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Basic Principles and Ecological Consequences of Changing Water Regimes: Riparian Plant Communities[1]

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ABSTRACT / Recent research has emphasized the importance of riparian ecosystems as centers of biodiversity and links between terrestrial and aquatic systems. Riparian ecosystems also belong among the environments that are most disturbed by humans and are in need of restoration to maintain biodiversity and ecological integrity. To facilitate the completion of this task, researchers have an important function to communicate their knowledge to policy-makers and managers. This article presents some fundamental qualities of riparian systems, articulated as three basic principles. The basic principles proposed are: (1) The flow regime determines the successional evolution of riparian plant communities and ecological processes. (2) The riparian corridor serves as a pathway for redistribution of organic and inorganic material that influences plant communities along rivers. (3) The riparian system is a transition zone between land and water ecosystems and is disproportionately plant species-rich when compared to surrounding ecosystems. Translating these principles into management directives requires more information about how much water a river needs and when and how, i.e., flow variables described by magnitude, frequency, timing, duration, and rate of change. It also requires information about how various groups of organisms are affected by habitat fragmentation, especially in terms of their dispersal. Finally, it requires information about how effects of hydrologic alterations vary between different types of riparian systems and with the location within the watershed.

Riparian systems are transition zones between land and water ecosystems, organized in networks across landscapes. The characteristics of natural riparian zones vary with the size of the river, from narrow and relatively simple strips of land along headwater streams, to heterogeneous floodplains many kilometers wide along lower reaches of major rivers. Riparian ecosystems encompass the stream channel between the low- and high-water marks. They also encompass the terrestrial landscape above the high-water mark where vegetation may be influenced by elevated water tables or flooding and by the ability of the soils to hold water (Naiman and Décamps 1997). Geomorphic structures are helpful in delimiting riparian ecosystems, and also distribution limits of plants that are intolerant to either flooding or drought (Nilsson 1983).

Riparian ecosystems are unusually complex, dynamic, and diverse and possess numerous economic, societal, and biological values (Sharitz and others 1992). These qualities make them key ecosystems for preserving biodiversity (Naiman and others 1993) and for understanding how environmental change may affect interactions between adjacent landscape elements (Décamps 1993). Recent research has begun to express these roles as ecosystem "goods and services", and has also started elucidating their connections with human health issues (e.g., Gregory 1997).

Natural riparian ecosystems include a variety of community types, ranging from strips of spruce forest on periodically frozen ground with dense moss carpets, to floodplain landscapes with deciduous trees and shrubs on heterogeneous substrates, and to deltas with distinct plant zonation and well-developed forests having diverse animal communities. Some floodplain landscapes, such as those in South America, Europe, Africa, and Asia, cover tens of thousands of square kilometers of land (Welcomme 1979, Petts 1984).

Streams and their riparian zones are nonequilibrium ecosystems that provide habitat for a wide range of plants with a variety of adaptations. Naiman and Décamps (1997) grouped riparian plants into four major categories: (1) invaders—produce large numbers of wind- and water-disseminated propagules that colonize

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Table 1. Summary of some concepts in river ecology and their relation to riparian mechanisms[a]

Major mechanisms	Concept/model	General idea	Major predictions
Flow (1)	The natural flow regime (Poff and others 1997)	The natural flow regime sustains ecosystem integrity and biodiversity in rivers and organizes the ecosystem. Every river has a characteristic pattern of flow components (magnitude, frequency, duration, timing and rate of change).	A wide range of ecological and physical responses to alterations of the five flow components is listed, including both animal and vegetation responses.
Flow (1) Landscape interactions (3)	The flood pulse concept (Junk and others 1989)	The flood pulse is the principal driving force in river-floodplain systems. Local generation and rapid cycling of nutrients on floodplains are emphasized. Lateral exchange between the river channel and floodplains makes important impact on biota. Littoral movement creates a dynamic edge effect.	In large rivers, the major riverine animal biomass is produced within the floodplains. Small rivers have short and unpredictable pulses to which organisms are little adapted. Large rivers with predictable and long duration pulses are easier to adapt to.
Pathway/corridor (2)	The river continuum concept (Vannote and others 1980)	Longitudinal nutrient/energy transport and decomposition along the river. A physical gradient leads to a continuum of biotic adjustments in space and time. Based on the energy equilibrium theory.	Total community diversity is greatest in medium-sized streams (3rd–5th order) where temperature variations are maximized. Downstream communities capitalize on inefficiencies of upstream communities.
Pathway/corridor (2) Landscape interactions (3)	The boundary/interface perspective (Naiman and others 1988, Naiman and Décamps 1997)	A boundary is comparable to a semipermeable membrane regulating flow of energy and matter between resource patches. For example, riparian forests control N and P movement. Boundaries also distinctively limit processes in resource patch zones.	A biodiversity maximum occurs where the mixture of edge and patch habitat is at maximum. Boundaries between terrestrial and freshwater ecosystems show early responses to human influence.
Pathway/corridor (2) Landscape interactions (3)	Four-dimensional framework (Ward 1989b)	The spatiotemporal hierarchy is a distinguishing feature of lotic ecosystems. Four dimensions are described: longitudinal (channel-channel), lateral (channel-floodplain), vertical (channel-aquifer) and temporal. Disturbances are explained as forces disrupting major interactive pathways.	The intermediate disturbance hypothesis as a possible model for diversity patterns.

[a]The numbers in the first column indicate the three basic principles outlined in the paper.

alluvial habitats; (2) endurers—resprout after breakage or burial of either the stem or roots from floods or after being partially eaten; (3) resisters—withstand flooding for weeks during the growing season, moderate fires, or epidemics; and (4) avoiders—lack adaptations to specific disturbance types: individuals germinating in an unfavorable habitat do not survive. Riparian plant communities are generally arranged along the local elevation gradient into more or less distinct zones. In many parts of the world growth form ranges from a forest margin, succeeded by shrub communities, and herbaceous plants from highest to lowest positions along this gradient (Junk and Piedade 1993, Hughes 1997, Nilsson 1999).

Several processes and characteristics at both landscape and local levels govern the attributes and functions of riparian plant communities. The basin characteristics (topography, geology, climate, etc.) set the stage (Stanford and others 1996, Hughes 1997), connections along the river and with adjacent systems regulate the openness of the system (what is imported or exported), and animals and the frequency and magnitude of physical disturbances determine the patterns of succession and rate of species turnover. At the local scale, biotic interactions are also important (Wilson and Keddy 1985, Bertness and Ellison 1987).

The various connections within the watershed provide an important framework for understanding the ways in which rivers function. During recent years, a number of conceptual models have been proposed to explain these patterns (Table 1). Basically, rivers interact in three dimensions—along their course [i.e., upstream–downstream connections, (Vannote and others 1980, Ward and Stanford 1983)], with their floodplains (Junk and others 1989, Bayley 1995, Naiman and Décamps 1997), and with their soil and groundwater environment (Stanford and Ward 1988). The three spatial dimensions—longitudinal, lateral, and vertical—together with the temporal dimension have been described as the four dimensions of rivers (Ward 1989b). Each of the three spatial dimensions can be viewed as gradients, albeit sometimes with a patchy organization (Townsend 1989). On a continental scale, the river itself is also a gradient, mediating between the terrestrial system and the sea (Bretschko 1995).

