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Reviewed work(s):
Source: *BioScience*, Vol. 50, No. 11 (November 2000), pp. 996-1011
Published by: University of California Press on behalf of the American Institute of Biological Sciences
Stable URL: http://www.jstor.org/stable/10.1641/0006-3568%282000%29050%5B0996%3AREAMIT%5D2.0.CO%3B2
Accessed: 29/12/2011 13:20

Riparian Ecology and Management in the Pacific Coastal Rain Forest

ROBERT J. NAIMAN, ROBERT E. BILBY, AND PETER A. BISSON

FUNDAMENTAL RIPARIAN RESEARCH HAS SUBSTANTIALLY IMPROVED WATERSHED MANAGEMENT ON THE NORTHERN PACIFIC COAST

The last two decades have seen an enormous global research effort focused on understanding the dynamics and managerial uses of riparian zones. *Riparius*, a Latin word meaning "belonging to the bank of a river," refers to biotic communities living on the shores of streams, rivers, ponds, lakes, and some wetlands. Riparian zones strongly influence the organization, diversity, and dynamics of communities associated with aquatic ecosystems (Gregory et al. 1991, Décamps 1996). Riparian areas possess distinct ecological characteristics because of their interaction with the aquatic system. Thus, their boundaries can be delineated by changes in soil conditions, vegetation, and other factors that reflect this aquatic–terrestrial interaction (Naiman and Décamps 1990, 1997).

Riparian zones vary widely in their physical characteristics, which are vividly expressed by an array of life history strategies and successional patterns. Consequently, these areas are among the biosphere's most complex ecological systems and also among the most important for maintaining the vitality of the landscape and its rivers (Naiman and Décamps 1990, 1997). The variability of natural riparian zones reflects the inherent physical heterogeneity of the drainage network, the processes shaping stream channels, and the characteristics of the biotic community (Figure 1). In effect, riparian biota are the products of past and present interactions among biophysical factors. In turn, the biota themselves have strong, long-term influences on the geological structures and processes that shape them.

The riparian forests of the Pacific Coastal Ecoregion (PCE) of North America are floristically and structurally its most diverse vegetation (Pollock 1998, Pollock et al. 1998), and their maintenance has become an integral component of watershed management strategies (Naiman and Bilby 1998). Since 1990, significant advances in understanding the structure and dynamics of riparian zones in the PCE have led to their being recognized as key components of land and water management. Many of the region's management guidelines are based on these recent scientific advances as well as on the strong foundation of knowledge built by S.V. Gregory and his colleagues (Gregory et al. 1991). In this article, we summarize the scientific advances of the last decade in understanding the ecology of PCE riparian zones and show how this understanding directly contributes to better stream and watershed management.

The Pacific Coastal Rain Forest

The PCE, also known as the Pacific Coastal Rain Forest, extends from northern California to south-central Alaska and east to the crests of the Cascade Mountains in the south and the Coastal Mountains in the north (Figure 2). This region is characterized by high precipitation (more than 1 m/year) and a maritime climate with cool, dry summers and warm, wet winters. The PCE encompasses an abundance of rivers, many of which support biota of considerable economic importance, such as Pacific salmon (*Oncorhynchus* spp.). It is also one of the most rapidly

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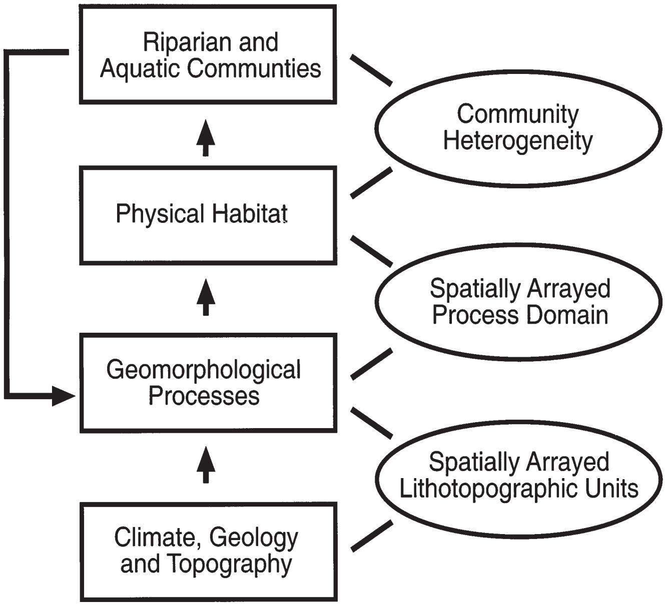

Figure 1. Schematic representation of the relationships among hydrogeomorphic processes, habitat dynamics, and riverine communities. Lithotopographic units are areas with similar topography and geology, and within which similar suites of geomorphic processes occur. Other terms are addressed in the text. Modified from Montgomery (1999).

developing regions of North America, bringing high levels of national and international attention to many conflicts involving stream and river environments.

