e., a key member) which can resist most flow regimes and physically capture smaller pieces of wood, making the pile even larger. Pile density may be quite high, up to 160/km of stream bank in temperate forests (Steel 1993). In tropical regions, where termites are prevalent, the density of woody debris piles is reduced substantially (Naiman and Rogers 1997). Further, some of this wood, especially the larger pieces, may be quite old. Nanson et al. (1995), measuring radiocarbon dates on logs within the channel and floodplain of a Tasmanian stream, found ages ranging from the present up to 17,000 years BP. Similar ages have been measured for large wood in streams of the Pacific coastal rainforest (Montgomery and Abbe, unpublished). The principal biophysical functions of woody debris piles are energy dissipation, trapping moving materials, and habitat formation.

Woody debris piles, depending on size, position in the channel and geometry, are able to resist and redirect water currents to various degrees. The net result is that the erosive power of water (in the presence of woody debris) becomes spatially heterogeneous, creating a mosaic of erosional and depositional patches in the riparian corridor. The potential energy in the water is either dissipated or redirected to do work, such as eroding banks or forming pools (Nakamura and Swanson 1993, Montgomery et al. 1995). The role of woody debris in pool formation, however, is dependent on channel slope with the spatial arrangement of pools in steeper channels being independent of the amount of woody debris (Montgomery et al. 1995). The physical consequences of redirecting water currents is to widen the channel and capture erosional materials (Maser and Sedell 1994). These processes have been examined extensively by geomorphologists in alluvial rivers (Richards 1982).

Woody debris, by dissipating and redirecting energy, not only forms areas where bed shear stress is greatly reduced but also results in longer water residence times (Ehrman and Lamberti 1992). These result in temporary storage of materials, which can be substantial. Experimental removal of wood from channels allows sediment and organic matter export rates in the first year to exceed baseline conditions by several hundred percent (Bilby 1981, Macdonald and Keller 1987). Analogous experiments with the addition of organic materials have produced similar insights. Ginkgo leaves and small pieces of wood added to a stream with woody debris moved only 65% and 8%, respectively, of the distance travelled by leaves and small wood in streams without large woody debris (Ehrman and Lamberti 1992). Likewise, 80% of the salmon carcasses added to nutrient poor coastal rainforest streams were retained by woody debris within 200 m of the release sites (Cederholm and Peterson 1985).

Woody debris, as habitat for fish and macroinvertebrates within the stream channel, has been the subject of several reviews (Harmon et al. 1986, Anderson and Sedell 1979, Maser and Sedell 1994, Meehan book). In contrast, its role as habitat within the terrestrial portion of the riparian corridor only now is receiving intense investigation. Woody debris physically retains plant propagules (seeds and plant fragments) and further protects them from erosion, abrasion and, in some cases, drought and herbivory (Hupp et al. 1995, Fetherston et al. 1995). On exposed cobble bars most of the successful seedling germination and survivorship is associated with woody debris as it provides a relatively moist and nutrient rich microenvironment that is somewhat protected from herbivores. Woody debris also affords protection for small mammals and birds in an otherwise hostile environment. The diversity and abundance of small mammal populations (e.g., shrews, voles, and mice) are significantly greater in areas with woody debris piles while several bird species preferentially use woody debris for perching and feeding (Doyle reference, Steel 1993).

Microclimate

Riparian forests are known to exert strong controls on the microclimate of streams but, surprisingly, there are few comprehensive studies of the forest microclimate itself. This topic could pay rich research dividends in the future as human activities intensify around riparian zones.

The results to date suggest strong differences between upland and riparian microclimates, stream water temperatures highly correlated with riparian soil temperatures, microclimatic gradients in the riparian zone for air, soil and surface temperatures and for relative humidity but not for short-wave solar radiation or wind speed, and the understory light regime (often < 2% of total solar radiation) not effecting seedling densities (MacDougall and Kellman 1992, Brosofske et al. 1997). Secondly, riparian forests, especially in warmer climates and seasons, influences stream discharge through evapotranspiration. The reduced streamflow decreases the amount of rearing habitat, causing physiological difficulties for organisms preferring cooler temperatures (Hicks et al. 1991).

Riparian Zones As Ecological Corridors

Even though riparian zones are shaped like corridors it is not clear that they function as dispersal corridors in all cases, especially for terrestrial animals. Certainly, many plants have adaptations which allow vegetative fragments and seeds to float for various distances (Sauer 1988, Nilsson et al. 1991) while many other riparian species are dispersed by wind or animals (especially in the feces of **birds**). Schneider and Sharitz (1988), for example, examining the importance of hydrochory in *Taxodium distichum* and *Nyssa aquatica*, found that their seeds could float for 42 and 85 days, respectively, and cover downstream distances of up to 2 km. Species that are wind-dispersed are more often r-selected and are successful pioneers of newly opened sites with high ambient light and bare mineral soils (e.g., *Populus*, *Salix*). However, perhaps the best evidence for plants using riparian zones as corridors comes from exotic invasions. DeFerrari and Naiman (1994), and several other investigators, have found exotic plants rapidly moving both up and down riparian corridors in preference to overland routes.

The use of riparian zones as corridors by terrestrial animals is problematic. Logically, it would make sense that the large number of riparian obligates would use riparian zones for dispersal but there are few data to support that assumption. **Seldom** have investigators actually documented the movements of individuals to validate this assumption, despite wide use of the assumption in models. One notable exception is the use of the riparian forest along the

Garonne River, France, which acts as a corridor for birds moving between the Central Massif and the Pyrenees (Decamps et al. 1987).

ECOLOGICAL FUNCTIONS OF RIPARIAN ZONES

Sources of Nourishment: Allochthonous Inputs and Herbivory

The importance of organic matter from riparian vegetation as a source of nourishment for aquatic communities was recognized by Thienemann (1912) and was revisited by Hynes (1963). In temperate zones, frequently reported figures vary from about 500 g AFDM of litter per m² in small and medium streams to about 50 g AFDM per m² in larger rivers. Higher figures of above 1000 g AFDM of litter per m² are given for tropical streams. A main characteristic of this source of nourishment is its non-uniform distribution in space and in time.

As a general trend, the proportion of coarse particulate organic matter (CPOM; >1 mm diameter) decreases as river size increases. For example, in a 673 km² undisturbed watershed of eastern Quebec, annual litterfall per unit area of stream surface declined exponentially from 307-539 g AFDM m⁻² in a first order stream to 15-17 g AFDM m⁻² in a sixth order stream (Connors and Naiman 1984). However, lateral inputs from the soil surface were not related to stream size but strongly influenced by riparian structure and entrainment of organic matter during spring flooding.

Similar local effects were found also important in an intermittent prairie stream in Kansas where total annual input of CPOM was lowest in the headwater reaches in comparison to forested reaches downstream (Gurtz et al. 1988). Prior to the wet season, storage of benthic CPOM in the dry channel and on the bank was 320-341 g AFDM m⁻² in the upstream reaches and 999 g AFDM m⁻² in the fourth and fifth order gallery forest reaches. The storage of CPOM increased during the wet season in headwater channels where retention was high, resulting in these reaches having more CPOM than downstream reaches, although bank storage was always highest in downstream reaches.

Riparian structure appears to be the main factor influencing litter entering streams either directly or transported laterally from the forest floor. For example, depending on

the vegetative cover of the riparian zone, annual inputs ranged from 52 to 295 g AFDW/m² in Alaskan streams (Duncan and Brusven 1985) and from 63 to 474 g AFDW/m² in a Moroccan stream (Maamri et al. 1994). In an Australian rainforest stream, laterally transported litter formed 6.8% of the total annual input, varying in response to bank slope and microtopography (REFERENCE?). The proportion of direct and laterally transported litter entering streams has been suggested to influence significantly in-stream community dynamics as a consequence of the quality and timing of the input (Cummins et al. 1989). Even though laterally transported litter may not exceed 10 % of the total litter input, it may be qualitatively important as a source of nourishment, due to a higher nitrogen concentration than that of leaves falling directly into the stream (Benson and Pearson 1993). However, the organic material may be rearranged only during high discharge periods and not during the leaf fall period (Maridet et al. 1995), and the forest floor litter may require the cumulative effects of several floods to move measurable amounts of litter laterally to the channel (Moller et al. 1995).

