

THE ECOLOGY OF INTERFACES: Riparian Zones

Robert J. Naiman and Henri Décamps

School of Fisheries, Box 357980, University of Washington, Seattle, Washington 98195 USA, naiman@u.washington.edu and Centre National de la Recherche Scientifique, Centre d'Ecologie des Systèmes Aquatiques Continentaux, 29, rue Jeanne Marvig, 31055 Toulouse, France; e-mail: decamps@cemes.cemes.fr

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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, geographically unique channel processes, altitudinal climate shifts, and upland influences on 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. Innovations in riparian zone management have been effective in ameliorating many ecological issues related to land use and environmental quality. Riparian zones play essential roles in water and landscape planning, in restoration of aquatic systems, and in catalyzing institutional and societal cooperation for these efforts.

INTRODUCTION

First described nearly a century ago (36), interfaces between environmental patches occur where structural or functional system properties change discontinuously in space or time.

The terms transition zone, ecotone, and boundary, which describe interfaces (91, 182), are used synonymously in this review. Interfaces between adjacent ecological systems have a set of characteristics uniquely defined by space and time scales and by the strength of interactions between the adjacent ecological systems (102). Thus, interfaces possess specific physical and chemical attributes, biotic properties, and energy and material flow processes, but they are

unique in their interactions with adjacent ecological systems (183, 231). The strength of these interactions, which vary over wide temporal and spatial scales, is 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 environmental patches (183). Interfaces have resources, control energy and material flux, are potentially sensitive sites for interactions between biological populations and their controlling variables, have relatively high biodiversity, maintain critical habitat for rare and threatened species, and are refuge and source areas for pests and predators (91, 102, 183, 231). Some interfaces may also be sites for longitudinal migration (e.g. along windbreaks or riparian zones) and genetic pools or sites for active microevolution (e.g. forest/agricultural interfaces—76). Interfaces between terrestrial and freshwater ecosystems are particularly sensitive to environmental change (155, 182). Examples include riparian forests, marginal wetlands, littoral lake zones, floodplain lakes and forests, and areas with groundwater–surface water exchanges. This article reviews riparian zones associated with streams and rivers because they encompass most of the characteristics important for interfaces.

Natural riparian zones are some of the most diverse, dynamic, and complex biophysical habitats on the terrestrial portion of the planet (184, 185). This article provides an overview of important characteristics of riparian zones, describes physical effects on adjacent environments, summarizes ecological characteristics, and discusses consequences of environmental alterations on ecosystem 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 1976). The anglicized term *riparian* refers to biotic communities on the shores of streams and lakes. Riparian zones are an unusually diverse mosaic of landforms, communities, and environments within the larger landscape, and they serve as a framework for understanding the organization, diversity, and dynamics of communities associated with fluvial ecosystems (53, 84, 183, 184, 185). A variety of natural disturbances creates a spatial and temporal environmental mosaic with few parallels in other systems.

Defining and Delineating Riparian Zones

The spatial extent of the riparian zone may be difficult to delineate precisely because the heterogeneity is expressed in an array of life-history strategies and successional patterns, while the functional attributes depend on community

composition and the environmental setting. The riparian zone encompasses the stream channel between the low and high water marks 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 (184, 185; exact definitions differ among researchers). 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 (53, 126, 182, 236, 238). The riparian zone may be 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 (>50 years) channel dynamics and the annual discharge regime. Riparian zones of 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 (155, 240). Vegetation outside the zone that is not directly influenced by hydrologic conditions but that contributes organic matter (e.g. leaves, wood, dissolved materials) to the floodplain or channel, or that influences the physical regime of the floodplain or channel by shading, may be considered part of riparian zones (26, 84). These attributes suggest that riparian zones are key systems for regulating aquatic-terrestrial linkages (182, 271) and that they may provide early indications of environmental change (52, 183, 230).

Defining riparian zones is important for both ecological and managerial reasons. Riparian buffer zones, a defined distance from a stream where land use activities are restricted for stream protection purposes, are becoming an increasingly common management tool (20, 80, 136, 242). Definitions generally incorporate ecological characteristics such as the spatial extent of herbaceous plants adapted to wetted soils, production of nutritional resources for aquatic systems, local geomorphology, and area of sediment generation (84, 136, 242). Increasingly, geographic information systems (GIS) and digital elevation models (DEM) are being used to provide an initial estimate of riparian zone area and distribution in drainage networks (13, 274). Where the riparian vegetation has been removed, methods are being developed to determine the spatial potential for its regeneration (136, 210).

Life-History Strategies

Streams are nonequilibrium systems that have strong effects on the biotic characteristics of riparian communities. The active channel and floodplain are harsh environments for the establishment of plants and animals (185). Here 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 225).

Seasonal variations in discharge and wetted areas create environmental conditions that challenge even the most tolerant species. Nearly every year, most riparian plants are subjected to floods, erosion, abrasion, drought, freezing, and occasionally toxic concentrations of ammonia in addition to the normal biotic challenges; the life-history strategies of most riparian plants are such that extreme conditions are either endured, resisted, or avoided (4, 86, 185).

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 (185). The classification of plants into four broad categories of functional adaptations is useful for understanding processes leading to riparian forest succession and distributional patterns.

1. Invader—produces large numbers of wind- and water-disseminated propagules that colonize alluvial substrates.
2. Endurer—resprouts after breakage or burial of either the stem or roots from floods or after being partially eaten.
3. Resister—withstands flooding for weeks during the growing season, moderate fires, or epidemics.
4. Avoider—lacks adaptations to specific disturbance types; individuals germinating in an unfavorable habitat do not survive.

Some widely distributed species illustrate the variety of life-history strategies. Sitka willow (*Salix sitchensis*) and Scouler's willow (*Salix scouleriana*) are pioneer plants well adapted to living under a number of disturbance regimes. Individuals of these species invade post-fire landscape or resprout if the root system remains intact in a fire (185). They are well suited as invaders, endurers, or resisters depending upon local environmental conditions. In contrast, Sitka spruce (*Picea sitchensis*), which can colonize woody debris and mineral substrata on the floodplain (94, 165) and resist both flooding and sediment deposition, does not persist where fire is a regular occurrence.

MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS Flood tolerance in trees includes both morphological and physiological adaptations. In general, morphological adaptations such as adventitious roots, stem buttressing, and root flexibility in riparian plants are a response to either soil anoxia or unstable substrata. Morphological adaptations to anoxia by vascular plants in periodically flooded areas include air spaces (aerenchyma) in the roots and stems that allow

for the diffusion of oxygen from aerial portions of the plant to the roots and 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 ethylene, the production of which is initiated by anaerobic soil conditions (17). Root and stem aerenchyma are common in species of families 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*, *Sequoia*) living in riparian environments where sediment deposition and wetted soils are common (17, 248, 252).

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 (73).

Anoxic conditions are challenging to plants not only because they need oxygen, but also because anoxic conditions mobilize soluble reduced ions (such as manganese) that are toxic (171). 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 klotzchyana* accelerates glycolysis with ethanol as the major end product of anaerobic metabolism but without detectable oxygen diffusion to the root system (123), whereas *Hymenaea courbaril* maintains aerobic root metabolism (with a 50% decrease in metabolism) through oxygen diffusion from the aboveground stem system. *Chorisia speciosa* develops hypertrophic lenticels to improve the aeration of the root system, although it does not reach full metabolism. A fourth species, *Schyzolobium parahyba*, which does not accelerate glycolysis enough to maintain the rate of energy production required by the roots, does not grow in that environment (123).

REPRODUCTIVE ADAPTATIONS Plant life-history strategies include a suite of co-adapted characters that enhance reproductive success in specific environments (9). The primary reproductive characteristics of riparian plants are trade-offs 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, ensuring moist seedbeds for successful germination and plant colonization (120, 248). Many species use transport by flowing water, a phenomenon known as hydrochory, for dispersal of seeds as well as vegetative fragments to new sites (116, 196, 198). Bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) in a South Carolina swamp forest rely on water

more than wind to disperse seeds (244). Further, small increases in water levels tend to introduce seeds from adjacent plant communities. Dispersal by animals (zoochory) and by wind (anemochory) may be even more important, but little empirical data exist for comparison.

The mechanism for propagule dispersal also structures riparian flora and may help explain species distribution patterns. In Sweden, Johansson et al (116) found a positive relationship between floating capacity of the diaspores and species occurrence in the riparian vegetation. Seeds of water-dispersed species floated better than other seeds. Floating time did not differ between seeds dispersed by animals or wind.

Many riparian plants reproduce vegetatively (e.g. asexually). Otherwise healthy branch tips, of cottonwood, for example, which are shed in the process of branch abscission, or cladoptosis (59, 81), may develop adventitious roots and grow into genetically identical trees (164).

Successional and Vegetative Patterns

PHYSICAL CONTROLS Complex interactions among hydrology, geomorphology, light, temperature, and fire influence the structure, dynamics, and composition of riparian zones (23, 155). The literature suggests that hydrology (and its interactions with local geology) is the most important factor. For example, in riparian floodplains having a ridge-and-swale topography, vegetative patch types alternate between those on topographic lows adapted to long hydroperiods and those on topographic highs with species also found in mesic uplands (23, 168, 240).

Brinson's (23) conceptual model is that 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. The former create 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 many tree species have similar generation times (8, 96, 109). The low-power floods that occur annually determine short-term patterns such as seed germination and seedling survival (8, 137, 138). For example, in southwestern Colorado, seedlings of cottonwood (*Populus angustifolia*) 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, but a persistent late-summer Arizona monsoon is needed for survival (8). Good seedling years occur more frequently (about every 3–4 years) than stand-origin years (about every 10–15 years).

The ability of soils and sediments to hold water and the existence of tributary and groundwater flows are equally important in determining vegetative distribution (23, 50, 109, 131, 262). Distance from the river and microtopographic variations determine lag times between rising discharge in the main channel and arrival of water on-site. Once 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. External water sources can allow vegetation to persist largely independent of the flood regime (14, 50, 131, 262). Indeed, older cottonwood, river red gum (*Eucalyptus camaldulensis*), and most mature riparian trees use groundwater rather than nearby creek water, presumably because groundwater is a more reliable source (50, 155).

The geomorphic template upon which the riparian forest develops is constantly undergoing change induced by the discharge regime (23, 180). The drainage network, from headwaters to the estuary, represents a mosaic of sites that 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 down-valley so that the physical features of the riparian zone continue to change (68). 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.

A rich and comprehensive literature describes fluvial geomorphology (68). Two aspects particularly important for understanding patterns and processes in riparian vegetation are site-specific erosion and deposition, and lateral channel migration. Lateral channel migration may be slow (cm yr^{-1}) to fast (10^2 m yr^{-1}), depending on the type of stream and channel hydraulics (12, 23, 239); this substantially influences the composition and demography of the vegetative communities (111, 113, 127).

Sediment supply depends upon land use, climate, and tectonic activity. Rates of erosion and deposition range from a few millimeters to several meters annually. Tectonic activity, which has been occurring in the Andes Mountains for millennia, appears to be a central speciation mechanism for riparian forest communities in the floristically rich upper Amazonian basin (226, 239).

The physical influences of light and temperature on the vegetative community are less well investigated than either hydrology or geomorphology. Understory light tends to be highest at the riparian forest edge but rapidly declines toward the forest interior (unless gaps have been created by fallen trees), 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 (152, 219, 220). The temperature regime is markedly different from upland forests, but no studies have attempted to link this difference to the vegetation (26). Compass orientation does influence light and temperature regimes, and significant floristic differences appear between riparian zones on north- and south-facing slopes (256).

Fire occurs rarely in the riparian zones of humid regions where most vegetation cannot withstand even mild fires (185) but plays a significant role in drier climates (4). In the lower Colorado River, nearly 40% of the riparian vegetation burned within 12 years, with halophytic shrubs recovering faster than mesophytic trees (30).

BIOTIC PATTERNS As corridors within watersheds, riparian zones have a unique longitudinal pattern that exerts substantial controls on the movements of water, nutrients, sediment, and species (76, 155). Forman (76) recognized eight common shapes for riparian corridors, ranging from strictly linear (mostly uplands) to highly variable (low-elevation valley bottoms). Cross-sectional profiles that provide an important third dimension depend upon the local geographic setting. The simplest tend to be upstream and the more complex ones downstream (76, 235).

Despite strong hydrologic and geographic influences on riparian vegetation, ecological influences (such as competition, herbivory, soils, and disease) are significant in shaping communities. Even though competition is probably reduced because of frequent disturbance, a competitive hierarchy does exist. There is evidence that some species could exist in environments beyond their present range, specifically in the direction of less stress, except for the presence of competitors (129).