In sum, rivers are viewed as continuous systems that redistribute material across landscapes and show terrestrial–aquatic interplay all along their lengths (Naiman and others 1988, Ward 1989b). River communities exhibit predictable downstream change in various structural and functional properties, including biotic diversity, organic matter characteristics, and metabolism (Vannote and others 1980). These concepts do not treat plants and riparian systems in any great detail, but because many river processes are common to both aquatic and riparian biota, some information about

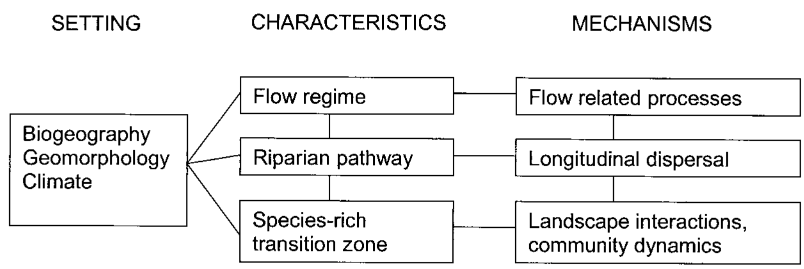

Figure 1. Simplified conceptual model showing how the three basic characteristics of riparian ecosystems are governed by their biogeographic, geomorphic and climatic settings, and how they relate to mechanisms operating at various spatial and temporal scales. The three sets of mechanisms are the same as those in Tables 1 and 2. A summary of how these mechanisms are represented in the general concepts of river ecology is given in Table 1. Ecological responses to alterations of these mechanisms are summarized in Table 2. Feedbacks are not included.

riparian plant communities can be outlined (Table 1). On a local scale, however, more detailed models on vegetation dynamics are available (e.g., Naiman and others 2000).

Because of their great values, riparian ecosystems belong among the environments most disturbed by humans and with the longest history of human disturbance. Today, the majority of the world's large rivers have a regulated water flow (Petts 1984, Dynesius and Nilsson 1994), and this has changed riparian conditions dramatically (Jansson and others 2000a; Nilsson and Berggren 2000). Embanking, clear-cutting, trenching, channelization, and pollution have also contributed to damaging riparian habitats. For example, only 2% of the 5.2 million km of streams in the contiguous 48 states of the United States are of sufficiently high quality to warrant federal protection status (Benke 1990). To reduce the threats to biodiversity and natural ecosystem functions, and to favor a sustainable use of rivers, restoration of riparian systems will become increasingly important (e.g., Naiman and others 1993, Stanford and others 1996, Ward and others 1999).

We here present three basic principles that determine the important qualities of riparian vegetation. The principles are:

1. The flow regime determines the ecological processes and the successional evolution of riparian plant communities and ecological processes.
2. The riparian zone serves as a pathway for redistribution of organic and inorganic material that influences plant communities along rivers.
3. The riparian system is a transition zone between land and water ecosystems and is disproportionately plant species-rich when compared to surrounding ecosystems.

In sum, these principles are governed by the biogeographic, geomorphic, and climatic settings and deal primarily with how the flow regime, especially floods, determines local riparian communities; the corridor function of the riparian zone; and the riparian system as a center of biodiversity and landscape interactions (Figure 1). Additionally, these principles are complementary to those proposed for rivers as ecological systems (Naiman and others 2002), for nitrogen cycling (Pinay and others 2002), and for biodiversity (Bunn and Arthington 2002) in the accompanying articles. Table 1 indicates how these principles relate to the general concepts of river ecology. In the next three sections, examples to illustrate each of these three principles will be given.

Flow Regime Shapes Successional Evolution of Riparian Plant Communities and Ecological Processes

There is general agreement within the scientific community that the flow regime is the grand structuring factor in rivers (Walker and others 1995, Hughes 1997, Poff and others 1997, Richter and others 1997, Ward 1998). Running water determines river form and is the driving force in riparian habitats because of its temporal and spatial variability. In other words, rivers with stable flow would not at all be as complex as naturally hydrologically variable rivers. Running water also redistributes organic and inorganic matter among riparian reaches (see the next section), and variation in flow is a vital factor for determining nutrient dynamics and plant production in riparian ecosystems (Spink and others 1998). Individual rivers have different hydrographic signatures or "fingerprints." Puckridge and others (1998) analyzed 52 rivers from all over the world

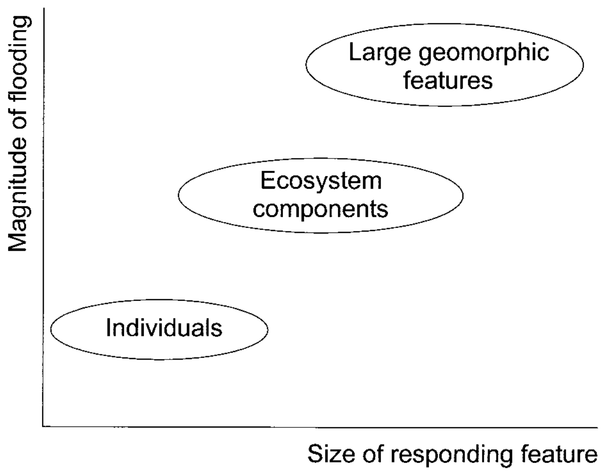

Figure 2. Simplified model showing the relationship between flooding magnitude and the size of the variable that is affected. High magnitude, infrequent floods influence large geomorphic features whereas small, frequent floods have effects at the level of individuals.

and identified 11 groups of rivers according to signature. Twenty-three hydrologic measures thought to be of ecological significance were used to identify the signature, corresponding mainly to five key facets: timing, duration, frequency, rate of change, and magnitude (Walker and others 1995, Richter and others 1996).

Floods of different magnitude affect different floodplain components and are differently frequent. Therefore, spatiotemporal hierarchy is useful for understanding the stability of riparian ecosystems (Brinson 1990, Hughes 1997). High-magnitude floods influence large geomorphic features such as deltas or new channels that persist for hundreds of years, floods of intermediate size determine ecosystem components such as plant community patches, and minor floods have effects at the plant species level (Kangas 1990, Hughes 1997) (Figure 2).

Water availability in the riparian zone is directly related to water stages and soils. It ranges from complete drowning of plants during high-water conditions to desiccation during periods of low water. When soil moisture conditions coincide with the water-level gradient along free-flowing rivers, zonation of riparian vegetation occurs (Stromberg 1997). However, not all plants are dependent on water availability in the river channel. For example, some mature riparian trees are phreatophytic, i.e., rely on groundwater (Dawson and Ehleringer 1991), and are thus able to cope with variable flows. Even small changes in water-level regime may induce detectable changes in vegetation structure. Increased flow, such as during large floods, may cause mechanical injury to plants, ranging from scarring of stems or the removal of single leaves, to uprooting and removal of entire plants. In rivers with ice formation, the erosive effect of water is further strengthened by ice floes (Bégin and Payette 1991, Nilsson and others 1993). Elimination of annual flooding in such rivers often leads to expansion of forest vegetation toward the waterline (Gill 1973, Grelsson and Nilsson 1980, Johnson 1994, Toner and Keddy 1997). In dry regions, however, substantial reduction in flow downstream of large dams may cause decline of floodplain forests because of water scarcity (Rood and Heinze-Milne 1989, Pettit and Froend 2000). Another change following flood elimination is that litter decomposition rate declines (Ellis and others 1999). The riparian areas thus become less biologically active.