In addition to particulate organic matter, riparian zones contribute substantial amounts of dissolved organic matter (DOM; <0.5 μ m) to river ecosystems. Soil water DOM may originate directly from unsaturated regions of riparian zones during floods or indirectly from the saturated through-flow at medium discharge rates (Neal et al. 1990). Soil water DOM originating farther away in the riparian zone also can influence stream communities through macroporous transfer of subsurface water.

At the scale of the Amazon basin, McClain and Richey (1996) recently identified four transfer pathways of terrigenous organic matter to streams: direct litterfall and blow-in from the soil surface (e.g., lateral movement), groundwater baseflow, stormflow, and seepage from fringing wetlands. Direct litterfall from overhanging canopies and blow-in contributions were similar between all landforms, amounting to 700 g AFDW/m²/yr, as was the elemental composition. Fresh and labile organic material dominated in all riparian zones examined. Groundwater baseflow DOM concentrations and proportions of hydrophobic organic acids were strongly correlated with soil type; old and refractory molecules characterized this DOM. Stormflow contributions were dominated by saturated overland flow originating in riparian areas which transferred a wide spectrum of dissolved and particulate organic matter dominated by fresh and labile

material. Fringing wetlands contributed high concentrations of DOM, particularly in the lowlands. In contrast to the other sites, here the organic matter is dominated by refractory hydrophobic dissolved compounds within a compositionally diverse molecular array. Although somewhat preliminary, their results and conceptual model may prove useful as a framework for quantifying organic matter concentrations and compositions between contrasting trophic pathways.

Litter breakdown constitutes a fundamental process in riparian and stream ecology, directly through in situ biological activity and indirectly through the production of dissolved and fine particulate organic matter. An exponential model of the $m_t = m_0 e^{-kt}$ type (Boulton and Boon 1991) is usually adopted to follow the dynamics of organic matter decomposition, where m_t represents the mass remaining at time t , m_0 the initial mass, and k the breakdown rate. This exponential breakdown rate varies with organic matter quality and with site characteristics. As an example, values of k (**d-1**) measured in the Garonne basin, France for beech (*Fagus silvatica*) and willow (*Salix alba*) leaves were, respectively, 0.0052 and 0.0147 in a third-order mountain stream, and 0.0027 and 0.0094 in a seventh-order lowland river (Chauvet et al. 1993).

Litter quality particularly affects the dynamics of decomposition in riparian zones as well as in other terrestrial systems. Typically, lower breakdown rates are found in wood than in leaf litter as a result of higher lignin and lower nitrogen content in wood (Melillo et al. 1983). The ratio of lignin to nitrogen is a useful indicator of relative litter decay rates acting primarily through effects on microbial activity (Melillo et al. 1992). Lignin being recalcitrant to enzymatic degradation reduces carbon availability to decomposers whereas the concentrations and absolute amounts of nitrogen increase as a consequence of accumulation in microbial biomass and accumulate in complexed products of microbial metabolism (Melillo et al. **1984**).

Litter breakdown also occurs in streams (Kaushik and Hynes 1971, Petersen and Cummins 1974, Barlocher [ACCENTS] and Kendrick 1974). It is recognized that several processes - leaching, microbial colonization, and fragmentation by physical forces and invertebrate feeding - contribute to litter breakdown (Cummins 1974, Webster and Benfield 1986, Boulton and Boon 1991). These processes are thought to act

simultaneously rather than successively in time (Gessner and Schwoerbel 1989, Gessner 1991, Barlocher [ACCENTS] 1992). They lead to the production of fungal, bacterial, and animal biomass, as well as the formation of carbon fractions such as CO₂, and dissolved and particulate organic matter. The relative importance of these processes and their interactions control the rate of organic matter oxidation and the characteristics of the organic byproducts of decomposition. As found in the early 1980's (Aber and Melillo 1981 19XX), litter quality as measured by the proportion of refractory substances (for example, lignin; Gessner and Chauvet 1994) as well as nitrate concentrations in the water (Suberkropp and Chauvet 1995) significantly influence rates of litter breakdown. Mechanistically, much of the influence is mediated through trophic interactions between microbes and invertebrate shredders feeding on the litter (see Suberkropp 1992, 1997 for **reviews**).

Comparisons of fungal and bacterial biomass during litter breakdown in streams [AND RIPARIAN ZONES?] indicate that fungal biomass may account for about 95% of the total microbial (fungi + bacteria) biomass associated with organic matter (Findley & Arsuffi 1989, Baldy et al. 1995). It seems that a similar difference holds when comparisons are made on a production basis (Weyers and Suberkropp 1996). Fungi currently are viewed as being most active in the early stages of organic matter decomposition with the microbial assemblage shifting towards the bacterial component later in the process. However, fungal sporulation and production continue as decomposition is progressing suggesting that, at advanced stages, bacteria complement rather than replace the fungi and that bacteria later govern the microbially mediated energy flow from organic matter to higher trophic levels (Baldy et al. 1995).

Since the first observations by Egglshaw (1964), freshwater ecologists have frequently reported high correlations 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 were found to be positively correlated with the amount of organic matter in riffles but not in pools in intermittent streams in Australia (Boulton and Lake 1992). This suggests that the abundant detritus may have deteriorated water quality and attracted predators; both phenomena reducing detritivore densities. In other respects, typical shredders may not be the only or even the major

users of organic matter accumulations. For example, leaves provide large surface areas, promoting a rich development of microorganisms, and hence abundant food for fine particle feeders such as naidid oligochaetes. Naidids are reported to represent up to 73% of the total number of organisms collected on willow leaves during the first 3 months of breakdown in a third order stream (Chauvet et al. 1993). Tubificid oligochaetes also represented more than 50 % of the animal biomass on willow leaves submerged in a seventh order stream. These worms were regularly encountered on the surface but also inside the leaf matrix, enhancing leaf breakdown by their activity (Chauvet et al. 1993).

Riparian vegetation is a source of nourishment for many animals, from insects to mammals who, by their feeding activities, can considerably alter system function. Sudden outbreaks of defoliating insects have the capability to alter riparian forest production and thereby alter water yield, nutrient cycling, and streamwater chemistry (Swank et al. 1981, Torossian and Rogues 1989). Through selective browsing large animals such as moose (*Alces alces*) can shift the riparian plant community from deciduous trees to conifers, thus altering soil formation and nutrient cycling, and ultimately affecting plant productivity and moose population dynamics (Pastor et al. 1988). Beaver (*Castor canadensis*) also exert a substantial impact on the structure and function of riparian systems, enhancing floodplain complexity and multiplying vegetative successional pathways, some of which affect the landscape for centuries (Naiman et al. 1988).

Riparian Zones as Nutrient Filters

Investigations on the effects of riparian zones on water quality intensified in the late 1970's after Karr and Schlosser (1978) demonstrated the role of the land-water interface in reducing nutrient movements to streams. These investigations quickly led to a new understanding of the role played by riparian zones in controlling nonpoint sources of pollution by sediment and nutrients in agricultural watersheds (Lowrance et al. 1983, Peterjohn and Correll 1984, Jacobs and Gilliam 1985). These articles formed the basis for a number of research projects on processes related to riparian zones as filters.

Indeed, riparian zones are areas of important biogeochemical processes that affect streamside as well as aquatic systems.