In regions with intact animal populations, herbivory exerts strong influences on vegetative characteristics (33, 190). The physical and trophic activities associated with herbivory have ecosystem-level consequences that go far beyond the requirements of individuals for food and habitat (121, 124, 179). The habitat is further modified by the activities of larger animals as they burrow and wallow in soils and build dams on streams, among other activities. The net result is that the heterogeneity of riparian habitats (or resource patches) is increased, and the distribution and cycling rates of elements (such as N and P) are modified.

Soil conditions (especially the degree of saturation) also coincide with patterns of sediment grain size and microtopography, affecting plant distribution from the river to the uplands (250) and are discussed later in this review. 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 (76).

In general, the basal area of riparian forests is as great or greater than that of upland forests (23). Although values vary widely within regions, largely due to stand age, the variation is usually less than an order of magnitude. 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 (23).

The aboveground biomass of riparian forests ranges between 100 and 300 tons ha^{-1} with few exceptions (23). Leaves represent 1–10% of the total. In general, belowground biomass tends to be less than aboveground biomass, ranging from 5% to 120% of it. Riparian forests have relatively high rates of production in comparison with upland forests. Much of the variation apparent in belowground biomass—12 to 190 tons ha^{-1} —may be due to sampling methods and site-specific conditions. Published values for aboveground production range from 6.5 to 21.4 t $\text{ha}^{-1} \text{yr}^{-1}$; litter fall averages 47% of the annual production. The limited data do not reveal latitudinal or successional gradients. Rates of belowground production have received virtually no attention in studies of riparian forests. The data suggest that there are no strong limiting factors associated with water or nutrients that would result in unusually low production.

Spatial zonation often exists as a transverse gradient perpendicular to the wetted channel that is made complex by vegetative responses to local variations in topography and susceptibility to flood (236). Vegetative patterns typically follow predictable patterns in physical features (273) and disturbance patterns (185). Décamps et al (54) presented a model of riparian forest succession for the Garonne River, France, in which 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 not reversible and internal autogenic forces dominate.

The earliest studies of vegetation dynamics in riparian zones did not refer to the concept of succession (75) but nevertheless illustrated the process. Many successional patterns in riparian areas are primary succession, but an equal number of successional patterns begin with plant fragments, propagules, or biomass remaining from previous communities (155). Avalanche, flood, wind, fire, drought, disease, herbivory, and other physical influences on the vegetation leave unique biotic legacies that are displayed in various successional patterns (185, 201). 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 depend on the type, intensity, frequency, and duration of the disturbance (53). Disturbances also prepare the site for invasion by additional species favored by the new conditions.

PHYSICAL FUNCTIONS OF RIPARIAN ZONES

Mass Movements of Materials and Channel Morphology

Material supplied to streams comes from erosion of stream banks, a process influenced by root strength and resilience (85), as well as from the uplands (178). Stream banks largely devoid of riparian vegetation are often highly unstable and subject to mass wasting, which can widen channels by several to tens of meters annually (111, 239). Major bank erosion is 30 times more prevalent on nonvegetated banks exposed to currents as on vegetated banks (11).

Riparian vegetation also modifies sediment transport either by physically entrapping materials, which appears to be most important in relatively low-gradient environments, or by altering channel hydraulics. In experimental channels, Kentucky bluegrass (*Poa pratensis*) entrains sediment at the base of the vegetation, with 30–70% retained dependent on blade length (3). Accretion of sediment and organic matter by vegetation can be substantial, especially during floods (107, 146). Sediment deposition from 1880 to 1979 on a coastal plain river in the southeastern United States averaged 35–52 Mg ha⁻¹ yr⁻¹ (146). Alteration of channel hydraulics is accomplished either by roots or by large woody debris in the channel at low flows and by stems at high flows. All provide physical structure that slows water, decreases stream power, and holds materials in place. Experimental manipulations involving the removal of large woody debris have resulted in dramatically increased erosion rates (16, 151, 191).

Erosional and depositional events shaping channel morphology are the subject of a large literature (68). In general, spatial heterogeneity introduced into the channel by either the vegetation or the large woody debris produced by the vegetation shapes channel morphology by redirecting flows of water and sediment, sorting sediments, and either retaining or moving materials (110).

Wood in Streams and Riparian Zones

Woody debris plays important biophysical roles at the land-water interface (95, 157). In the riparian forest, on exposed alluvial substrates, and in streams, it accumulates during floods in discrete and conspicuous piles. Each pile usually includes at least one large piece of dimensionally complex wood (i.e. a key member) which can resist most flow and physically capture smaller pieces of wood, making the pile even larger. In temperate forests, densities of up to 160 woody piles per km of stream bank may be found (251), but in tropical regions, where termites are prevalent, the density of woody debris piles is reduced substantially (190). Further, some of this wood, especially in the larger pieces, may be quite old. Nanson et al (192) found wood >17,000 years old in the floodplain of a Tasmanian stream; ages >300 years have been measured

for large wood in streams of the Pacific coastal rain forest (1). Woody debris piles dissipate energy, trap moving materials, and form habitat. Depending on size, position in the channel, and geometry, they can resist and redirect water currents, causing the erosive power of water to become spatially heterogeneous, thereby creating a mosaic of erosional and depositional patches in the riparian corridor (173, 191). In steeper channels, the spatial arrangement of pools is independent of the amount of woody debris (173), so redirected water currents widen the channel and capture erosional materials (157). Such processes have been examined extensively by geomorphologists in alluvial rivers (228).

Woody debris also results in longer water residence times (69), and the temporary storage of materials can be substantial. Experimental removal of wood allows sediment and organic matter export rates in the first year to exceed base-line conditions by several hundred percent (16, 151). Analogous experiments with the addition of organic materials have produced similar insights. Leaves and small pieces of wood added to a stream with woody debris move only 65% and 8%, respectively, of the distance traveled by leaves and small wood in streams without large woody debris (69); 80% of the salmon carcasses added to nutrient-poor coastal rainforest streams are retained by woody debris within 200 m of the release sites (34).