Riparian Corridor Serves as a Pathway for Downstream Redistribution of Organic and Inorganic Material that Influences Plant Communities

Many of the recent discoveries about river ecology have dealt with the importance of rivers as conduits for movement. Rivers transport water but also sediment, nutrients, contaminants, and carbon. Because of the downstream vector, the redistribution of material along rivers is not cyclic in the way that an atom or molecule returns to its starting point after having completed a cycle. Instead, the visualized cycle is stretched into the shape of a spiral along the river (Fisher and others 1998). The length of a spiral loop is the average distance required for a given material to complete a cycle. Because of the slope, form, successional stage, and other characteristics of a river, the longitudinal distance associated with one cycle varies among rivers (Fisher and others 1998, McClain and others 1998) (Figure 3).

The riparian corridor can also be a pathway for the upstream distribution of nutrients. For example, anadromous salmon (*Oncorhynchus* spp.) transport marine-derived nutrients in their bodies to streams when they return from the sea to spawn (Helfield and Naiman 2001). Fish carcasses may be removed from the stream channel by predators and deposited in riparian areas, thus adding nutrients to the terrestrial system. Nutrients from fish carcasses may also be deposited secondarily as predators' feces in areas quite far from the stream (Ben-David and others 1998). Such marine-derived nutrients may be a particularly significant

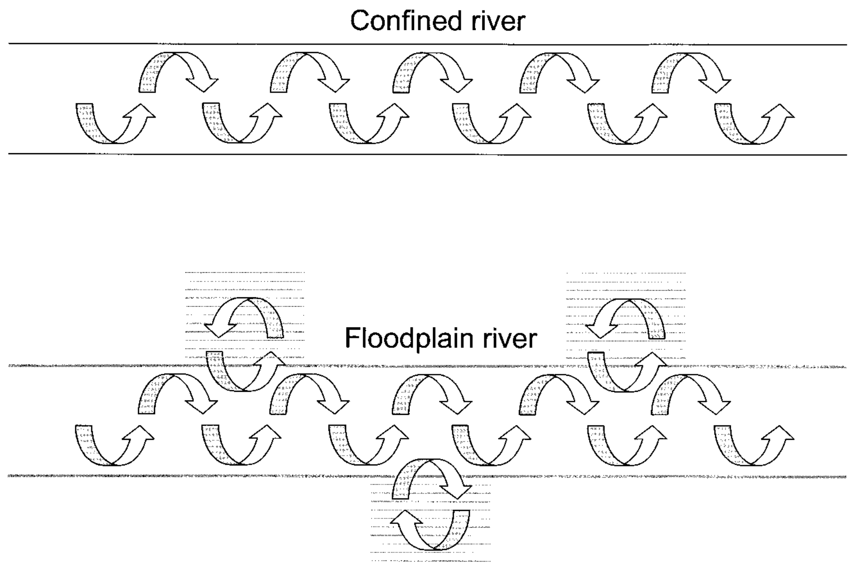

Figure 3. Conceptual model showing two contrasting examples of chemical cycles along rivers. Top: the confined river has internal nutrient spiraling but little interaction with its surroundings. Bottom: in the floodplain river nutrient spiraling in the channel interacts with chemical cycling in adjacent wetlands. Modified from Ward (1989a).

source of nutrients in oligotrophic systems (Bilby and others 2000).

Waterborne sediments usually carry adsorbed nutrients. When fine-grained sediments are deposited in the riparian ecosystem, soil fertility and, thus, productivity increase. The potential for nutrient supply in floodplains can be understood by an example from the Amazon Basin where the annual net production of a C_4 grass species on a floodplain was estimated to be 99 tons of dry matter per hectare (Piedade and others 1991). This value stands among the highest for natural vegetation. The C_4 physiology in combination with a continuous supply of nutrients during the several-months'-long flooding season, make productivity conditions excellent (Piedade and others 1991).

Virtually all fractions of soil can be redistributed within riparian zones, but fine soils constitute the dominant fraction by mass (e.g., Prosser and others 2001). The redistribution of sediment in a river can be described as an interplay between areas of erosion and deposition, both of which may disturb established plants but favor young and productive stages of vegetation. Dense riparian vegetation helps to minimize soil erosion, both by covering the soil, reducing current velocity during periods of high discharge, and by providing stability to underlying soils through root growth (Rowntree and Dollar 1999). Although vegetation cover reduces soil erosion, plants may eventually be uprooted and the ground opened for colonization by new plants. Waterborne sediments may be deposited as a thin veneer on plant leaves and stems, reducing photosynthesis and growth, or sediment may be deposited in much larger quantities, partially or completely burying plants and causing stress or mortality (Kent and others 2001). In the latter case, invasible patches are formed, but some riparian plants also have a great ability to withstand accretion. Xiong and others (2001) added up to 12 cm of alluvial silt to herbaceous vegetation in a floodplain along the Vindel River in northern Sweden and found a reduction of plant growth during the first season but no remaining effect after two growing seasons. Plants able to adventitiously root and to spread vegetatively were best fit to recover from silt burial.

For seeds, patterns are more complicated. One of the general questions that has remained unanswered for a long time is whether differences in floating ability among seeds regulate distribution patterns of riparian species. Andersson and others (2000a) used wooden cubes to mimic dispersal and deposition of seeds in a free-flowing river in northern Sweden. They found that species richness of established vegetation increased with the number of cubes that were deposited. In contrast, the proportions between long-floating and short-floating species in the established vegetation did not vary with cube deposition. If floating ability had been important, the riparian areas that trapped most waterborne cubes should have had a higher proportion of long-floating plants. Apparently, hydrochory is so effective in free-flowing rivers that even short-floating seeds are well dispersed. In regulated rivers of the same region, however, where current velocity has been reduced and the area of open water increased, both the number of plant species and the proportion of short-floating species have decreased (Jansson and others 2000a). The most likely explanation is that short-floating species do not float long enough to disperse successfully across impounded, lakelike river sections.

Plant debris ranges from leaves, buds, and flowers to entire tree trunks with attached root masses. The effects of redistribution of plant debris are somewhat similar to those of silt. Leaves and wood produced in the riparian belt are removed during floods, transported by the river, and deposited on the river bottom or in the riparian zone or delivered to the sea. Some of the litter is consumed or broken into smaller pieces by aquatic organisms. Much of the litter is also deposited along the high-water level, mostly on the ground but sometimes also in trees and other obstacles to flow. Accumulation of leaf litter buries plants, adds nutrients or phytotoxins following leaf decomposition, and provides plant propagules that are transported together with the litter (Xiong and Nilsson 1997). When large woody debris (LWD) is trapped, it can accumulate and sometimes block entire channels of small rivers, creating pools and waterfalls and affecting channel width and depth (Bilby and Bisson 1998). Woody debris in forest streams contributes to the maintenance of a more variable and complex range of habitats compared to streams with grass banks and no woody debris (Montgomery 1997). The masses of LWD can be extremely high, e.g., in the western United States, where figures ranging from 2.2 to 74.2 kg/m^2 have been reported (Bilby and Bisson 1998). The presence of LWD facilitates accumulation of finer sediment and organic matter that provides a substrate for early-successional plant species. In this way, the dynamics of LWD can have a major influence on the successional patterns of riparian plant communities. Its relative importance varies with stream size because logs are more easily trapped in small rivers (Gippel 1995, Gurnell and others 1995, Hughes 1997). LWD acts hydraulically as large roughness elements providing a varied flow environment and reducing average velocity (Gippel 1995).