Microbial activity, coupled with the slow diffusion of oxygen in saturated riparian soils, creates anaerobic conditions which encourage processes such as denitrification and phosphorus immobilization. These processes are well expressed within the dynamic terrestrial-aquatic interface between the terrestrial boundary controlled by watershed hydrology and the aquatic boundary strongly influenced by channel hydraulics (Triska et al. 1993). The subsurface transfer of water, as well as dissolved and particulate substances, is mostly unidirectional towards the channel across the terrestrial boundary whereas it is bi-directional across the aquatic boundary where oxidized hyporheic water from the streambed mixes with often reduced interstitial water coming from the riparian zone. Both boundaries appear to be major locations for regulating and diminishing the transfer of inorganic nitrogen and phosphorus from subsurface water to streamwater (McClain et al. 1994).

As riparian zones intercept run-off from agricultural land, they also retain sediments, encourage plant uptake and transformation of nutrients, and breakdown pesticides. These processes are optimized under certain conditions. Sediments are retained if the residence time of water is prolonged (and hence its erosive power is reduced). This is dependent on the topographic slope and the density of plant cover. Sediment retention is enhanced when water enters the riparian zone as uniformly shallow flows at low discharge, and not as channelized flow. Nutrients taken up by plants eventually are returned to the soil if harvesting does not take place. Transformation of nitrate through denitrification to nitrous oxide (a gas) is optimized providing the soils are wet and anaerobic, and a source of labile carbon exists. Pesticides decay if the residence time is long enough to allow solar radiation, microbial activity and other pesticide decay processes in the soil to proceed.

Sediments and sediment-bound pollutants carried in surface runoff are deposited effectively in mature riparian forests as well as in streamside grasses. In both cases sediment trapping is facilitated when runoff is primarily sheet flow, which allows deposition of sediment particles and prevents channelized erosion of accumulated sediments.

Riparian areas have been reported to remove 80-90% of the sediments leaving agricultural fields in North Carolina (Cooper et al. 1987, Daniels and Gilliam 1996). Sediment deposition may be substantial in the long term, with large amounts of coarse sediments deposited within a few meters of the field-forest boundary, and finer sediments deposited

further into the forest and near the stream where they mix with coarse sediments deposited in overbank flows (Lowrance et al. 1986, Cooper et al. 1987). These finer sediments carry higher concentrations of labile nutrients and adsorbed pollutants; their removal from the runoff occurs as a consequence of several interactive processes: deposition and erosion, infiltration, dilution, and adsorption/desorption reactions with forest soil and litter.

Grassy riparian areas trap more than 50% of sediments from uplands when overland water flows are <5 cm deep (Magette et al. 1989, Dillaha et al. 1989a). An interesting characteristic of grassy areas is their influence on the uniformity of runoff; channelized flows are transformed into expanded shallow flows which are more likely to deposit sediment. However, the performance of grassy vegetation seems to be highly variable and of short life span when several floods occur within a limited period. For example, in an experimental study, Dillaha et al. (1989a) found that sediment trapping efficiency decreased from 90% in a first rainfall simulation event to 5% in a sixth rainfall simulation event.

Plant uptake is an important mechanism for nutrient removal in riparian forests (Peterjohn & Correll 1984, Fail et al. 1986, Correll & Weller 1989, Groffman et al. 1992). It results in a short-term accumulation of nutrients in non-woody biomass as well as a long-term accumulation in woody biomass. Riparian forests are especially important sites for biotic accumulations of nutrients for two reasons. First, transpiration is often very high, increasing the mass flow of nutrient solutes toward root systems. Second, riparian communities include many flood-tolerant species whose morphological and physiological adaptations facilitate nutrient uptake under low-oxygen conditions. In some species, such as water tupelo (*Nyssa aquatica*), saturated conditions enhance nutrient uptake and growth (Hosner et al. 1965). In their paper of 1984, Peterjohn and Correll estimated vegetation uptakes of 77 and 10 kg **ha⁻¹ yr⁻¹** for N and P, respectively. Such rates are comparable with known upland rates. For example, a worldwide average N uptake rate of 70.5 kg/ha/yr has been suggested for deciduous tree species and 39 kg/ha/yr for conifers (Cole and Rapp 1980). However, potential N uptake rates may be much higher as shown by Cole (1981) for poplar (*Populus nigra*) that assimilated 913 kg N/ha/yr when fertilized with a **nutrient-rich** effluent at a rate of 400 kg N/ha/yr for three years. Sites not receiving any nutrient effluent assimilated only

16 kg N/ha/yr. Further, due to nitrogen saturation (Aber et al. 1989), phosphorus may become the limiting factor for tree growth, particularly in wetlands (Taylor et al. 1991) making vegetation an effective phosphorus sink.

Nevertheless, the importance of plants as nutrient filters may be reduced by restricting the accessibility of water, by the seasonal phenology of uptake and release of nutrients, and by the saturation of old plantations. Water is accessible to plants only if the water table is high in the soil profile or if transpiration demands moves water and solutes into the root zone. During intense rain storms, concentrated surface flow and macropore-dominated percolation may not be available to plants (Jaworski et al. 1992). Nutrient uptake declines or stops during the winter season precisely when high discharges occur. In addition, litter decomposition releases nutrients previously stored during the growing season to forest soils. Finally, the ability to sequester nutrients in woody biomass may decline as trees mature, leading to a phenomenon referred to as saturation (Aber et al. 1989, Groffman et al. 1992). A better knowledge is needed [FOR WHAT PURPOSE??] on the ability of individual riparian trees as nutrient filters.

In addition to vegetative processes, microbial processes also are important for nutrient removal. Microbial uptake of nutrients, similar to plant uptake, initially results in the immobilization of dissolved nutrients followed by cell growth, death, decomposition and eventual nutrient release. Nitrogen, in contrast to other nutrients, has an alternate pathway of major importance in most riparian forests: denitrification (Jacobs and Gilliam 1985b, Pinay and Decamps 1988, Correll and Weller 1989, Groffman et al. 1992, Haycock and Pinay 1993, Jordan et al. 1993). Denitrification is the anaerobic, microbial conversion of nitrate to nitrogen gases. The activation of denitrification depends on the presence of nitrate, a suitable carbon substrate, and the absence of oxygen. Soil temperature, moisture regime and the type of carbon also influence the reaction rate. Soil pH affects the nature of the gas produced, N₂O or N₂. In riparian zones, anaerobic microsites associated with decomposing organic matter fragments allows denitrification to occur in otherwise well drained soils. Denitrification rates of 30 to 40 kg N ha⁻¹ yr⁻¹ have been measured for natural riparian forests in the United States. Within a given riparian zone, the fastest rates occur at the riparian-stream boundary where nitrate enriched water enters

organic surface soil (Cooper 1990). Most denitrification occurs in the top 12-15 cm of the surface soil.

Denitrification of groundwater-borne nitrate is much less well established. Carbon availability usually limits subsurface microbial activity, preventing anaerobic conditions to develop (Hedin et al. manuscript). Since denitrification is concentrated in the upper soil layers (which are only occasionally part of the shallow aquifer), nitrate disappearance from shallow groundwater may require the riparian vegetation playing a primary role (Lowrance 1992). It has been suggested that groundwater derived nitrate may be eventually denitrified in surface soil after plant uptake of the nitrate from groundwater, litter decomposition and nitrogen release, followed by nitrification and denitrification in surface soil (Groffman et al. 1992, Hansen et al. 1994a,b). Therefore, microbial denitrification interacts with vegetation nitrogen uptake and organic carbon availability via litterfall and root decay to remove nitrate. Such an interaction varies within and between riparian forests under the influence of subsurface water, plant cover and soil characteristics (Hill 1990).