Woody debris provides habitat for fish and macroinvertebrates within the stream channel (5, 95, 157, 167); its role as habitat within the terrestrial portion of the riparian corridor is only now being investigated. Woody debris physically retains plant propagules (seeds and plant fragments) and further protects them from erosion, abrasion, and, in some cases, drought and herbivory (74, 110). On exposed cobble bars, most seedling germination and survivorship are associated with woody debris, which provides a protective and relatively moist, nutrient-rich microenvironment. Woody debris also affords protection for small mammals and birds; the diversity and abundance of small mammals such as shrews, voles, and mice are significantly greater in areas with woody debris accumulations, while several bird species preferentially use woody debris for perching and feeding (61, 251).

Microclimate

Riparian forests exert strong controls on the microclimate of streams, but there are few comprehensive studies of the forest microclimate itself. Stream water temperatures are highly correlated with riparian soil temperatures, and strong microclimatic gradients appear in air, soil, and surface temperatures and in relative humidity but not in short-wave solar radiation or wind speed (26). Riparian forests, especially in warmer climates and seasons, influence stream discharge through evapotranspiration. Reduced streamflow causes physiological difficulties for organisms preferring cooler temperatures (100).

Riparian Zones As Ecological Corridors

Riparian zones, as networks distributed over large areas, are key landscape components in maintaining biological connections along extended and dynamic environmental gradients (184, 218, 220). Perhaps the best evidence for plants using riparian zones as corridors comes from exotic invasions. Exotic plants rapidly move both up and down riparian corridors in preference to overland routes (58). However, it is not clear that riparian zones function as dispersal corridors in all cases. Certainly, adaptations of many plants allow vegetative fragments and seeds to float for various distances (196, 198, 241), while many other riparian species are dispersed by wind or animals (especially in the feces of birds). Schneider & Sharitz (244), for example, found that seeds of *Taxodium distichum* and *Nyssa aquatica* could float for 42 and 85 days, respectively, covering downstream distances of up to 2 km.

Few data document riparian zones as corridors for terrestrial animals, despite the common assumption in models. Two exceptions are the use of the riparian forest along the Garonne River, France, for birds moving between the Central Massif and the Pyrenees (55), and a three-year field experiment in Alberta, Canada, demonstrating enhanced movements of juvenile birds through riparian strips before and after harvest of adjacent forest (153).

ECOLOGICAL FUNCTIONS OF RIPARIAN ZONES

Sources of Nourishment: Allochthonous Inputs and Herbivory

Organic matter from riparian vegetation is a source of nourishment for aquatic organisms (112, 261). In temperate zones, values vary from about 200–900 g AFDM (ash-free dry mass) of litter m^{-2} in small and medium streams (1st to 3rd order) to about 20–50 g AFDM m^{-2} in larger rivers (35, 39, 272). As a general trend, the proportion of coarse particulate organic matter (CPOM; > 1 mm diameter) decreases as river size increases. For example, in eastern Quebec, annual litterfall declines exponentially from 307–539 g AFDM m^{-2} in a 1st-order stream to 15–17 g AFDM m^{-2} in a sixth-order stream (39). Lateral inputs from the soil surface are not related to stream size but are strongly influenced by riparian structure and entrapment of organic matter during spring flooding (272).

Similar local effects also are found in intermittent prairie streams in Kansas where total annual input of CPOM is lowest in the headwater reaches (90). Prior to the wet season, storage of benthic CPOM in the dry channel and on the bank is 320–341 g AFDM m^{-2} in the upstream reaches and 999 g AFDM m^{-2} in the 4th- and 5th-order gallery forest reaches. The storage of CPOM

increases during the wet season in headwater channels where retention is high, with the result that these reaches have more CPOM than do downstream reaches, although bank storage is 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. Depending on the vegetative cover of the riparian zone, annual inputs range from 52 to 295 g AFDM m^{-2} in Alaskan streams (64) and from 63 to 474 g AFDM m^{-2} in a Moroccan stream (150). In an Australian rainforest stream, laterally transported litter forms 6.8% of the total annual input, varying in response to bank slope and microtopography (15). The proportion of direct and laterally transported litter entering streams may significantly influence in-stream community dynamics as a consequence of input quality and timing (45). 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 (15). However, the organic material may be rearranged only during high discharge periods and not during the leaf fall period (156), and forest floor litter may require the cumulative effects of several floods to move measurable amounts of litter laterally to the channel (172).

In addition to particulate organic matter, riparian zones contribute substantial amounts of dissolved organic matter (DOM; $<0.5 \mu\text{m}$) 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 (193). Soil water DOM originating in the riparian zone also can influence stream communities through macropore transfer of subsurface water.

At the scale of the Amazon basin, McClain & Richey (158) identified five transfer pathways of terrestrial organic matter to streams: direct litterfall, 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 in mass and elemental composition among all landforms, amounting to 700 g $\text{m}^{-2} \text{yr}^{-1}$. 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 (characterized by old and refractory molecules). Stormflow contributions were dominated by saturated overland flow originating in riparian areas, which transferred a wide spectrum of dissolved and particulate organic matter, largely fresh and labile material. Fringing wetlands contributed high concentrations of DOM, particularly in the lowlands. In contrast to the other sites, the organic matter of wetlands is dominated by refractory hydrophobic dissolved compounds within a compositionally diverse molecular array. Although somewhat preliminary, the results and conceptual

model of McClain & Richey (158) may prove useful as a framework for quantifying organic matter concentrations and compositions between contrasting trophic pathways.

Living riparian vegetation is a source of nourishment for many animals, from insects to mammals, that can considerably alter system function by their feeding activities. Outbreaks of defoliating insects can alter riparian forest production and thereby alter water yield, nutrient cycling, and streamwater chemistry (254, 263). Through selective browsing, large animals such as moose (*Alces alces*) can shift the riparian plant community from deciduous trees to conifers, altering soil formation and nutrient cycling and ultimately affecting plant productivity and moose population dynamics (206). 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 (186).

Riparian Zones as Nutrient Filters

Karr & Schlosser's (128) demonstration that the land-water interface reduces nutrient movements to streams led to understanding the role played by riparian zones in controlling nonpoint sources of pollution by sediment and nutrients in agricultural watersheds (114, 147, 208).

Important biogeochemical processes that affect streamside as well as aquatic systems occur within the riparian zone, which is influenced on one hand by watershed hydrology and on the other hand by channel hydraulics (264, 265). The subsurface transfer of water and materials is mostly unidirectional toward the channel across the terrestrial boundary. In contrast, it is bidirectional 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 stream water (159).