Plants have several morphologies that facilitate dispersal by water (Johansson and Nilsson 1993, Malanson 1993), and long floating times have been documented for many plant propagules (Romell 1938, Danvind and Nilsson 1997). Free-flowing rivers carry whole plants; propagated modules such as rhizomes, stolons, tubers, and turions; and live seeds of many riparian plant species. Although hydrochory is one of the major dispersal mechanisms for plants along rivers (Johansson and others 1996), relatively few studies have linked such dispersal to the structure of riparian vegetation. Johansson and Nilsson (1993) studied the vegetatively dispersed plant *Ranunculus lingua* L. in a small river in northern Sweden and found a close correlation between the dispersal pattern of vegetative diaspores and the local distribution of individual clones. Barrat-Segretain and others (1999) studied aquatic plant species in the Rhone River, France, and found that species growing in frequently disturbed (flooded) habitats had higher regeneration and colonization abilities than plants in rarely disturbed habitats.

Riparian System Is a Transition Zone Between Land and Water Ecosystems and Is Disproportionately Plant Species-Rich When Compared to Surrounding Ecosystems

The riparian zone is unique in that it connects aquatic, terrestrial, and groundwater ecosystems and at the same time is ruled by dynamic hydrologic processes. Recent reports describe the complex nature of the riparian zone in terms of boundary, interface, ecotone, and transition zone (Naiman and Décamps 1990, 1997, Gregory and others 1991). Riparian communities are considered to be disproportionately species-rich compared to their surroundings (Naiman and others 1993, 2000). For example, in the Santa Monica Mountains in southern California in the United States, less than 1% of the land area consists of riparian communities and associated wetlands but approximately 20% of the native vascular plant species have their primary habitat there (Rundel and Sturmer 1998). Nilsson (1992) reports 13% (>260 species) of the entire Swedish flora of vascular plants occurring along the Vindel River in northern Sweden. Junk and others (1989) report that all periodically flooded forests in the Amazon Basin may have about 20% of the 4000–5000 estimated Amazonian tree species. Planty-Tabacchi and others (1996) report 1396 vascular plant species along the Adour River riparian corridor in France, representing 30% of the French flora (World Conservation Monitoring Centre 1992). An even more striking example is that the riparian corridor along the main channel of the Vindel River includes 60% of the vascular plant species in the entire Vindel River watershed (Nilsson personal observations).

There are several reasons why riparian communities of vascular plants are so species-rich, and all three principles outlined here are involved in explaining this richness (Naiman and others 1993, Pollock 1998, Pollock and others 1998): (1) Floods are intense and frequent resulting in spatial and temporal heterogeneity. (2) There are small-scale variations in topography, soils, and groundwater as a result of lateral migration of river channels. Disturbances caused by natural floods are interactive with geomorphic features, forming a mosaic of landforms with different disturbance history.

The individual elements of this mosaic show different stages of vegetation succession with different diversity (Harris 1999). (3) The climate varies as streams flow from high to low altitudes or across biomes, implying that a river will encounter a large proportion of a region's flora. (4) Upland environments impose various disturbance regimes on the riparian corridor, including fire, landslides, mud flows, and herbivory. (5) Plants have an excellent migration capacity along riparian corridors. Hydrochory is the most important means of dispersal, but anemochory (dispersal by wind) and zoochory (dispersal by animals) can also be important (Johansson and others 1996). Recent reports suggest that riparian communities are easily invaded by exotic plants (e.g., Planty-Tabacchi and others 1996), but there is also evidence that invasion by exotics is further promoted by flow alterations (e.g., Busch and Smith 1995, Friedman and others 1998).

Riparian corridors vary in species richness along the river's course. Ward (1998, see also Ward and Stanford 1995) identified three types of river landscape units or reaches that differ in terms of biodiversity: constrained river units increase in biodiversity downstream whereas braided river units have relatively low diversity, and meandering river units have high biodiversity. Nilsson and others (1989, 1991) examined entire rivers in northern Sweden and found that riparian vegetation was most species-rich in the middle reaches of free-flowing rivers. This pattern is analogous to that suggested for "total biotic diversity" in the river continuum concept (Vannote and others 1980), although this hypothesis was based on aquatic invertebrate communities. Décamps and Tabacchi (1994) found similar patterns in French rivers. The peak in plant species density along the free-flowing rivers in northern Sweden coincides with the former highest coastline formed during early Holocene, and in the French rivers with the piedmont area, thus providing another example of the importance of geomorphology in structuring plant communities.

How Can the Principles Be Incorporated into Management Strategies?

It is a key challenge for researchers to integrate the various models and information pieces about river ecosystems, thus revealing strengths and weaknesses of the present knowledge. Such an integrative modeling effort is necessary for a fuller understanding of the ways by which rivers and their riparian zones function (Walker and others 1995) and is also necessary for translating the present knowledge into proper management directives for riparian systems. This achievement should give full credit to the different spatial dimensions, their nature (continua or patch series), and their interactions within watersheds, but should also include interactions between adjacent watersheds and between watersheds and the sea (Nilsson and Berggren 2000, Helfield and Naiman 2001). It should deal with both short and long time scales to incorporate more regular as well as extreme events. A major shortcoming of the present concepts is that they are supported by few data and that only subsets of organisms and habitats are treated (Tockner and Ward 1999, Lorenz and others 1997). These limitations make it difficult to predict the more specific differences in ecological responses among different categories of rivers, and hence the different requirements for management. For example, seemingly simple questions such as which are the "toughest" and "weakest" rivers or river reaches, i.e., the rivers or river reaches that can be predicted to change little or a lot relatively independent of the degree of human impact, are difficult to answer with reasonable accuracy (cf., Rosgen 1994, Naiman 1998).

The three basic features of riparian zones outlined above are all affected by changing hydrologic regimes and all require specific management efforts to be restored. Table 2 summarizes the mechanisms related to each of the three principles, the alterations they are affected by, and the ecological responses to these alterations. It also summarizes some of the management measures that would restore the basic mechanisms. Some basic examples are given below:

1. The flow can be described in terms of its magnitude, frequency, timing, duration, and rate of change. Each modification of these variables affects the riparian plant communities, and the effects vary from increased scouring of vegetation to succession toward woodlands. Invasion of exotics also increases following such modification. The suggested management measures are straightforward and all imply flow manipulation toward more pristine flow conditions.
2. When dams disrupt the longitudinal pathway, plant dispersal is reduced and plant communities become fragmented. The dispersal process is difficult to restore without opening or removing the dams.