The influence of subsurface water characteristics was clearly demonstrated in the Coastal Plain of the Chesapeake Bay watershed (Lowrance et al. 1995). In several locations, average annual terrestrial boundary nitrate concentrations of 7 to 14 mg $\text{NO}_3\text{-N L}^{-1}$ were found to decrease to 1 mg $\text{NO}_3\text{-N L}^{-1}$ or less in shallow groundwater near streams. However, in the same area, a well with a nitrate concentration of 25 mg $\text{NO}_3\text{-N L}^{-1}$ was found to leave 18 mg $\text{NO}_3\text{-N L}^{-1}$ in shallow groundwater at the stream. Lowrance et al. (1984) estimated annual denitrification rates to average 31 kg N $\text{ha}^{-1} \text{yr}^{-1}$ in the top 50 cm of soil. But the measured denitrification rates varied between 1.4 kg N $\text{ha}^{-1} \text{yr}^{-1}$ in a riparian zone adjacent to an old field which received no fertilizer application to 295 kg N $\text{ha}^{-1} \text{yr}^{-1}$ under conditions of high nitrogen and carbon subsidies. Such results illustrate the potential for denitrification in surface soils as well as the high variability to be expected in field measurements. Most of this variability is driven by fine scale differences between rooted and non-rooted soil layers as well as between anoxic and oxic conditions. On the whole, enrichment of riparian zones may lead to significantly higher soil inorganic-nitrogen concentrations, litter nitrogen contents, and potentials for net nitrogen mineralization and nitrification; all suggesting nitrogen saturation.

Nevertheless, high rates of denitrification and storage usually maintain enriched riparian zones as sinks for upland derived nitrate (Hanson et al. 1994).

Differences in plant cover also influence the efficiency of riparian zones in filtering nutrients and pesticides. As might be expected, a riparian zone vegetated with poplar is more effective than one vegetated with grass for winter nitrate retention (Haycock and Pinay 1993). The capability of some trees is better than others in filtering nitrate, such as *Populus x canadensis* which effectively removes nitrate from saturated soils, with a subsequent accumulation of nitrogen in root biomass (O'Neill and Gordon 1994). Roots of alder, willow and poplar seem to favor colonization by proteolytic and ammonifying microorganisms and, particularly for alder roots, to inhibit nitrifying microorganisms (Pozuelo-Gonzalez et al. 1995). **Changing** plant cover may affect water quality as documented in a set-aside riparian zone in New Zealand where 12 years after retirement from grazing dominant vegetation returned to native tussock (*Poa cita*). This led to a zone likely to be a sink for sediment-bound nutrients and dissolved nitrogen but a source for dissolved phosphorus (Cooper et al. 1995).

Soil characteristics influence redox conditions and the availability of dissolved nitrogen to plant roots. For example, Pinay et al. (1995) calculated that uptake and denitrification retained 32% of the total organic nitrogen flux during a flood on sandy riparian forest soils but 70% on loamy riparian soils. McDowell et al. (1992) compared riparian nitrogen dynamics in two geomorphologically distinct tropical rain forest sites. At the first site, a deep layer of coarse sand conducted subsurface water to the adjacent stream below most plant roots, but through distinct oxic and anoxic zones from upslope to downslope, respectively. This horizontal oxidation-reduction zonation led to a spatial segregation of mineralization, nitrification, plant uptake and denitrification, causing ammonium and nitrate to accumulate in distinct zones. At the second site, a dense clay layer impeded infiltration and subsurface water rapidly moved through a shallow and variably oxidized rooting zone. Under such conditions, oxidation-reduction conditions change over fractions of centimeters. As a result of this spatial proximity, nitrogen transformation processes (i.e., mineralization, nitrification, plant uptake and denitrification) effectively coexist causing ammonium and nitrate concentrations to remain persistently low and variable. Although intense

biotic activity controlled hydrologic export of nitrogen at both sites, soil differences strongly modified interactions between the processes (McDowell et al. 1992). Such interactions have important consequences at watershed and landscape scales whenever the transient retention of ammonium or nitrate in riparian sediments influences biotic nitrogen cycling, thereby altering the timing and form of dissolved inorganic nitrogen export (Triska et al. 1994).

Riparian zones are generally effective in retaining sediment-borne phosphorus, in contrast to dissolved phosphorus. This is an important issue as the most readily available phosphorus components are transported in dissolved rather than particulate form (Pionke & Kunishi 1992). Significant amounts of phosphorus may first accumulate in riparian zones and then be transported to aquatic ecosystems via shallow groundwater flow possibly as a result of increased decomposition of organic matter (Vanek 1991).

In forested watersheds with relatively low nutrient concentrations, riparian zones can be sources or sinks for nutrients, depending on oxidation-reduction conditions. For example, the riparian zone of a small deciduous forest stream in eastern Tennessee proved to be a net source of inorganic phosphorus when dissolved oxygen concentrations in riparian groundwater were low, but a sink when dissolved oxygen concentrations in riparian groundwater were high (Mulholland 1992).

Wetlands are useful sites in retaining phosphorus as they often are P-limited. In a study of experimental freshwater riparian marshes in Illinois, Mitsch et al. (1995) showed that average phosphorus concentrations decreased 64-92% for low-flow and 53-90% for high-flow wetlands over three years. During the final growing season of the study, inflow averaged 176 $\mu\text{g P L}^{-1}$ while outflows averaged 34 $\mu\text{g P L}^{-1}$ and 45 $\mu\text{g P L}^{-1}$, respectively, for low- and high-flow wetlands. In this case, most of the inflowing phosphorus was retained through sedimentation. However, riparian buffer strips may act effectively as physical traps (sinks) for incoming particulate phosphorus while enriching runoff waters in available soluble phosphorus (Dillaho et al. 1989).

Biodiversity and Exotic Invasions

Riparian zones appear to be key landscape components in preserving species diversity (Naiman et al. 1993). As networks distributed over large areas, they have a large potential for maintaining biological diversity along extended and dynamic environmental gradients (Pollock et al. 1997 1997). They are also somewhat unique in that a wide variety of natural disturbances are an inherent part of the system, creating a spatial and temporal environmental mosaic with few parallels in other systems. Further, they provide physical corridors for the preferential establishment and movement of exotic and invasive species, as well as acting as long-term refuges for regional diversity. Finally, riparian forests affect the diversity of adjacent communities, especially aquatic communities, by influencing the flux and biochemical transformation of nutrients and organic matter across the landscape.

This section focuses on vegetative biodiversity and exotic invasions; animals associated with riparian zones are considered in subsequent sections of this review. Indeed, there is a great variety of fauna primarily linked to riparian habitats, and these animal-habitat linkages are a consequence of vegetative development and diversity.

Vegetative Patterns of Diversity. Riparian forests insights into how plant species richness varies at regional scales with respect to natural disturbances. For example, longitudinal profiles along river courses have proved to be especially effective in evaluating the intermediate disturbance hypothesis for explaining biodiversity patterns (Nilsson et al. 1989). The original concept was that plant species richness should be highest in median sections of river courses where flood disturbances were at intermediate levels of intensity and duration. Results obtained from European rivers in northern Sweden (Nilsson et al. 1989) and in southern France (Decamps and Tabacchi 1994, Tabacchi et al. 1996), as well as along American rivers (Baker 1990), suggest that the intermediate disturbance hypothesis relevant along river courses only in certain places, on certain spatial scales, and for certain groups of species.

Currently, it is difficult to formulate a general theory explaining the spatial distribution of vegetative diversity in riparian zones. In northern Sweden, post glacial history of the landscape results in species diversity peaking where rivers begin to downcut into sediments deposited during a higher coastal stage 9200 yr BP (Nilsson et al. 1991). In southern Spain, semi-arid rivers show very irregular patterns of species richness along their courses, as a

consequence of irregular water availability (Tabacchi et al. 1996). Differences also occur when comparing main channels and their tributaries such as in the Adour basin of France where exotic species were more numerous in the main channel and display different longitudinal patterns than native species (Planty-Tabacchi 1993, Decamps and Tabacchi 1994). In the Vindel basin, northern Sweden, the main channel also has a higher species richness than the tributaries and, in addition, differences occur in altitudinal patterns where species richness is greatest at mid-altitude in the main channel but least in the tributaries (Nilsson et al. 1994). Likewise, plant groups differ markedly in longitudinal profiles of richness; for example, the distributions of native and exotic flora (Tabacchi et al. 1990, 1996, Tabacchi 1995, Planty-Tabacchi et al. 1996, DeFerrari and Naiman 1994), or when comparing long-lived with ruderal species (Nilsson et al. 1989, 1991, 1994 Nilsson and Jansson 1995).