PHYSICAL BUFFERS Sediments and sediment-bound pollutants carried in surface runoff are deposited effectively in mature riparian forests as well as in streamside grasses. Sediment trapping is facilitated by sheet flow runoff, which allows deposition of sediment particles and prevents channelized erosion of accumulated sediments. Riparian areas remove 80–90% of the sediments leaving agricultural fields in North Carolina (42, 47). Sediment deposition may be substantial in the long term, with 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 (42, 146).

Finer sediments carry higher concentrations of labile nutrients and adsorbed pollutants; their removal from the runoff occurs as a consequence of the interactive processes of deposition and erosion, infiltration, dilution, and adsorption/desorption reactions with forest soil and litter. 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 was a net source of inorganic phosphorus when dissolved oxygen concentrations in riparian groundwater were low, but a sink when dissolved oxygen concentrations were high (174).

Phosphorus dynamics may be particularly complex. Although riparian zones may act effectively as physical traps (sinks) for incoming particulate phosphorus, they may enrich runoff waters in available soluble phosphorus (60). Significant amounts of phosphorus may first accumulate in riparian zones, then be transported to aquatic ecosystems in a different form via shallow groundwater flow, possibly as a result of increased decomposition of organic matter (71, 268).

Grassy riparian areas trap more than 50% of sediments from uplands when overland water flows are <5 cm deep (60, 154). Grassy areas influence the uniformity of runoff by transforming channelized flows 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 duration when several floods occur within a limited period. For example, sediment trapping efficiency may decrease from 90% in a first rainfall simulation event to 5% in a sixth rainfall simulation event (60).

BIOLOGICAL BUFFERS Plant uptake, an important mechanism for nutrient removal in riparian forests (43, 72, 88, 208), results in a short-term accumulation of nutrients in nonwoody biomass and a long-term accumulation in woody biomass. Riparian forests are especially important sites for biotic accumulations of nutrients because transpiration may be quite high, increasing the mass flow of nutrient solutes toward root systems, and because morphological and physiological adaptations of the many flood-tolerant species facilitate nutrient uptake under low-oxygen conditions. In some species, such as water tupelo, saturated conditions enhance nutrient uptake and growth (103). Peterjohn & Correll (208) estimated vegetation uptakes of 77 and 10 kg ha⁻¹ yr⁻¹ for N and P, respectively, rates that are comparable with upland rates. However, potential N uptake rates may be much higher, as shown by Cole (37): Poplar (*Populus nigra*) assimilated 213 kg N ha⁻¹ yr⁻¹ when fertilized with a nutrient-rich effluent at a rate of 400 kg N ha⁻¹ yr⁻¹ for three years, but sites not receiving nutrient effluent assimilated only 16 kg N ha⁻¹ yr⁻¹. Further, due to nitrogen saturation

(2), phosphorus may become the limiting factor for tree growth, particularly in wetlands (260), making vegetation an effective phosphorus sink.

The importance of plants as nutrient filters may be reduced by restricted accessibility to water, by the seasonal phenology of uptake and release of nutrients, and by the saturation of mature forests. Water is accessible to plants only if the water table is high or if transpiration demand 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 (115). Nutrient uptake declines or stops during the winter, precisely when high discharges occur. In addition, litter decomposition releases nutrients to forest soils stored during the growing season. Finally, the ability to sequester nutrients in woody biomass may decline as trees mature, leading to saturation (2, 88). The contribution of individual riparian tree species to nutrient retention remains to be elucidated.

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 (43, 88, 114, 125, 212, 214) depends on the presence of nitrate, a suitable carbon substrate, and the absence of oxygen. Soil temperature, moisture, and the type of carbon influence the reaction rate. Soil pH affects whether N_2O or N_2 is produced. In riparian zones, anaerobic microsites associated with decomposing organic matter fragments allow denitrification in otherwise well-drained soils. Within a riparian zone, denitrification rates of 30–40 $kg\ ha^{-1}\ yr^{-1}$ have been recorded; the fastest rates occur at the riparian-stream boundary where nitrate-enriched water enters organic surface soil (40).

Denitrification of groundwater-borne nitrate is less well established. Carbon availability usually limits subsurface microbial activity, preventing anaerobic conditions from developing (99). Since denitrification is concentrated in the upper 12–15 cm of the soil (which is only occasionally part of the shallow aquifer), nitrate disappearance from shallow groundwater may require the riparian vegetation to play a primary role (144). Groundwater-derived nitrate may be eventually denitrified in surface soil after plant uptake of the nitrate from groundwater, litter decomposition, and ammonium release, followed by nitrification (88, 92, 93). 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 (101).

BUFFER VARIABILITY Subsurface water flow paths have strong effects on nutrient characteristics. In several locations of the Coastal Plain of the Chesapeake

Bay watershed, average annual terrestrial boundary nitrate concentrations of 7 to 14 mg NO₃-N L⁻¹ decrease to 1 mg NO₃-N L⁻¹ or less in shallow groundwater near streams (145). However, in the same area, a single site with a nitrate concentration of 25 mg NO₃-N L⁻¹ at depth had a concentration of 18 mg NO₃-N L⁻¹ in shallow groundwater at the stream. Lowrance et al (148), who estimated annual denitrification rates to average 31 kg N ha⁻¹ yr⁻¹ in the top 50 cm of soil, measured denitrification rates between 1.4 kg N ha⁻¹ yr⁻¹ in a riparian zone adjacent to an old field (which received no fertilizer) to 295 kg N ha⁻¹ 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 nonrooted soil layers as well as between anoxic and oxic conditions, and it depends on subsurface flow paths. 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 suggest nitrogen saturation. Nevertheless, high rates of denitrification and storage usually maintain enriched riparian zones as sinks for upland-derived nitrate (92).

Plant cover also influences the efficiency of riparian zones in filtering nutrients and pesticides. A riparian zone vegetated with poplar is more effective for winter nitrate retention than one vegetated with grass (97). Some trees are better than others in filtering nitrate: *Populus x canadensis* effectively removes nitrate from saturated soils with a subsequent accumulation of nitrogen in root biomass (203). Roots of alder, willow, and poplar seem to favor colonization by proteolytic and ammonifying microorganisms and, particularly for alder roots, to inhibit nitrifying microorganisms (221). Changing plant cover may affect water quality: In a set-aside riparian zone in New Zealand 12 yr after retirement from grazing, dominant vegetation returned to native tussock (*Poa cita*), leading to a zone likely to be a sink for sediment-bound nutrients and dissolved nitrogen but a source for dissolved phosphorus (41).