Many rivers have been converted to stairs of lake like waterbodies interrupted by dams and underground passages. In Sweden, nine of 13 major river channels have been altered this way (Jansson and others 2000b). Dams are barriers to the movement of fish and waterborne vascular-plant propagules, and regulated riparian zones harbor fewer vascular plant species than free-flowing ones (Nilsson and others 1991). In free-flowing rivers, floating propagules are rapidly transported far downstream during floods. Andersson and others

Table 2. Ecological responses of vegetation to alterations in riparian mechanisms (section 1 modified from Poff and others 1997)

Mechanisms	Specific alteration	Ecological response	References	Management measure action
1. Flow/hydrology				
1 1. Magnitude/frequency	Increased variation	Increased scour and washout of plants and organic matter	Petts 1984, Rørslett and Johansen 1996	Reduce frequency of flow variation
	Stabilized flow	Invasion of exotic plants	Ward and Stanford 1979, Busch and Smith 1995, Stanford and others 1996	Increase seasonal variation in flow (Springer and others 1999, Hill and others 1998), remove exotics
		Reduced water and nutrients to floodplain vegetation, leading to reduced disturbance, ineffective seed dispersal and reduced regeneration	Fenner and others 1985, Shankman and Drake 1990, Johnson 1994, Rood and others 1995, Scott and others 1997, Cordes and others 1997.	
1 2. Timing	Loss of seasonal flow peaks	Reduced plant recruitment and plant growth rates	Reily and Johnson 1982, Fenner and others 1985, Rood and Mahoney 1990	Reintroduce seasonal flow peaks and higher minimum flows (Rood and Mahoney 1990, Richter and others 1997)
		Invasion of exotic plants	Horton 1977, Friedman and others 1998	Remove exotics
		Succession towards wooded wetlands	Toner and Keddy 1997	Reintroduce second flow peak (Toner and Keddy 1997)
1 3. Duration	Prolonged low flows	Reduced plant cover and diversity	Busch and Smith 1995, Stromberg and others 1996	Increase seasonal high flows (Richter and others 1997, Galat and Lipkin 2000)
		Physiological stress leading to reduced plant growth rates, morphological change, and mortality	Reily and Johnson 1982, Perkins and others 1984, Kondolf and Curry 1986, Stromberg and others 1992, Rood and others 1995	
	Prolonged inundation	Altered plant communities	Connor and others 1981, Bren 1992, Crivelli and others 1995, Toner and Keddy 1997, Friedman and Auble 1999	Reduce high flows, especially when badly timed (Toner and Keddy 1997, Galat and Lipkin 2000)
1 4. Rate of change	Rapid changes in river stage	Washout of riparian plants, failed seedling establishment	Grelsson 1986, Rood and others 1995, 1999	Reduce rates of water-level change
2. Pathway/corridor				
2 1. Dispersal	Longitudinal pathway disrupted by dams, impoundments and diversions	Fragmented and altered plant communities and reduced plant migration	Andersson and others 2000b, Jansson and others 2000b	Remove dams, restore riparian corridors (Shafroth and others 1998)
3. Landscape interactions				
3 1. Connectivity	Riparian zones disconnected from surrounding habitats	Reduced plant diversity and compromised ecological integrity	Sparks and others 1990, Theiling 1995, Ward and Stanford 1995, Brunke and Gonser 1997, Ward and others 1999	Reconnect riparian zones with their environments (Galat and others 1998, Schiemer and others 1999)
3 2. Disturbance	Altered disturbance regime	Reduced diversity of plant communities and landscapes	Ward and others 1999, Marston and others 1995	Reintroduce seasonal floods (Hill and others 1998), remove dams, allow minimum flows

(2000b) showed that in a free-flowing river, the species composition of drifted propagules was similar to the riparian vegetation of sites upstream. In a regulated river, this similarity was significantly lower (Andersson and others 2000b). The underlying mechanism is probably that the effective dispersal makes it possible for any riverbank site to be colonized by species from a large portion of the river valley, thus favoring homogenization of the floristic composition.

In impounded rivers, current velocity is low and floating propagules either sink or become swept ashore by winds (Jansson and others 2000b). Very few propagules pass dams through turbines or spillways because passages are hard to hit, but long floating-times increase the probability of success. Therefore, about 30 years after dam erection, adjacent impoundments in similar environmental settings in northern Sweden have been found to develop different riparian floras because species with poor floating capacity become unevenly distributed among impoundments (Jansson and others 2000b). Such discontinuities have not been observed in free-flowing rivers, suggesting effective dispersal of riparian plants in the absence of dams. Given that dams regulate most of the world's rivers, floristic disruptions of riparian corridors may be a global phenomenon. The extensive fragmentation of other ecosystems may have caused similar obstructions to organism dispersal, with subsequent changes in species composition.

3. When riparian communities are disconnected from the rivers, they no longer receive and release plant propagules as during natural conditions. They thus become more isolated in a landscape context and overall diversity decreases (Bravard and others 1997).

Alterations to the riparian disturbance regime may give similar results. The suggested management measure is to reconnect the riparian zones with their environments, a target that is easiest to achieve by reintroducing seasonal floods.

The lower third of the Missouri River in the United States was channelized and diked between 1937 and 1955, while the middle third was impounded (Galat and others 1998, Schiemer and others 1999). River water was used for navigation, hydropower, and flood control, causing disconnection of the river from its floodplain. In 1993 the "Great Midwest Flood" overtopped the levees of the Missouri River, reconnecting the river with most of its floodplain. Record flooding also occurred in 1995 and 1996. This provided an opportunity for restoring riparian wetlands along the Missouri River.

Large areas of floodplain have been protected since the flooding, by state and federal programs, potentially to be rehabilitated (Galat and others 1998, Schiemer and others 1999). "Passive" management can recreate braided channels and wetlands. This management strategy is based on nonstructural techniques such as reconstruction of natural river floodplain geometry by "letting the river do the work" and only allowing a few low-elevation structures. For the Missouri River, this means taking advantage of the many scours produced by the high floods during the 1990s. In other rivers, such as the Danube, more active restoration measures have been undertaken. For example, riverside embankments have been lowered, and completely opened at inflow channels, and weirs in side channels have been lowered (Schiemer and others 1999).

The vegetation responded quickly to the reconnection of the lower Missouri River with its floodplain (Galat and others 1998, Schiemer and others 1999). For example, perennial plants recovered, and new opportunities were provided for invasive plants on sites scoured by the 1993 flood. However, flooding in 1995 and 1996 removed many plants established after the 1993 flood.

Most of the suggested management actions could be implemented without further research. However, because the measures will interfere with societal interests, and compromises are likely to be asked for, further research will be needed to provide an understanding about the ecological responses that are likely to result from each individual management measure (Jackson and others 2001). There are also uncertainties about long-term effects and more holistic responses. Some examples of required research efforts are given in Table 3.

In sum, riparian zones are an integral part of river ecosystems and a landscape component that has to function well if ecologically vital rivers are to be maintained in the long term. This task may require a combination of measures, such as protection, restoration, rehabilitation and substitution (Naiman and others 2000), but also the integration of many different societal institutions. Restoration of highly altered riparian areas will be constrained by structures such as dams, dikes, and pavements that prevent reestablishment of natural functions. Restoration will also be confined by conservative policies and laws governing the commodity of instream flow, by a complexity of institutions managing water resources, and also by an increasing human population demanding more and more water. Despite such obstacles, however, there are several recent examples of major advances that offer hope for significant improvements of watershed management during the 21st century (Naiman and others 2000). Researchers must realize the potential of such a development and design their work in such a way that their science will be used, for the mutual benefit of both humans and the environment.