It still remains to be demonstrated, however, if riparian forests maintain biodiversity through continuous upstream movement of species from other watersheds or from extension of species distributions downstream during favorable environmental periods (Nilsson et al. 1994). Clearly propagule dispersal by water has a role in structuring the riparian flora (Johansson et al. 1996), but other dispersion mechanisms such as anemochory and ornithochory deserve consideration (Metzger 1995) as does consideration of the different stages of a plant's life cycle which are important for successful establishment and growth (Decamps et al. 1995).

Black cottonwood (*Populus trichocarpa*) from Pacific river banks in North America responds to climatic selection pressures at regional as well as local scales with significant variations in survival, growth, and photosynthesis in high light regimes; additionally, leaf and crown traits respond to whether the habitat is mesic or xeric (Dunlap et al. 1993, 1994, 1995). Of special interest is the discovery that genetic discontinuities are expressed among riparian populations of *P. trichocarpa* along the same river, coinciding with upstream-downstream changes in atmospheric moisture levels. This is despite the capacity of *Populus trichocarpa* to disperse sexual and asexual propagules over wide areas by water and indicates complex genetic relationships of some *Populus* populations among riparian zones

Natural Disturbances. Floods, in particular, influence plant species diversity through their capacity to create heterogeneity within the riparian zone. Such heterogeneity, in addition to inherent variations in flood characteristics, create distinct regeneration niches facilitating the coexistence of congeneric species. For example, six species of *Salix* co-occur, despite similar adult ecology, along the Sorachi River, Hokkaido, Japan (Niiyama 1990). Dispersal periods of these species overlap as water levels decrease following spring floods, thus allowing seedlings of all species to establish on the remaining wet soils. The dominant species, *S. sacchalinensis*, is maintained by general regeneration traits allowing this species to establish on a wide range of soil textures. The subordinate species *S. rorida* and *S. subfragilis* coexist with the dominant *S. sacchalinensis* on the finest and coarsest soils, respectively, where the dominant species does not grow as efficiently. The occurrence of the three other rarer subordinate species also is related to the fitness of early stages to flooding and soil characteristics.

Once established, plant species diversity also depends on periodic floods for maintenance. An interesting example is provided by the lowland floodplain podocarp forests in New Zealand (Duncan 1993). This forest is dominated by four tree species: *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Prumnopitys ferruginea* (conifers), and *Weinmannia racemosa* (angiosperm). The two former species are upper canopy trees, and the two latter species are sub-canopy trees. Tree-canopy diversity is maintained primarily through the effect of floods of contrasting intensities on site availability. Intense floods denude large areas, allowing *D. dacrydioides* to establish on silt substrates and *D. cupressinum* to establish on elevated microsites covered with organic debris. Less intense floods expose debris, providing sites more suitable for *D. cupressinum* and occasionally for *P. ferruginea*. Minor floods do not disturb the canopy, but provide opportunities for establishment of *P. ferruginea* under canopy cover and *W. racemosa* in small canopy openings. Periodic flood disturbances of various intensities are thus critical for maintaining the four dominant trees, whereas lack of major flooding leads to an increasing domination by *W. racemosa* as a result of its ability to colonize canopy gaps caused by non-flood mortality of the mature conifers.

At local scales, floods affect species diversity of herbaceous plants through heterogeneities created by the erosion and deposition of litter and silt. In northern

Sweden, leaf litter accumulations of approximately 150 g m⁻² result in a maximum number and diversity of adult vascular plant species at the upper elevational limit of riparian zones (Nilsson and Grelsson 1990). Likewise, in southern France, organic matter accumulations of 150 to 300 g m⁻² result in high rates of germination and decrease rates of mortality, whereas accumulations of 600 to 1200 g m⁻² decrease germination rates. Around 150 g m⁻² of litter correspond to maximal density and species richness (Langlade and Decamps 1994). Similarly, silt accumulations of about 500 g m⁻² correspond to maximal density and species richness of seedlings (Langlade and Decamps 1995).

Invasion by exotic species.- Riparian corridors are routes for invasions by exotic plant species across landscape path types (DeFerrari and Naiman 1994). Comparing the Adour River, France with the Mackenzie River, Oregon, **Planty-Tabacchi** et al. (1996) discovered about 1400 species (24% exotic) and about 850 species (30% exotic), respectively, constitute the riparian plant communities of these rivers. More woody species are exotic along the Adour (46%) than along the Mackenzie (17%). In contrast, herbaceous communities of the Mackenzie are more invasible (32%) than the Adour (21%). Although these differences parallel more intensive forest management in Oregon than in France the ecological mechanisms explaining these similarities remain obscure. The richest communities also have the greatest proportion of exotics, both along the rivers as well as within specific sites. This suggests that the richest communities in riparian corridors may be the most invasible because of the substantial environmental heterogeneity created by moderate floods and, therefore, most likely to allow native and exotic species to coexist.

Several interactive processes appear to the control establishment of exotic species in riparian zones (Decamps et al. 1995). Most importantly, biological invasions, although common in nature, have been accelerated through human activities (Lodge 1993). In addition, specific life history characteristics control the various stages of establishment, stabilization and expansion. For example, Pysek and Prach (1993) report that the shorter the life span, the higher the rate of invasion when comparing four species alien to central Europe: *Impatiens glandulifera*, *Heracleum mantegazzianum*, *Reynoutria japonica*, and *R. sacchalinensis*. A third level of control depends on landscape characteristics such as connectivity along rivers (Johansson et al. 1996) and historical development of

landscape patch structure (Pysek and Prach 1994). These different levels of control, and their interactions, are fundamental in predicting the patterns and consequences of riparian plant invasions.

Natural environmental features, however, may slow the rate of invasion. This has been suggested for the exotic *Mimosa nigra* in northern Australia (Lonsdale 1993). Between 1980 and 1986 the area occupied by these species increased with a doubling time of 1.2 years, with the rate of areal expansion being related to the amount of rainfall in the previous wet season. A much slower areal doubling time of 6.7 years was observed at the regional scale, probably due to the spatial isolation of wetland habitats by eucalyptus savannah. Seed predation combined with folivores are also likely to slow the rate of expansion since the seeds of this species are dispersed by flotation.

Logical reasoning suggests that exotic invasions have the potential to reduce native plant species diversity. Nevertheless, there is no clear resolution of this issue. Currently, *Impatiens glandulifera*, the tallest annual plant in Europe is expected to reduce species diversity and to out compete native light-demanding species in riparian habitats (Beerling & Perrins 1993, Planty-Tabacchi 1993, Pysek & Prach 1995). Similarly, *Tamarix* spp, an invasive exotic woody plant in arid and semi-arid riparian habitats of western United States is expected to replace or inhibit much of the native flora (Brock 1994). However, clear data supporting or refuting these expectations does not appear to exist.

Refuges for regional diversity.- Riparian forest patches, comparable to those occurring in present day neotropical savannas, have acted as safe sites for regional flora during drought periods. Although some present day humid tropical zones appear to have experienced Pleistocene droughts, there is no indication of mass extinctions but there is indication of rapid species re-expansion during the early Holocene. It has been suggested, for example, that riparian forest patches may have been refuges for the maintenance of mesic plant diversity in Central America (Meave and Kellman 1994). The floristic attributes of the riparian forest are similar to those characterizing continuous forests in the area, whereas their stem density is higher and biomass lower thus increasing their potential to maintain species richness. Moreover, riparian forest communities in a savanna matrix are often younger because more frequent disturbances by wind and fire (as compared to continuous forests) which remove

mature trees (Kellman and Tackaberry 1993). Frequent removal of mature trees reduces the rate of competitive exclusion from the community while enhancing the potential for greater numbers of coexisting species.