The PCE supports some of the most extensive temperate rain forests in the world (Schoonmaker et al. 1997), some of them containing massive coniferous trees. These include the biggest and longest lived redwoods (*Sequoia* spp.), spruces (*Picea* spp.), firs (*Abies* spp.), and hemlocks (*Tsuga* spp.). These forests support thousands of identified (and many unidentified) species and supply wood and other materials that are vital to stream and river integrity. The wettest forests in the region contain more living and dead plant matter than even tropical rain forests.

The biota of the aquatic systems also reaches large sizes, great ages, and high densities. The legendary spawning runs of salmon have both cultural and economic importance. Chinook salmon (*Oncorhynchus tshawytsha*) may reach 55 kg and number in the hundreds of thousands in a single river system (NRC 1996), while sturgeon (*Acipenser* spp.) may live for a century and reach lengths of 6 m and a mass of 700 kg. The endemic diversity of aquatic organisms is not as well known as that of other ecoregions (Pollock 1998). However, the lack of known inventories offers unique research opportunities, especially if the diversity of aquatic organisms parallels that of the terrestrial landscape.

At a global scale, the PCE is sufficiently homogeneous to be considered a single ecoregion, and indeed there is regional consistency in aquatic community structure (especially fishes) and vegetation (Naiman and Bilby 1998). However, at the smaller scales relevant to resource management and conservation, there are ecologically significant variations in genetic diversity, evolutionary processes, life history strategies, and other biotic characteristics. Individual species are well adapted to the wide variations in physical properties and to the disturbance regimes associated with individual river systems (Naiman and Anderson 1997).

Moreover, several important latitudinal gradients in the PCE have significant ecological implications for population and community processes, for life history strategies, and for the behavior of riparian biota (Naiman and Anderson 1997). First, watershed size, at the marine interface, decreases from south to north. Ninety-five percent of the 608 major watersheds in the north (above 48° N latitude) are less than 100 km^2 compared with only 52% in the southern region. Second, the mean annual runoff from

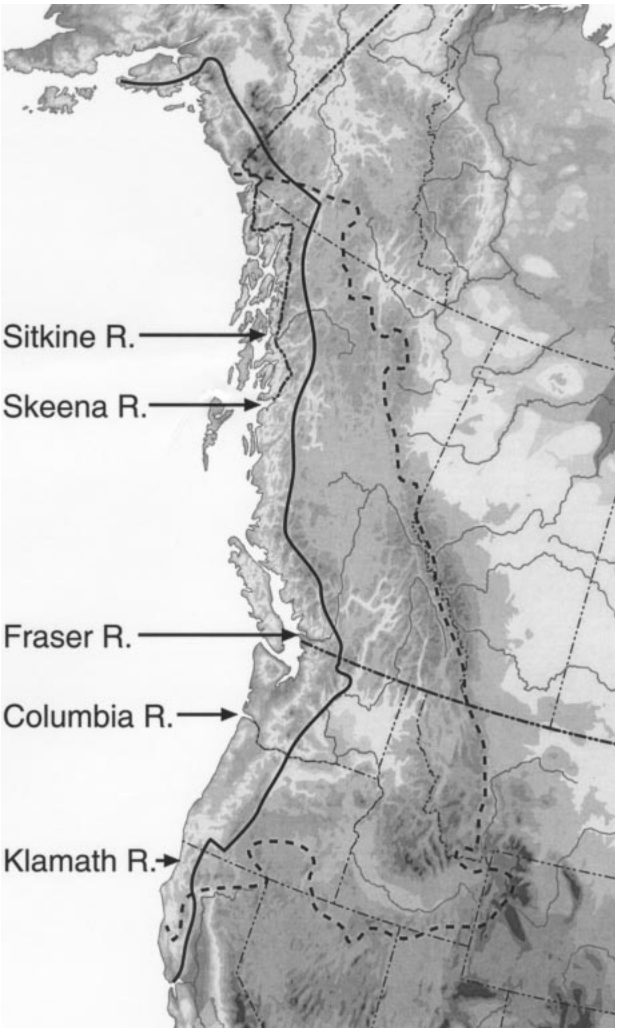

Figure 2. Watershed-based boundary of the Pacific Northwest (dashed line) region of North America and approximate boundary of the Pacific coastal ecoregion (solid line). Modified from Ryan (1994).