Table 3. Examples of research needed for improving the ecological understanding of various management measures in riparian areas[a]

1. Flow/hydrology Relationships between effect and response variables: Are there certain thresholds of water needs that cannot be exceeded (in both directions) without devastating environmental effects?
2. Pathway/corridor Effects of fragmentation by dams on organism dispersal: How do effects vary between different organisms? Which organisms are most (or least) susceptible to fragmentation by dams? Does genetic diversity show similar fragmentation patterns as species diversity? Which parts of a river are most affected ecologically by dam fragmentation? Which are the results of various approaches to reducing fragmentation effects without removing dams?
3. Landscape interactions Effects of hydrologic alterations on land-water interactions: How do responses vary with the location along a river? How do responses vary between different types of riparian systems (substrate, slope width, ecoregion)? Which are the effects of short-term artificial floods on riparian integrity?

[a]Needs for knowledge about long-term effects and of patterns of change on the scale of watersheds are common for all three groups of principles. Many research topics require integrative approaches to principles 1–3.

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Literature Cited

Andersson, E., C. Nilsson, and M. E. Johansson. 2000a. Plant dispersal in boreal rivers and its relation to the riparian flora. *Journal of Biogeography* 27:1095–1106.

Andersson, E., C. Nilsson, and M. E. Johansson. 2000b. Effects of river fragmentation on plant dispersal and riparian flora. *Regulated Rivers: Research and Management* 16:83–89.

Barrat-Segretain, M. H., C. P. Henry, and G. Bornette. 1999. Regeneration and colonization of aquatic plant fragments in relation to the disturbance frequency of their habitats. *Archiv für Hydrobiologie* 145:111–127.

Bayley, P. B. 1995. Understanding large river-floodplain ecosystems. *BioScience* 45:153–158.

Bégin, Y., and S. Payette. 1991. Population structure of lakeshore willows and ice-push events in subarctic Québec, Canada. *Holarctic Ecology* 14:9–17.

Ben-David, M., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* 83:47–55.

Benke, A. C. 1990. A perspective on America's vanishing streams. *Journal of the North American Benthological Society* 9:77–88.

Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt-marsh plant community. *Ecological Monographs* 57:129–147.

Bilby, R. E., and P. A. Bisson. 1998. Function and distribution of large woody debris. Pages 324–346 *in* R. J. Naiman and R. E. Bilby (eds.), River ecology and management. Springer-Verlag, New York.

Bilby, R. E., B. R. Fransen, J. K. Walter, C. J. Cederholm, and W. J. Scarlett 2000. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. *Fisheries* 26:6–14.

Bravard, J. P., C. Amoros, G. Pautou, G. Bornette, M. Bournaud, M. C. desChatelliers, J. Gibert, J. L. Peiry, J. F. Perrin, and H. Tachet. 1997. River incision in south-east France: Morphological phenomena and ecological effects. *Regulated Rivers: Research and Management* 13:75–90.

Bren, L. J. 1992. Tree invasion of an intermittent wetland in relation to changes in the flooding frequency of the River Murray, Australia. *Australian Journal of Ecology* 17:395–408.

Bretschko, G. 1995. River land ecotones: scales and patterns. *Hydrobiologia* 303:83–91.

Brinson, M. 1990. Riverine forests. Pages 87–141 *in* A. E. Lugo, S. Brown and M. Brinson (eds.) Ecosystems of the world 15. Forested wetlands. Elsevier, Amsterdam, The Netherlands.

Brunke, M., and T. Gonser. 1997. The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* 37:1–33.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30:492–507.

Busch, D. E., and S. D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecological Monographs* 65:347–370.

Connor, W. H., J. G. Gosselink, and R. D. Parrondo. 1981. Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. *American Journal of Botany* 68:320–331.

Cordes, L. D., F. M. R. Hughes, and M. Getty. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: The Red Deer River, Alberta, Canada. *Journal of Biogeography* 24:675–695.

Crivelli, A. J., P. Grillas, P., and B. Lacaze. 1995. Responses of vegetation to a rise in water-level at Kerkini Reservoir (1982–1991), a Ramsar site in northern Greece. *Environmental Management* 19:417–430.

Danvind, M., and C. Nilsson. 1997. Seed floating ability and distribution of alpine plants along a northern Swedish river. *Journal of Vegetation Science* 8:271–276.

Dawson, T. E., and J. R. Ehleringer. 1991. Streamside trees that do not use stream water. *Nature* 350:335–337.

Décamps, H. 1993. River margins and environmental change. *Ecological Applications* 3:441–445.

Décamps, H., and E. Tabacchi. 1994. Species richness in vegetation along river margins. Pages 1–20 *in* P. S. Giller, A. G. Hildrew and D. G. Rafaelli (eds.), Aquatic ecology: Scale, pattern and process. Blackwell, London.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266:753–762.

Ellis, L. M., M. C. Molles, and C. S. Crawford. 1999. Influence of experimental flooding on litter dynamics in a Rio Grande riparian forest, New Mexico. *Restoration Ecology* 7:193–204.

Fenner P., W. W. Brady, and D. R. Patten. 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. *Journal of Range Management* 38:135–138.

Fisher, S. G., N. B. Grimm, E. Marti, R. M. Holmes, and J. B. Jones, Jr. 1998. Material spiraling in stream corridors: A telescoping ecosystem model. *Ecosystems* 1:19–34.

Friedman, J. M., and G. T. Auble. 1999. Mortality of riparian box elder from sediment mobilization and extended inundation. *Regulated Rivers: Research and Management* 15:463–476.

Friedman, J. M., W. R. Osterkamp, M. L. Scott, and G. T. Auble. 1998. Downstream effects of dams on channel geometry and bottomland vegetation: regional patterns in the Great Plains. *Wetlands* 18:619–633.

Galat, D. L., and R. Lipkin. 2000. Restoring ecological integrity of great rivers: Historical hydrographs aid in defining reference conditions for the Missouri River. *Hydrobiologia* 422:29–48.

Galat, D. L., L. H. Frederickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, G. T. Gelwicks, J. E. Havel, D. L. Helmers, J. B. Hokker, J. R. Jones, M. F. Knowlton, J. Kubisiak, J. Mazourek, A. C. McColpin, R. B. Renken, and

R. D. Semlitsch. 1998. Flooding to restore connectivity of regulated, large-river wetlands. *BioScience* 48:721–733.

Gill, D. 1973. Modification of northern alluvial habitats by river development. *Canadian Geographer* 17:138–153.

Gippel C. J. 1995. Environmental hydraulics of large woody debris in streams and rivers. *Journal of Environmental Engineering* 121:388–395.

Gregory, S. V. 1997. Riparian management in the 21st century. Pages 69–85 *in* K. A. Kohm and J. F. Franklin (eds.), Creating a forestry for the 21st century: The science of ecosystem management. Island Press, Washington, DC.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* 41:540–551.