Riparian forests in Central America average 52 species ha^{-1} (trees >10 cm dbh), which is comparable or slightly lower than upland forests in the area (Meave and Kellman 1994). However, extremely diverse forests occur in other tropical rain forests such as in Amazonia (225 tree species ha^{-1}) and in southeast Asia (283 tree species ha^{-1}) where the refuge role of riparian forests may have been more limited (Dumont et al. 1990).

Macroinvertebrate communities.- Riparian vegetation affects macroinvertebrate aquatic communities in many ways. Evidence is so strong that it has been suggested that macroinvertebrate community characteristics could be predicted from a knowledge of riparian vegetation (Cummins et al. 1989), and that the presence or absence of trees adjacent to stream channels could be the single most important factor altered by human activity that affects macroinvertebrate communities (Sweeney 1993).

Streamside forests influence aquatic biodiversity by creating benthic habitat through the addition of woody debris and possibly by supplying food in the form of plant litter and terrestrial DOM (Sweeney 1993). Recent investigations argue strongly that riparian vegetation affects macroinvertebrate diversity primarily through its effects on benthic habitat (Ormerod et al. 1993, Glova and Sagar 1994, Lester et al. 1994, Richards and Host 1994, Brewin et al. 1995). In contrast, the effect of riparian vegetation as a source of nourishment on invertebrate biodiversity is not so well established. Much of the woody debris is unpalatable, thus preventing a diverse consumer community from developing (O'Connor 1992). Also, changes in species composition, rather than diversity, often follow changes in riparian composition. For example, a gatherer-collector community of chironomids may replace a shredder community when there is a reduction in slowly decomposing riparian litter in small woodland streams (Grubbs and Cummins 1994).

Habitat

It is widely recognized, for several reasons, that riparian zones provide valuable wildlife habitat. First is proximity

to a high energy aquatic environment. With variations in flood duration and frequency, and concomitant changes in water table depth and plant succession on new substrata, the resulting environment becomes a complex of shifting habitats created and destroyed on different spatio-temporal scales (Malanson 1993). Second, most riparian zones are covered with woody vegetation. This gives rise to a remarkable variation from shrubs serving as refuges for small mammals to trees offering nesting and perching sites for birds. Also, sustained herbivory develops as a result of enhanced productivity and food quality, and fallen woody debris provides stability for terrestrial as well as aquatic invertebrate communities. Third, riparian forests act as refuges where feeding in adjacent areas is facilitated and as corridors for migration and dispersal (Brinson et al. 1981).

The importance of riparian forests as wildlife habitat is exemplified in the lower Mississippi River where more than 60 species of mammals, about 190 species of reptiles and amphibians, and about 100 species of birds are seasonally associated with riparian habitats (Klimas et al. 1981). Mammals include 4 shrews and voles, 17 bats, 2 rabbits, 27 rodents (including beaver), 14 carnivores (including wolves, bears and cougars), two hoofed mammals (deer and boar), opossum, and armadillo; reptiles and amphibians include crocodile, 20 turtles, 10 lizards, 36 snakes, 21 salamanders, and 25 frogs and toads.

Drinking water is obviously an important reason for mammals to be in riparian zones. However, small mammals may respond more to differences in tree communities than proximity to streams. For example, higher capture rates for some small mammals have been reported in streamside habitat dominated by red alder (*Alnus rubra*) adjacent to uplands dominated by Douglas-fir (*Pseudotsuga menziesii*?) (McComb et al. 1993a), but no difference was detected where upland and streamside habitats were similar in vegetative structure and composition (McComb et al. 1993b). One large mammal (i.e., the white-tailed deer *Odocoileus virginianus*) uses riparian zones almost twice as much as non-riparian areas, supposedly as an anti-predation strategy (Larue et al. 1994). Nevertheless, several interrelated reasons are probably needed to explain the occurrence of any species in riparian areas. Consider juvenile wood turtles (*Clemmys insculpta*) which preferentially remain near stream channels where they can move comparatively short distances to find appropriate

thermal and moisture conditions and at the same time are less exposed to predation (Brewster and Brewster 1991).

Like mammals, more individuals and species of birds generally are found in riparian habitats than in adjacent ones. For example, 82% of the breeding birds of northern Colorado occur in riparian vegetation (Knopf and Samson 1994). In addition, seasonal migratory birds utilize riparian vegetation as transitory habitats. However, bird individuals and species may not be more numerous in situations where the riparian habitat is similar to upland habitat, or not clearly delineated (Murray and Stauffer 1995).

In reality, bird assemblages of riparian zones and adjacent uplands are interdependent, and the number of shared species varies seasonally and longitudinally along river courses with apparently greater interdependence at intermediate elevations (Knopf and Samson 1994). Such an interdependence results in dynamic bird communities. About 90% of the present bird fauna along the Platte River in northern Colorado has arrived since the development of a gallery forest within the last 90 years (Knopf 1986). In boreal forests, bird densities reportedly increase 30 to 70% in protected riparian forest strips the year after clear-cutting, and then decline during the following years, while regeneration of the adjacent clear-cuts occurs (Darveau et al. 1995).

Bird communities also are sensitive to the quality of riparian vegetation (Croonquist and Brooks 1993). Destruction of riparian vegetation causes local extinction but also reduces the ability of some populations to recolonize sites (Knopf and Samson 1994). Replacement of tree species is also important. For example, along the Colorado River, in the Grand Canyon, black-chinned hummingbirds (*Auriparus flaviceps*) nest only in exotic tamarisk-dominated habitats that are greater than 0.5 ha in size (Brown 1992). Even modest changes in plant communities are likely to produce substantial changes in bird communities (Croonquist and Brooks 1993).

Various widths of riparian zones have been reported as desirable for maintenance of bird communities. In disturbed areas, woody strips 2 m wide permit only portions of reduced bird populations to occur, but widths > 25 m on each bank are necessary to maintain sensitive species (Croonquist and Brooks 1993). In a survey of 117 corridors ranging from 25 to 800 m wide, Keller et al. (1993) concluded that the probability-of-occurrence increased most rapidly between 25

and 100 m. An important conclusion of recent work on riparian habitat for birds is that conservation must be based on specific bird species, and account for differences in behavior (for example, between generalist-opportunistic and riparian-obligate species). A drainage basin perspective is absolutely necessary (Knopf and Samson 1994).

Another important discovery is the realization of how the inhabitants of riparian zones - large, but also small mammals and birds - have the capacity to modify habitat structure and function. Beaver (*Castor canadensis*) is one well known habitat modifier in temperate North America (Naiman et al. 1986, 1988, 1994). Through ponding water and storing sediments, they create diverse wetlands and alter the vegetative composition of in channel and riparian communities, strongly influencing riparian landscapes. Through selective cutting of trees they change the composition of riparian communities. For example in Minnesota, under beaver influence, trembling aspen (*Populus tremuloides*) has been reported to decrease in abundance while alder (*Alnus rugosa*) and black spruce (*Picea glauca*) increase (Johnston & Naiman 1990). Besides beaver, species such as moose (*Alces alces*), elk (*Cervus canadensis*), brown bear (*Ursus arctos*) create and maintain tight networks of trails along river banks. In southern Africa, hippopotamus (*Hippopotamus amphibius*) appears as a powerful modifier of riparian habitats, gathering in pools during the day where they stir up sediments and deepen aquatic habitats, and following the same paths during the night between pools and terrestrial grazing areas, thus creating channels maintaining connectivity between patches (Naiman and Rogers 1997). Warthog (*Phacochoerus aethiopicus*) transform tens of hectares to apparently ploughed fields by digging soils 10-15 cm deep to feed on underground plant storage organs in riparian forests and wetlands (Rickard 1993) and, as a consequence, favor the replacement of perennial rhizomatous grasses by annual grasses and forbs.