Soil characteristics influence redox conditions and the availability of dissolved nitrogen to plant roots. Pinay et al (215) calculated that sandy riparian forest soils retained 32% of the total organic nitrogen flux during a flood, but 70% was retained on loamy riparian soils. McDowell et al (162) compared riparian nitrogen dynamics in two geomorphologically different tropical rain forest sites. At one site, a deep layer of coarse sand conducted subsurface water to the adjacent stream below most plant roots, through oxic and anoxic zones from upslope to downslope, respectively, whereas at the other site, a dense clay layer impeded infiltration, and subsurface water rapidly moved through a shallow and variably oxidized rooting zone. Although intense biotic activity controlled hydrologic export of nitrogen at both sites, soil differences strongly

modified interactions. 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 (266).

VEGETATIVE PATTERNS OF DIVERSITY Riparian forests provide insights into how plant species richness varies at regional scales with respect to natural disturbances (218). Profiles along river courses are especially effective in evaluating the intermediate disturbance hypothesis for explaining biodiversity patterns (199). Plant species richness is not always highest in median sections of river courses where flood disturbances are at intermediate levels of intensity and duration (8, 57, 199, 259).

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; 198). In southern Spain, semi-arid rivers show irregular patterns of species richness along their courses, as a consequence of irregular water availability (259). Main channels and their tributaries may differ as in the Adour basin of France, where exotic species are more numerous in the main channel and display different longitudinal patterns than native species (57, 216). In the Vindel basin, northern Sweden, the main channel also has a higher species richness than the tributaries; in addition, species richness is greatest at mid-altitude in the main channel but least in the tributaries (195). The distributions of native and exotic flora (58, 217, 257, 258, 259), or long-lived ruderal species (195, 196, 199, 200) differ markedly in longitudinal profiles of richness.

It remains to be demonstrated whether riparian forests maintain biodiversity through continuous upstream movement of species from other catchments or from extension of species distributions downstream during favorable environmental periods (195). Clearly, propagule dispersal by water has a role in structuring the riparian flora (116), but dispersion mechanisms such as anemochory and ornithochory deserve consideration (169), as do the different stages of a plant's life cycle, which are important for successful establishment and growth (56).

Black cottonwood (*Populus trichocarpa*) from Pacific river banks in North America respond 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 (65, 66, 67). Genetic discontinuities among riparian populations of *P. trichocarpa* along the same river coincide with upstream-downstream changes in atmospheric moisture levels (66, 67). Such discontinuities occur

even though black cottonwood can disperse sexual and asexual propagules over wide areas.

NATURAL DISTURBANCES Floods create heterogeneity within the riparian zone and thereby create distinct regeneration niches that facilitate the coexistence of congeneric species. For example, six species of *Salix* co-occur, despite similar adult ecology, along the Sorachi River, Hokkaido, Japan (194). Dispersal periods of these species overlap as water levels decrease following spring floods. The dominant species, *S. sacchalinensis*, establishes on a wide range of soil textures. The subordinate species *S. rorida* and *S. subfragilis* coexist with *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.

Periodic flood disturbances of various intensities are also critical for maintaining the four dominant tree species of the lowland floodplain podocarp forest in New Zealand (63)—*Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Prumnopitys ferruginea* (conifers), and *Weinmannia racemosa* (angiosperm). The two former are upper-canopy trees, and the two latter are sub-canopy trees. 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 gaps caused by nonflood mortality of the mature conifers.

At local scales, floods affect species diversity of herbaceous plants through physical 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 (197). Likewise, in southern France, organic matter accumulations of 150 to 300 g m^{-2} result in high germination rates and decreased mortality rates, whereas accumulations of 600 to 1200 g m^{-2} decrease germination rates. Around 150 g m^{-2} of litter corresponds to maximal density and species richness (137). Similarly, silt accumulations of about 500 g m^{-2} correspond to maximal density and species richness of seedlings (138).

INVASION BY EXOTIC SPECIES The richest communities also have the greatest proportion of exotics, 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. Comparing the riparian plant communities of the Adour River, France, with the Mackenzie River, Oregon, Planty-Tabacchi et al (217) discovered about 1400 (24% exotic) and 850 (30% exotic) constituent species, respectively. 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 those of the Adour (21%). Although these differences parallel more intensive forest management in Oregon than in France, the ecological mechanisms explaining these similarities remain obscure.

Several interactive processes appear to control establishment of exotic species in riparian zones (56). Although common in nature, biological invasions have been accelerated through human activities (142). Life-history characteristics of invaders control the various stages of establishment, stabilization, and expansion. For example, Pysek & Prach (222) reported that the shorter the life span, the higher the rate of invasion among four species alien to central Europe, *Impatiens glandulifera*, *Heracleum mantegazzianum*, *Reynoutria japonica*, and *R. sacchalinensis*. Landscape characteristics such as connectivity along rivers (116) and historical development of landscape patch structure (223) also exert control.

Natural environmental features may also slow the rate of invasion. For example, in the subarctic environment of northern Sweden, exotic plants from other continents are rare in riparian zones. In northern Australia, where the area occupied by the exotic *Mimosa nigra* doubles every 1.2 yr, the rate of expansion is related to the amount of rainfall in the previous wet season (143). At the regional scale, the areal doubling time is 6.7 yr, probably due to the spatial isolation of wetland habitats by eucalyptus savanna. Seed predation combined with folivores is also likely to slow the rate of expansion because the seeds of this species are dispersed by flotation.

Although exotic invasions can reduce native plant species diversity, there is no clear evidence it does. However, *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 (10, 216, 224). Similarly, *Tamarix* spp., invasive exotic woody plants in arid and semi-arid riparian habitats of western United States, are expected to replace or inhibit much of the native flora (25). However, clear data supporting or refuting these expectations do not appear to exist.

REFUGES FOR REGIONAL DIVERSITY Riparian forest patches have acted as safe sites for regional flora during dry periods. Some present-day humid tropical zones appear to have experienced Pleistocene droughts, but there is no indication of mass extinctions, whereas there is indication of rapid species re-expansion

during the early Holocene. Riparian forest patches may have been refuges for the maintenance of mesic plant diversity in Central America (166). The floristic attributes of the riparian forest are similar to those characterizing continuous forests in the area, while their stem density is higher and biomass lower, thus increasing their potential to maintain species richness. Moreover, riparian trees in a savanna matrix are often younger because more mature trees are removed by wind and fire as compared to continuous forests (132). 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 (trees with > 10-cm diameter at breast height), a richness comparable to or slightly lower than for upland forests in the area (166). 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 (62).