Grelsson, G. 1986. Vegetational changes on two eroding banks of a short-term regulated river reservoir in northern Sweden. *Nordic Journal of Botany* 5:581–614.

Grelsson, G., and C. Nilsson. 1980. Colonization by *Pinus sylvestris* of a former middle-geolittoral habitat on the Umeälven river in northern Sweden, following river regulation for hydro-electric power. *Holarctic Ecology* 3:124–128.

Gurnell, A. M., K. J. Gregory, and G. E. Petts. 1995. The role of coarse woody debris in forest aquatic habitats: Implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5:143–166.

Harris, R. R. 1999. Defining reference conditions for restoration of riparian plant communities: Examples from California, USA. *Environmental Management* 24:55–63.

Helfield, J. M., and R. J. Naiman. 2001. Nutrients from salmon carcasses enhance streamside forest growth and long-term salmon production. *Ecology* 82:2403–2409.

Hill, N. M., P. A. Keddy, and I. C. Wisheu. 1998. A hydrological model for predicting the effects of dams on the shoreline vegetation of lakes and reservoirs. *Environmental Management* 22:723–736.

Horton, J. S. 1977. The development and perpetuation of the permanent tamarisk type in the phreatophyte zone of the Southwest. *United States Department of Agriculture, Forest Service, General Technical Report RM* 43:124–127.

Hughes, F. M. R. 1997. Floodplain biogeomorphology. *Progress in Physical Geography* 21:501–529.

Jackson, R. B., S. R. Carpenter, C. N. Dahm, D. M. McKnight, R. J. Naiman, S. L. Postel, and S. W. Running. 2001. Water in a changing world. *Ecological Applications* 11:1027–1045.

Jansson, R., C. Nilsson, M. Dynesius, and E. Andersson. 2000a. Effects of river regulation on river-margin vegetation: A comparison of eight boreal rivers. *Ecological Applications* 10: 203–224.

Jansson, R., C. Nilsson, and B. Renöfält. 2000b. Fragmentation of riparian floras in rivers with multiple dams. *Ecology* 81: 899–903.

Johansson, M. E., and C. Nilsson. 1993. Hydrochory, population dynamics and distribution of the clonal aquatic plant *Ranunculus lingua*. *Journal of Ecology* 81:81–91.

Johansson, M. E., C. Nilsson, and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science* 7:593–598.

Johnson, W. C. 1994. Woodland expansion in the Platte River, Nebraska: Patterns and causes. *Ecological Monographs* 64:45–84.

Junk, W. J., and M. T. F. Piedade. 1993. Herbaceous plants of the Amazon floodplain near Manaus: Species diversity and adaptations to the flood pulse. *Amazonia* 12:467–484.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Canadian Special Publication Fisheries and Aquatic Sciences* 106:110–127.

Kangas, P. C. 1990. An energy theory of landscape for classifying wetlands. Pages 15–23 *in* A. E. Lugo, M. Brinson and S. Brown (eds.), Ecosystems of the world 15. Forested wetlands. Elsevier, Amsterdam.

Kent, M, N. W. Owen, P. Dale, R. M. Newnham, and T. M. Giles. 2001. Studies of vegetation burial: a focus for biogeography and biogeomorphology? *Progress in Physical Geography* 25:455–482.

Kondolf, G. M., and R. R. Curry. 1986. Channel erosion along the Carmel River, Monterey County, California. *Earth Surface Processes and Landforms* 11:307–319.

Lorenz, C. M., G. M. Van Dijk, A. G. M. Van Hattum, and W. P. Cofino. 1997. Concepts in river ecology: Implications for indicator development. *Regulated Rivers: Research and Management* 13:501–516.

Malanson, G. P. 1993. Riparian landscapes. Cambridge University Press, Cambridge, UK, 296 pp.

Marston, R. A., J. Girel, G. Pautou, H. Piegay, J. P. Bravard, and C. Arneson. 1995. Channel metamorphosis, floodplain disturbance, and vegetation development: Ain River, France. *Geomorphology* 13:121–131.

McClain, M. E., R. E. Bilby, and F. J. Triska. 1998. Nutrient cycles and responses to disturbance. Pages 347–372 *in* R. J. Naiman and R. E. Bilby (eds.), River ecology and management. Springer-Verlag, New York.

Montgomery, D. R. 1997. River management: What's best on the banks? *Nature* 388:328–329.

Naiman, R. J. 1998. Biotic stream classification. Pages 97–119 *in* R. J. Naiman and R. E. Bilby (eds.), River ecology and management. Springer-Verlag, New York.

Naiman, R. J., and H. Décamps (eds.). 1990. The ecology and management of aquatic–terrestrial ecotones. Man and the biosphere series. UNESCO, Paris, France.

Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics* 28:621–658.

Naiman, R. J., H. Décamps, J. Pastor, and C. A. Johnston. 1988. The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society* 7:289–306.

Naiman, R. J., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209–212.

Naiman, R. J., R. E. Bilby, and P. A. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. *BioScience* 50:996–1011.

Naiman, R.J., S.E. Bunn, C. Nilsson, G.E. Petts, G. Pinay, and L.C. Thompson. 2002. Legitimizing fluvial systems as users of water: An overview. *Environmental Management* 30:455–467.

Nilsson, C. 1983. Frequency distributions of vascular plants in the geolittoral vegetation along two rivers in northern Sweden. *Journal of Biogeography* 10:351–369.

Nilsson, C. 1992. Conservation management of riparian communities. Pages 352–372 *in* L. Hansson (ed.) Ecological principles of nature conservation. Elsevier, London.

Nilsson, C. 1999. Rivers and streams. *Acta Phytogeographica Suecica* 84:135–148.

Nilsson, C., and K. Berggren. 2000. Alterations of riparian ecosystems resulting from river regulation. *BioScience* 50: 783–792.

Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. *Ecology* 70:77–84.

Nilsson, C., A. Ekblad, M. Gardfjell, and B. Carlberg. 1991. Long-term effects of river regulation on river margin vegetation. *Journal of Applied Ecology* 28:963–987.

Nilsson, C., E. Nilsson, M. E. Johansson, M. Dynesius, G. Grelsson, S. Xiong, R. Jansson, and M. Danvind. 1993. Processes structuring riparian vegetation. Pages 419–431 *in* J. Menon (ed.) Current topics in botanical research. Council of Scientific Research Integration, Trivandrum, India.

Perkins, D. J., B. N. Carlsen, M. Fredstrom, R. H. Miller, C. M. Rofer, G. T. Ruggerone, and C. S. Zimmerman. 1984. The effects of groundwater pumping on natural spring communities in Owens Valley. Pages 515–527 *in* R. E. Warner and K. M. Hendrix (eds.), California riparian systems: Ecology, conservation, and productive management. University of California Press, Berkeley.

Pettit, N. E., and R. H. Froend. 2000. Variability in flood disturbance and the impact on riparian tree recruitment in two contrasting river systems. *Wetlands Ecology and Management* 9:13–25.

Petts, G. E. 1984. Impounded rivers: Perspectives for ecological management. Wiley, Chichester, UK, 285 pp.

Piedade, M. T. F., W. J. Junk, and S. P. Long. 1991. The productivity of the C_4 grass *Echinochloa polystachia* on the Amazon floodplain. *Ecology* 72:1456–1463.