Feeding activities may have serious long-term consequences for riparian forests structure and function. A well known example is zoochory, particularly ornithochory, which facilitates the expansion of certain species through selective feeding and propagule transport. Moose browsing has been reported as indirectly affecting decomposers through changes in the quality of litterfall in North American riparian systems (McInnis et al. 1992, Pastor et al. 1993). Similar effects occur in riparian corridors in Africa through bulk grazing by hippopotamus, selective

browsing by kudu (*Tragelaphus strepsicerous*), giraffe (*Giraffa camelopardalis*), and bushbuck (*Tragelaphus scriptus*), and bulk browsing by elephant (*Loxodonta africana*) (Naiman and Rogers 1997).

ENVIRONMENTAL ALTERATIONS

Human alterations

The impact of Man's activities on riparian systems began with the settlement of societies in floodplains. Along European rivers, the succession of human induced alterations includes neolithic deforestations and clearing land during Gallo-Roman and medieval periods (Pautou et al. 1992). Civil engineering works in the 19th century and hydroelectric developments in the 20th century accelerated these alterations (Petts et al. 1989). A similar story occurred in North America on a reduced time-scale since the European settlement (Sedell and Froggatt 1984). Papers of the last few years have illustrated some of the mechanisms involved in modern human impact on riparian systems [ADD REFERENCE?].

Flow variability and fluctuations in channel width are necessary for maintaining the biodiversity of riparian systems (Friedman et al. 1996). These natural disturbances have been dramatically decreased in many parts of the world through river impoundment, water management, and lowering of water tables. Substantial changes in riparian vegetation may occur, however, without changing mean annual flows, as riparian vegetation is especially sensitive to changes in minimum and maximum flows (Auble et al. 1994). In many cases, hydrologic alterations result in shifts in riparian plant community composition as well as senescence of woody communities (Bravard et al. 1986, Franklin et al. 1987, Decamps et al. 1988, Rood and **Heinz-Milne** 1989, Howe and Knopf 1991, Nilsson et al. 1991, Busch et al. 1992, Pautou et al. 1992).

Hydrological alterations in the southwestern United States has facilitated rapid invasion of floodplain ecosystems by *Tamarix ramossissima* (Busch and Smith 1995). This species can dessicate water courses (Vitousek 1990), inducing other disturbances such as fire (Busch and Smith 1993) and displacement of native species (e.g., *Salix gooddingii* and *Populus fremontii*; Vitousek 1990, Stromberg et al. 1991). Along the Colorado River floodplain, ecophysiological tolerances and competition for moisture may be at the origin of shifts in riparian community structure from a gallery forest to riparian thickets with *Tamarix*

dominating or replacing *Salix* and the disappearance of *Populus* (Busch and Smith 1995).

Native upland tree species also can invade riparian zones as a result of flow regulation. Along the River Murray in Australia, flood frequency and duration historically prevented native redgums (*Eucalyptus camaldulensis*) from establishing on grass plains. By reducing depth and duration of flooding, river regulation has favored a redgum invasion that is expected to cause a complete extinction of the once extensive grass plains in the near future (Bren 1992).

Alterations of water regimes also have contributed to dramatic declines and losses of cottonwood forests throughout western North America as a consequence of drought-induced mortality from abrupt flow reductions and lowering of water tables (Rood & Mahoney 1990, Rood et al. 1995). A possible mechanism for this decline is that a reduction of flooding diminishes the rate of recruitment of new stands (Miller et al. 1995).

In fact, the maintenance of phreatophytic riparian woodlands depends heavily on the relationship between river flow and life history traits of cottonwood (Rood and Heinz-Milne 1989, Mahoney and Rood 1991b, 1992, Stromberg and Patten 1991, 1992, Scott et al. 1996, Segelquist et al. 1993, Hughes 1994). [PERHAPS CHOOSE JUST 1-2 OF THE BEST REFERENCES] For example, as growth conditions vary widely within and between years for the same site, an important factor for survival is the ability of seedlings to establish over a range of moisture conditions (Segelquist et al. 1993) while river flow interacts with species-specific characteristics. Tyree et al. (1994) demonstrated this for several *Populus* species that differ in xylem water potentials and consequent cavitation.

Even though alterations to water regimes often result in declines of cottonwood forests, at least temporary increases occur in some other situations (Snyder and Miller 1991). An interesting example occurs in the northern part of the Great Plains of the United States associated with the poplar-willow communities of the Missouri and Platte rivers (Johnson 1992, 1993, 1994). In the Missouri River, after completion of the Garrison dam in 1953, regeneration sites progressively disappeared downstream, resulting in a continuous decrease in pioneer stages and an increase in older stages. In this meandering river, poplar-willow communities depend on flow peaks which erode outer banks and deposit sediments on inner banks. A reduction of peak flows prevents meandering and thus the formation of suitable areas

for poplar-willow establishment (Johnson 1993). On the contrary, poplar-willow communities have dramatically expanded along the Platte River after completion of dams on its two main tributaries, the North and South Platte rivers. In this braided river flow reduction exposes large areas suitable for seedling establishment and survival (Johnson 1994).

In turn, invading riparian trees may have an impact on channel morphology, particularly when they replace formerly grassy areas (Rowntree 1991). The specific consequences of such dynamic interactions between invading trees and channel morphology depends on complex relationships between the physical characteristics of the channel, the biological characteristics of the invasive vegetation, and the section of channel considered (Friedman et al. 1996b). Active investigations are needed on mechanisms linking water, landforms and species in different landscape settings in order to predict the effects of manipulating flow on floodplain forests (Décamps 1997).

The entire riparian plant community, not only the trees, is modified by flow regulation. For example, in northern Sweden, species-richness and the percentage vegetative cover are both lower per site in a regulated as compared to a non-regulated river (Nilsson et al. 1991). Subtle changes also occur within the communities with the proportion of annual plus biennial species-richness being higher, and perennial species-richness being lower, along the regulated river. Water level regime and mean annual discharge are among the most important variables for maintaining species richness and plant cover.

The species composition of the riparian plant community, before the water is regulated, is also an important variable to consider in predicting responses to alterations (Bravard et al. 1986, Nilsson et al. 1991, Pautou et al. 1992). Several different scenarios may be expected for a plant community as a result of flow alterations: self-reproduction by on-site regeneration, duplication MOT SURE WHAT IS MEANT] in other parts of the floodplain, or replacement by a new type of plant community (Pautou et al. 1992).

Alterations of riparian plant communities obviously affect aquatic macro-invertebrates and fishes as a consequence of their role as source of nourishment and instream habitat (Davies & Nelson 1994, Salo & Cundy 1987), as well as the species diversity of amphibians, birds and

mammals (Croonquist & Brooks 1993, Keller et al. 1993, Naiman & Bilby 1997).

Management (and Restoration)

An important goal for the management of riparian zones is to control diffuse pollution from agriculture. One model suggests that multi-species riparian buffer strips provide the best protection of streams against agricultural impact (Hubbard & Lowrance 1994, Lowrance et al. 1995, Schultz et al. 1995). This model uses three interactive zones that are in consecutive **upslope** order from the stream: (1) a permanent forested zone, about 10 m wide, (2) a zone of shrubs and trees, up to 4 m wide (and managed so that biomass production is maximized), (3) a herbaceous zone, up to 7 m wide. The first zone influences the stream environment (e.g., temperature, light, habitat diversity, channel morphology, food webs and species richness). The second zone controls pollutants in subsurface flow and surface runoff. It is an area where biological and chemical transformations are maximized, as well as storage in woody vegetation, infiltration and deposited sediments. These first two zones contribute to nitrogen, phosphorus and sediment pollution removal. The third zone, herbaceous plants next to cropland, provides spreading of overland flow thus facilitating deposition of coarse sediments. Clearly this basic model must be adapted to various catchment conditions and stream orders to provide effective management.