MACROINVERTEBRATE COMMUNITIES Stream macroinvertebrate community characteristics may be predicted from a knowledge of riparian vegetation (45). The presence or absence of riparian trees could be the single most important factor altered by human activity that affects these communities (255) since riparian vegetation affects macroinvertebrate diversity primarily through its effects on benthic habitat (21, 82, 140, 204, 227). In contrast, the effect of riparian vegetation as a source of nourishment for invertebrates is not so well established. Much of the woody debris is unpalatable, thus preventing a diverse consumer community from developing (202). 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 (89).

Habitat

With variations in flood duration and frequency, and concomitant changes in water table depth and plant succession, the environment is a complex of shifting habitats created and destroyed on different spatio-temporal scales (155). Most riparian zones are covered with a remarkable variety of woody vegetation 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. Riparian forests act as refuges in adjacent areas and, in some cases, as corridors for migration and dispersal (24).

The occurrence of any species in riparian areas is probably due to several interrelated reasons. Juvenile wood turtles (*Clemmys insculpta*) prefer to 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 (22). Drinking water is obviously an important reason for mammals to visit riparian zones. However, small mammals may respond more to differences in tree communities. 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*) (160), but no difference was detected where upland and streamside habitats were similar in vegetative structure and composition (161). The white-tailed deer (*Odocoileus virginianus*) uses riparian zones almost twice as much as nonriparian areas, supposedly as an antipredation strategy (139).

Like mammals, more individuals and species of birds are found in riparian habitats than in adjacent ones. In the lower Mississippi River, 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 (133). For example, 82% of the breeding birds of northern Colorado occur in riparian vegetation (135).

Bird assemblages of riparian zones and adjacent uplands are interdependent; the number of shared species varies seasonally and longitudinally along river courses with apparently greater interdependence at intermediate elevations (135, 141). However, bird individuals and species may not be more numerous where the riparian habitat is either similar to upland habitat or not clearly delineated (176). 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 (134). In boreal forests, bird densities reportedly increase 30% to 70% in protected riparian forest strips the year after clear-cutting; they then decline during the following years while the adjacent clear-cut regenerates (48).

Bird communities are sensitive to the quality of riparian vegetation (44, 141). Destruction of riparian vegetation causes local extinction and also reduces the ability of some populations to recolonize sites (135). Along the Colorado River in the Grand Canyon, black-chinned hummingbirds (*Archilochus alexandri*) nest only in exotic tamarisk-dominated habitats that are greater than 0.5 ha in area (27). In disturbed areas, woody strips 2 m wide permit only portions of bird populations to occur; widths >25 m on each bank are necessary to maintain sensitive species (44). In a survey of 117 corridors ranging from 25 m to 800 m wide, Keller et al (130) concluded that the probability-of-occurrence increased most rapidly between 25 m 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 (135).

The inhabitants of riparian zones can modify habitat structure and function. Through ponding water and storing sediments, beaver create wetlands and alter the vegetative composition of in-channel and riparian communities in temperate North America, strongly influencing riparian landscapes (186, 188, 189). Through selective cutting of trees, they change the composition of riparian communities. For example in Minnesota, under beaver influence, trembling aspen (*Populus tremuloides*) decreased in abundance, whereas alder (*Alnus rugosa*) and black spruce (*Picea glauca*) increased (122). Besides beaver, species such as moose, elk (*Cervus canadensis*), and brown bear (*Ursus arctos*) create and maintain tight networks of trails along river banks. In southern Africa, hippopotamus (*Hippopotamus amphibius*) modify riparian habitats, gathering in pools during the day where they stir up sediments and deepen aquatic habitats; during the night they create paths between pools and terrestrial grazing areas, thus maintaining connectivity between patches (190). Warthog (*Phacochoerus aethiopicus*) transform tens of hectares to ploughed fields by digging soils 10–15 cm deep to feed on underground plant storage organs in riparian forests and wetlands (229); consequently the replacement of perennial rhizomatous grasses by annual grasses and forbs is favored.

Feeding activities have long-term consequences for the structure and function of riparian forests. Zoochory, particularly ornithochory, facilitates the expansion of certain species through selective feeding and propagule transport. Moose browsing reportedly affects decomposition indirectly through changes in the quality of litterfall in North American riparian systems (163, 205). Similar effects occur in riparian corridors in Africa through bulk browsing by elephant (*Loxodonta africana*), bulk grazing by hippopotamus, and selective browsing by kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*), and bushbuck (*Tragelaphus scriptus*) (190).

ENVIRONMENTAL ALTERATIONS

Human Alterations

Along European rivers, human-induced alterations include neolithic deforestation and land-clearing during Gallo-Roman and medieval periods (207). Civil engineering works in the nineteenth century and hydroelectric developments in the twentieth century accelerated these alterations (211). Similar events have occurred in North America on a reduced time scale since European settlement (246).

Flow variability and fluctuations in channel width, which are necessary for maintaining the biodiversity of riparian systems (78), 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 without changing mean annual flow, as riparian vegetation is especially sensitive to changes in minimum and maximum flows (6). In many cases, hydrologic alterations result in shifts in riparian plant community composition as well as senescence of woody communities (18, 31, 54, 77, 104, 196, 198, 207, 232).

The rapid invasion of floodplains in the southwestern United States by *Tamarix ramossissima* has desiccated water courses (269), inducing other disturbances such as fire (32) and displacement of native species (e.g. *Salix gooddingii* and *Populus fremontii*; 253, 269). 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* (32).

Along the River Murray in Australia, flood frequency and duration historically prevented native red gum (*Eucalyptus camaldulensis*) from establishing on grass plains. By reducing depth and duration of flooding, river regulation has favored a red gum invasion that is expected to cause a complete extinction of the once-extensive grass plains in the near future (19). 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 (233, 234). A possible mechanism for this decline is that a reduction of flooding diminishes the rate of recruitment of new stands (170).

In fact, the maintenance of phreatophytic riparian woodlands depends heavily on the relationship between river flow and life-history traits of cottonwood (108). For example, as growth conditions vary widely within and between years at the same site, an important factor for survival is the ability of seedlings to establish over a range of moisture conditions (247). Tyree et al (267) demonstrated species-specific responses to water regimes for several *Populus* species that differ in xylem water potentials and consequent cavitation.