Pinay, G., J.C. Clément, and R.J. Naiman. 2002. Basic principles and ecological consequences of changing water regimes on nitrogen cycling in fluvial ecosystems. *Environmental Management* 30:481–491.

Planty-Tabacchi, A.-M., E. Tabacchi, R. J. Naiman, C. DeFerrari, and H. Décamps. 1996. Invasibility of species-rich communities in riparian zones. *Conservation Biology* 10:598–607.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769–784.

Pollock, M. M. 1998. Biodiversity. Pages 430–452 *in* R. J. Naiman and R. E. Bilby (eds.), River ecology and management. Springer-Verlag, New York.

Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology* 79:94–105.

Prosser, I. P., I. D. Rutherfurd, J. M. Olley, W. J. Young, P. J. Wallbrink, and C. J. Moran. 2001. Large-scale patterns of erosion and sediment transport in river networks, with examples from Australia. *Marine and Freshwater Research* 52:81–99.

Puckridge, J. T., F. Sheldon, K. F. Walker, and A. J. Boulton. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* 49:55–72.

Reily, P. W., and P. W. Johnson. 1982. The effects of altered hydrologic regime on tree growth along the Missouri river in North Dakota. *Canadian Journal of Botany* 60:2410–2423.

Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* 10:1163–1174.

Richter, B. D., J. V. Baumgartner, R. Wigington, and D. P. Braun. 1997. How much water does a river need? *Freshwater Biology* 37:231–249.

Romell, L.-G. 1938. Växternas spridningsmöjligheter. Pages 279–448 *in* C. Skottsberg (ed.), Växternas liv. IV. Nordisk Familjeboks Förlags A.-B., Stockholm.

Rood, S. B., and S. Heinze-Milne. 1989. Abrupt downstream forest decline following river damming in southern Alberta (Canada). *Canadian Journal of Botany* 67:1744–1749.

Rood, S. B., and J. M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation. *Environmental Management* 14:451–464.

Rood, S. B., J. M. Mahoney, D. E. Reid, and L. Zilm. 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. *Canadian Journal of Botany* 73:1250–1260.

Rood, S. B., K. Taboulchanas, C. E. Bradley, and A. R. Kalischuk. 1999. Influence of flow regulation on channel dynamics and riparian cottonwoods along the Bow river, Alberta. *Rivers* 7:33–48.

Rørslett, B., and S. W. Johansen. 1996. Remedial measures connected with aquatic macrophytes in Norwegian regulated rivers and reservoirs. *Regulated Rivers: Research and Management* 12:509–522.

Rosgen, D. L. 1994. A classification of natural rivers. *Catena* 22:169–199.

Rowntree, K. M., and E. S. J. Dollar. 1999. Vegetation controls on channel stability in the Bell River, Eastern Cape, South Africa. *Earth Surface Processes and Landforms* 24:127–134.

Rundel, P. W., and S. B. Sturmer. 1998. Native plant diversity in riparian communities of the Santa Monica Mountains, California. *Madroño* 45:93–100.

Schiemer, F., C. Baumgartner, and K. Tockner. 1999. Restoration of floodplain rivers: The "Danube restoration project." *Regulated Rivers: Research and Management* 15:231–244.

Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications* 7:677–690.

Shafroth, P. B., G. T. Auble, J. C. Stromberg, and D. T. Patten. 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands* 18:577–590.

Shankman D., and D. L. Drake. 1990. Channel migration and regeneration of bald cypress in western Tennessee. *Physiological Geography* 11:343–352.

Sharitz, R. R., L. R. Boring, D. H. Van Lear, and J. E. Pinder, III. 1992. Integrating ecological concepts with natural resource management of southern forests. *Ecological Applications* 2:226–237.

Sparks, R. E., P. B. Bayley, S. L. Kohler, and L. L. Osborne. 1990. Disturbance and recovery of large floodplain rivers. *Environmental Management* 14:699–709.

Spink, A., R. E. Sparks, M. Van Oorschot, and J. T. A. Verhoeven. 1998. Nutrient dynamics of large river floodplains. *Regulated Rivers: Research and Management* 14:203–216.

Springer, A. E., J. M. Wright, P. B. Shafroth, J. C. Stromberg, and D. T. Patten. 1999. Coupling groundwater and riparian vegetation models to assess effects of reservoir releases. *Water Resources Research* 35:3621–3630.

Stanford, J. A., and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. *Nature* 335:64–66.

Stanford, J. A, J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers: Research and Management* 12:391–413.

Stromberg, J. C. 1997. Growth and survivorship of Fremont cottonwood, Goodding willow, and salt cedar seedlings after large floods in central Arizona. *Great Basin Naturalist* 57:198–208.

Stromberg, J. C., J. A. Tress, S. D. Wilkins, and S. Clark. 1992. Response of velvet mesquite to groundwater decline. *Journal of Arid Environments* 23:45–58.

Stromberg, J. C., R. Tiller, and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro River, Arizona, USA. *Ecological Applications* 6:113–131.

Theiling, C. H. 1995. Habitat rehabilitation on the Upper Mississippi River. *Regulated Rivers: Research and Management* 11:227–238.

Tockner, K., and J. V. Ward. 1999. Biodiversity along riparian corridors. *Archiv für Hydrobiologie* 3, *Supplement* 115:293–310.

Toner, M., and P. Keddy. 1997. River hydrology and riparian wetlands: A predictive model for ecological assembly. *Ecological Applications* 7:236–246.

Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8:36–50.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.

Walker, K. F., F. Sheldon, and J. T. Puckridge. 1995. A perspective on dryland river ecosystems. *Regulated Rivers: Research and Management* 11:85–104.

Ward, J. V. 1989a. Riverine-wetland interactions. Pages 385–400 *in* R. R. Sharitz and J. W. Gibbons (eds.), Freshwater wetlands and wildlife. CONF-8603101, DOE Symposium Series No. 61, USDOE Office of Scientific and Technical Information, Oak Ridge, Tennessee.

Ward, J. V. 1989b. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8:2–8.

Ward, J. V. 1998. Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* 83:269–278.

Ward, J. V., and J. A. Stanford (eds.). 1979. The ecology of regulated streams. Plenum Press, New York, 398 pp.

Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 *in* T. D. Fontaine III and S. M. Bartell (eds.), Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

Ward, J. V., and J. A. Stanford. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research and Management* 11:105–119.

Ward, J. V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers: Research and Management* 15:125–139.

Welcomme, R. L. 1979. Fisheries ecology of floodplain rivers. Longman, London, 317 pp.

Wilson, S. D, and P. A. Keddy. 1985. Plant zonation on a shoreline gradient: Physiological response curves of component species. *Journal of Ecology* 73:851–860.

World Conservation Monitoring Centre. 1992. Global biodiversity: Status of the earth's living resources. Chapman and Hall, London, 585 pp.

Xiong, S., and C. Nilsson. 1997. Dynamics of leaf litter accumulation and its effects on riparian vegetation: A review. *Botanical Review* 63:240–264.

Xiong, S., C. Nilsson, M. E. Johansson, and R. Jansson. 2001. Responses of riparian plants to accumulation of silt and plant litter: The importance of plant traits. *Journal of Vegetation Science* 12:481–490.