In using riparian zones for management, hydrological characteristics are of primary importance. Riparian buffer zones retain surface runoff pollutants as a result of their water storage capacity and infiltration rate (Cooper et al. 1995). However, a key factor is that riparian buffer zones intercept the dominant hydrological pathways which are dependent on soil type and permeability, adjacent land use, slope, potential run-off generation areas, and land drainage installations. For example, nitrate removal requires that the bulk of the water moves across the surface and shallow groundwater through biologically active soil zones (Lowrance et al. 1995), and sediment removal requires that surface runoff does not overwhelm the buffer system. An important issue is that hydrological pathways are likely to change widely in space and time. Forest growth or weather variations may affect the degree of saturation of the riparian zone and the proximity of the water table to the soil surface (Haycock et al. 1993, Emmett et al. 1994),

still complicating the intricacy of groundwater routes and how they encounter roots and soil microbes.

A second consideration in the management or restoration of riparian zones is biophysical connections within the entire catchment. Although riparian zones are valuable tools in reducing diffuse pollution, they are more effective over the long term when upstream pollution has been limited through good agricultural practice at the catchment level (DeBano & Schmidt 1990, Baillie 1995). Within a catchment, the integrated effects of riparian zones on water quality will also differ according to stream order, smaller streams having a greater potential than larger ones to buffer against diffuse pollution (Lowrance et al. 1995). The control of water quality in headwater catchments is an effective management strategy since, once a river is contaminated, few inexpensive possibilities remain to improve water quality (Haycock et al. 1993).

Increasing loading rates may affect riparian zones differentially according to the type of pollution (Emmett et al. 1994, Lowrance et al. 1995). For nitrate, higher rates of N-removal generally occur with higher loading rates as a consequence of denitrification and vegetative uptake. Nevertheless, buffering capacity may be limited by inefficient nitrate uptake rates, limited duration of anaerobic conditions, or organic carbon availability for microbial respiration (Haycock et al. 1993). For other nutrients and metals, biological processes similar to denitrification are lacking, and higher rates of loading may result in excess release when the immobilization capacity of the riparian buffer is exhausted. In such cases it is necessary to manage riparian systems to facilitate sediment removal and infiltration so as to prevent these systems from becoming sources of pollutants. Also, flooding and erosion of riparian soils during winter may be a general limitation to buffering capacities for nutrients and metals (Haycock et al. 1993).

Long-term sustainability is likely to occur when managed systems imitate natural ones. For example, the zone 1 of the multi-species riparian buffer strip (located near the stream) functions better if zone 2 is harvested infrequently; and zone 3 near the cropland also functions better if accumulated sediment is removed and herbaceous vegetation re-established periodically (Lowrance et al. 1995). The literature, however, offers divergent examples ranging from efficient removal of nitrogen after 20 years of

high nutrient loading (Baillie 1995) to exhaustible sinks (Cooper et al. 1995). Whatever the example, improved land use practices within the catchment and the maintenance of riparian zones for interception of groundwater flows by various stages of vegetation succession (each having different absorption capacity) are key factors for the long-term sustainability of buffer strips (Vitousek and Reiners 1975, Haycock et al. 1993).

Other benefits obtained from creative management and restoration of riparian zones include provision of diversified habitat for terrestrial and aquatic wildlife, corridors for plants and animals dispersion, input of organic matter to streams, and so forth. Enhancement of the visual quality and amenity of the landscape is also an important benefit derived from management efforts. Management has been used positively to influence communities of aquatic animals upland streams throughout Wales and Scotland (Ormerod et al. 1993) and managed and natural floodplain forests are recommended in British river and floodplain restoration projects (Peterken & Hughes 1995). Indeed, management and restoration of riparian zones are important tools for the future catchment quality.

Tools for the Future

In the near future, riparian systems will have to accommodate dramatic changes in population density, resource consumption and environmental conditions. Even more so than today, they will be expected to fulfill various ecological functions related to biodiversity, habitat, information flow, biogeochemical cycles, microclimate, and resistance and resilience to disturbance (Naiman et al. 1995). They will be also expected to fulfill more social functions, including economics, recreation, culture and aesthetics. Clearly, no single riparian system will perform all these functions, but each will be likely to perform at least one function.

Riparian systems, as future management tools, may be useful under three main approaches: (1) a linear extensive approach at the scale of river courses, (2) a site specific intensive approach within a riparian system, and (3) a catchment approach at various scales from **hillslopes** to the entire drainage basin.

An extensive linear approach is needed to delineate and classify riparian systems along streams. Significant progress has already been made in mapping riparian systems

using remotely sensed data (Muller 1995). Lowrance et al. (1995) recommend that linear forests be characterized at a resolution of 10 to 20 m. In combination with hydrogeomorphic data, such precise maps help in assessing the potential for riparian systems to intercept surface- and subsurface-borne pollutants. Management-initiated investigations, such as those conducted on poplar trees of the Platte River, demonstrate the need for considering entire river courses to understand various aspects of the dynamics of riparian systems (Johnson 1994), to restore the ecosystem integrity of rivers and floodplains (Dahm et al. 1995), and to manage international greenways (Burley 1995). In all these examples, strategies for creating or restoring vegetation along river courses focus on conditions suitable for the natural regeneration of riparian habitats. Both landscape and detailed site perspectives are required to judge whether planted trees will survive for more than a few years and reach the expected sizes. The landscape perspective may be attained through a knowledge based on mapping past and present extents of floodplain plant communities, characterizing the ecology of appropriate species, and determining priorities at both landscape and site scales (Howell et al. 1994). The detailed site perspective may be attained through a knowledge based on water regimes, suitable soil conditions, long-term survival and growth rates, as well as the effects of variable water levels on tree metabolism (Johnson et al. 1990).

An intensive site-specific approach is necessary to integrate research, demonstration, and application of riparian zone buffers (Lowrance et al. 1995). Such an integration will aid in discovering the effects of vegetation type and management approach on the long-term control of nutrient and sediment pollution, the response of riparian zones to acute stresses such as large storms and extremes in temperature or growing season rainfall, the consequences of chronic stress leading to saturation of riparian zones by nutrients, and the processes controlling groundwater microbial dynamics (Lowrance et al. 1995, Groffman 1997). Insights into these issues are requisite for developing models of risk assessment (Lowrance & Vellidis 1995) and decision making (Hubbard & Lowrance 1994). Intensive site specific studies also should improve the ability to model important functional issues such as the influence of soil wetness on key nutrient transformation processes (Gold 1997). Finally, site specific studies should improve the ability to evaluate the performances of restored

processes (Gold 1997). Finally, site specific studies should improve the ability to evaluate the performances of forested riparian habitats through a better knowledge of hydrologic, geomorphic and biologic conditions.

Research at the catchment scale, or at least at the representative hillslope scale, is essential to assess the effect of riparian systems on hydrologic inputs from uplands (Lowrance et al. 1995). As many buffer processes operate most effectively in headwater basins, downstream cumulative effects involving many small catchments must be given proper emphasis (Burt 1997). The catchment is also the appropriate scale to improve hydrologic conditions within riparian zones (Schmidt & DeBano 1990) and to assess the potential of narrow riparian zones that are remnants of previously wider ones in most rural and urban European landscapes (Décamps et al. 1988, Petersen 1992).

Finally, considering riparian zones as management tools for the future, requires the adoption of flexible, adaptive management schemes to cope with surprises related to discontinuities and synergism's (Myers 1995). Discontinuities in riparian systems may occur where nutrient accumulations reach disruptive thresholds that suddenly change the system from a sink to a source. Synergism may result from an interaction between two chronic stresses such as nutrient loading and global warming or between a chronic and an acute stress such as a large storm. In addition to such "anticipatable surprises", entirely unforeseeable future issues require increased efforts in research. After all, as quoted from the Freshwater Imperative (Naiman et al. 1995) "the important role of riparian forests in maintaining environmental quality in streams and rivers was the result of investigations into the fate of fertilizer placed on agricultural fields (Peterjohn and Correll 1984) and studies of the effects of logging (Gregory et al. 1991)".

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