Even though alterations to water regimes may result in declines of cottonwood forests, at least temporary increases occur in some other environmental situations (249). Along the meandering Missouri River, poplar-willow communities depend on flow peaks that erode outer banks and deposit sediments on inner banks (118, 119, 120). A reduction of peak flows after completion of the Garrison Dam in 1953 prevented meandering and thus the formation of suitable areas for poplar-willow establishment, resulting in a continuous decrease in pioneer stages and an increase in older stages (119). In contrast, 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, reduced flow and exposed large areas suitable for seedling establishment and survival (120).

Invading riparian trees may have an impact on channel morphology, particularly when they replace formerly grassy areas (79, 237). Active investigations are needed on mechanisms linking water, landforms, and species in various landscape settings in order to predict the specific effects of manipulating flow on floodplain forests (53).

In northern Sweden, species-richness and the percentage vegetative cover are both lower per site in a regulated as compared to a nonregulated river (196, 198). The proportion of annual plus biennial species-richness is higher and perennial species-richness is lower along regulated rivers. Water level regime and mean annual discharge certainly are among the most important variables for maintaining species richness and plant cover.

The species composition of the riparian plant community is also important to consider in predicting responses to alterations (18, 196, 198, 207). Several scenarios may be expected for a plant community as a result of flow alterations: reproduction by on-site regeneration, colonization of other parts of the floodplain, or replacement by a new type of plant community (207). Alterations of riparian plant communities obviously affect aquatic macroinvertebrates and fishes as a consequence of modifying trophic pathways and in-stream habitat (49, 238) as well as the species diversity of amphibians, birds, and mammals (44, 130, 181).

Management and Restoration

Hydrological characteristics are of primary importance in managing riparian zones. Riparian buffer zones retain surface runoff pollutants as a result of their water storage capacity and infiltration (41). Riparian buffer zones intercept the dominant hydrological pathways that 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 either across the surface or as shallow groundwater through biologically active soil zones (145), and sediment removal requires that surface runoff does not overwhelm the buffer system. 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 (70, 98), thereby complicating the intricacy of groundwater routes and the ways water-borne nitrate encounters roots and soil microbes.

Increasing loading rates may affect riparian zones differentially according to the type of pollution (70, 145). 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 (98). 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 (98).

An increasingly important managerial use of riparian zones is to control diffuse pollution. Riparian zones are more effective over the long term when upstream pollution has been limited through good agricultural practices at the catchment level (7, 51). 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 (145). The control of water quality in headwater catchments is an effective management strategy because, once a river is contaminated, few inexpensive possibilities remain for improvement (98).

One model suggests that multi-species riparian buffer strips provide the best protection of streams against agricultural impact (106, 145, 245). This model uses three interactive zones that are in consecutive up-slope order from the stream: 1. a permanent forest about 10 m wide, 2. shrubs and trees up to 4 m wide (and managed so that biomass production is maximized), and 3. herbaceous vegetation 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, which controls pollutants in subsurface flow and surface runoff, is where biological and chemical transformations, storage in woody vegetation, infiltration, and deposited sediments are maximized. The first two zones contribute to nitrogen, phosphorus, and sediment pollution removal. The third zone 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.

Long-term sustainability is likely to occur when managed systems imitate natural ones. For example, zone 1 of the multispecies 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 is reestablished periodically (145). The literature, however, offers divergent examples ranging from efficient removal

of nitrogen after 20 years of high nutrient loading (7) to exhaustible sinks (41). Whatever the example, improved land use practices within the catchment and the maintenance of riparian zones for interception of groundwater flows by vegetation in various stages of succession (which differ in absorption capacity) are key factors for the long-term vitality of buffer strips and streams (98, 270).

Other benefits obtained from creative management and restoration of riparian zones include provision of diversified habitat for terrestrial and aquatic wildlife, corridors for plant and perhaps animal dispersion, and input of organic matter to streams. Enhancement of the visual quality and increase in recreational value of the landscape are also important benefits. Management has been used positively to influence communities of aquatic animals in upland streams throughout Wales and Scotland (204), and managed and natural floodplain forests are recommended in British river and floodplain restoration projects (209).

Tools for the Future

Riparian systems are increasingly expected to fulfill ecological functions related to biodiversity, habitat, information flow, biogeochemical cycles, microclimate, and resistance and resilience to disturbance (187). They will be expected also to fulfill more social functions, including provision of resources, recreation, culture, and aesthetics. Clearly, no single riparian system will perform all these functions, but each will be likely to perform at least one.

An extensive linear approach to management, at the scale of river courses, is needed to delineate and classify riparian systems along streams. Significant progress has already been made in mapping riparian systems using remotely sensed data (175). Lowrance et al (145) recommended that linear forests be characterized at a resolution of 10 m 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 the poplars of the Platte River, demonstrate the need for considering entire river courses to understand various aspects of the dynamics of riparian systems (120), to restore the ecosystem integrity of rivers and floodplains (46), and to manage international greenways (28).

Both landscape and detailed site perspectives are required to judge whether planted trees will survive to reach the expected sizes. The landscape perspective may be attained through 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 (105). Detailed site perspective may be attained through knowledge based on water regimes, suitable soil conditions, and long-term survival and growth rates as well as on the effects of variable water levels on tree metabolism (117).

An intensive site-specific approach integrates research, demonstration, and application of riparian zone buffers (145). 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 (87, 145). Insights into these issues are requisite for developing models of risk assessment (149) and decision-making (106). 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 (83). Finally, site-specific studies should improve the ability to evaluate the performances of restored 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 (145). As many buffer processes operate most effectively in headwater basins, downstream cumulative effects involving many small catchments must be given proper emphasis (29). The catchment is also the appropriate scale to improve hydrologic conditions within riparian zones (243) and to assess the potential of narrow riparian zones that are remnants of previously wider ones in most rural and urban temperate zone landscapes (54, 210).

Finally, considering riparian zones as management tools for the future requires the adoption of flexible, adaptive schemes to cope with surprises related to discontinuities and synergisms (177). Discontinuities in riparian systems may occur where nutrient accumulations reach disruptive thresholds that suddenly change the system from a sink to a source. Synergism also may occur from interactions 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 and management (187).

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