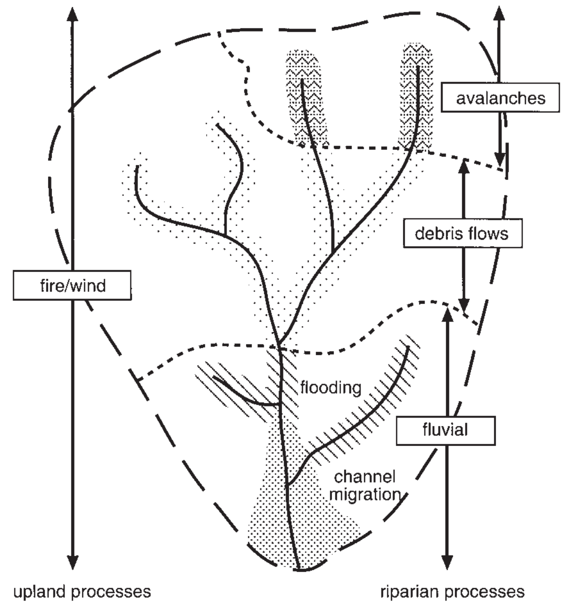

Figure 3. General process domains of origin, transport, and deposition of materials in mountainous watersheds of the Pacific Coastal Ecoregion. Modified from Montgomery (1999).

rivers increases from south to north, varying from 0.5 m/year in northern California to 7.4 m/year in southeastern Alaska. Third, seasonal patterns of discharge vary significantly with latitude. Nearly 70% of the annual discharge occurs in winter in California, but only about 25% occurs in winter in British Columbia and Alaska. In California, less than 2% of the annual discharge occurs in summer, while in British Columbia and Alaska, summer discharge is as high as 60% of the annual total. Finally, average annual water temperature decreases from south to north, varying from about 15°C in northern California to about 3°C in Alaska.

Understanding riparian zones (circa 1990)

Gregory et al. (1991) summarized the riparian dynamics based on information gathered before 1990. They proposed a conceptual model of riparian zones in which physical processes shaping valley-floor landforms are integrated with the formation of habitat, the succession of riparian plant communities, and the production of nutritional resources for aquatic systems. This model synthesized a diverse and often-confusing array of information into a coherent understanding that formed a base for much subsequent research.

Gregory and his colleagues showed, moreover, how the geomorphic structure of valley-floor landforms resulted from interactions among basin geology, hydrology, and inputs of materials from adjacent hillslopes and vegetation. Furthermore, they showed that similar physical habitat contained similar biological communities, and pointed out how site-specific characteristics of the riparian vegetation reflect histories of both fluvial disturbance from floods and nonfluvial disturbances (e.g., fire, wind, plant disease, and herbivory). Finally, they articulated how variations in soil properties and microtopography on the valley floor affect the biotic composition of the riparian community.

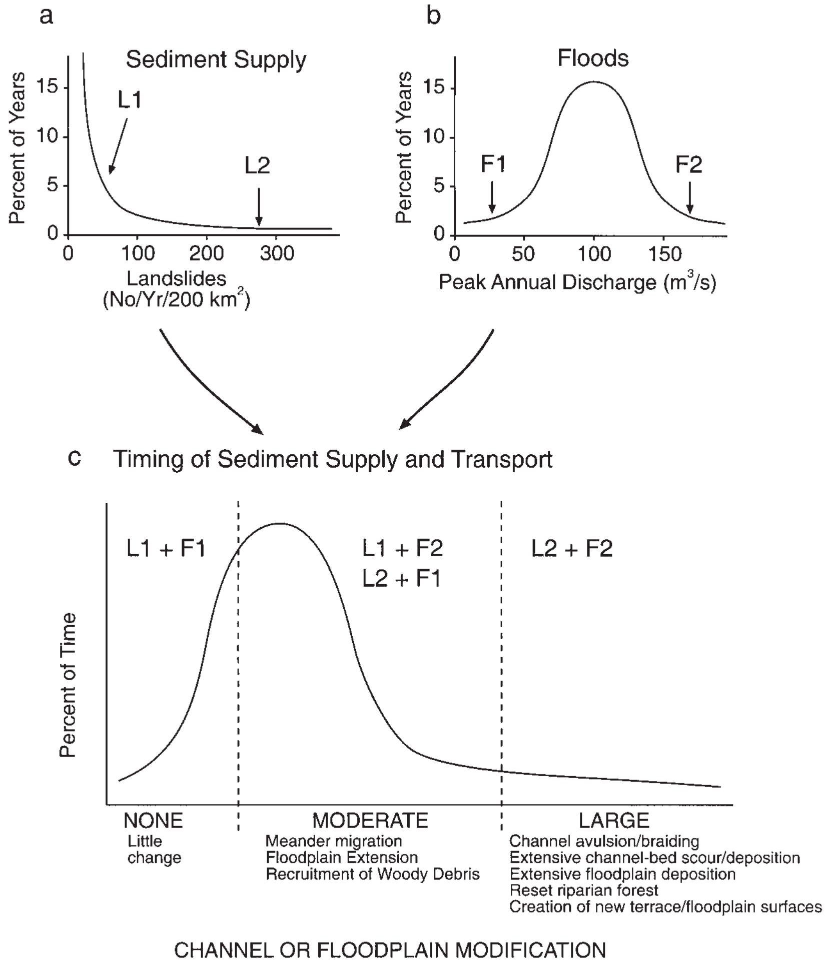

Figure 4. The extent to which floods affect channel and floodplain characteristics depends on the volume of sediment and the size of the flood (i.e., temporal sequencing). Hence, the frequency with which impacts of a given magnitude occur depends on (a) the frequency distribution of sediment input to the channel system, (b) the frequency distribution of floods, and (c) the persistence of sediment in the channel and the relative timing between these events. Relative timing between flooding (F) and sediment supply from landslides (L) is indicated by L1 and F1, and so on. From Benda et al. (1998).

In combination, the biophysical factors shape system-level biodiversity and productivity. Thus, Gregory et al. (1991) postulated that the great variety of microsites and complex, high-frequency disturbance regimes along river valleys lead to greater plant species diversity in riparian zones than in uplands. Likewise, the favorable juxtaposition of water, nutrients, temperatures, and light regimes contributes to unusually high levels of plant production, with a significant portion contributed to aquatic communities in the form of leaves, needles, and wood. And the addition of large, dead wood to streams further enhances habitat and the overall retentive abilities of the system.

Important advances in the last decade

The major advances of the last decade are built on this fundamental understanding of riparian dynamics in the PCE. These advances relate to hydrogeomorphic processes, controls on the structure and diversity of plant communities, hyporheic-riparian linkages, and the influences of animals on vegetative characteristics.

***Hydrogeomorphic processes*.** The PCE is a dynamic landscape in which watershed and geomorphic processes such as fire, sediment, and flow regimes continuously shape the drainage network (e.g., Benda et al. 1998, Montgomery and Buffington 1998, Swanson et al. 1998, Montgomery 1999). Important advances have clarified how these processes affect the riparian vegetation and how vegetation may modify stream channels through the delivery and routing of woody debris and sediment.

Watershed-scale processes. Improved understanding of the consequences of watershed-scale disturbances to PCE riverine corridors has been attained by shifting the focus from individual watershed elements to populations of watershed elements and from short to long time scales (Benda et al. 1998, Montgomery 1999). Linking the behavior of watershed elements—major sediment sources and large woody debris (LWD)—and their interaction with other elements (i.e., a network of linked stream reaches) allows one to model the movement of materials between hillslope sources and stream deposits.

One approach to understanding watershed-scale processes is the concept of "process domains" in which multiscale spatial variability in geomorphic processes governs the temporal pattern of disturbances that influence riparian structure and dynamics (Montgomery 1999). Conceptually, the drainage network can be divided into discrete regions with distinctly different disturbance regimes (e.g., initiation, transport, and deposition). Simply, the Process Domain Concept allows one to define and map domains within a watershed characterized by different geomorphic processes, disturbance regimes, response potential, recovery time, and ecological properties (Figure 3).

Another approach is to use probability and frequency distributions to simulate long-term patterns of watershed behavior and natural disturbance. Patterns are projected as probabilities of possible disturbances and environmental conditions. For example, using a watershed in the Oregon Coast Range where shallow landslides and debris flows are dominant erosion processes, Benda et al. (1998) showed that the sequence of rainstorms and fires governs the sequence of erosional events (Figure 4). Sediment supply and routing are presented as frequency distributions of the proportion of time when water or sediment production is at given levels. Considering the sediment supply in concert with the distribution of floods makes it possible to determine the frequency distribution of channel and floodplain changes (Figure 4c). The scenario in Figure 4 illustrates how often channel and floodplain changes are likely to occur, projecting channel and riparian floodplain conditions over time and space.

Figure 5. Debris flow on a tributary of the Hoh River, Olympic Peninsula, Washington. Notice the person in the photo for scale. Photo: Robert J. Naiman.

Debris flows. Debris flows are primary agents moving sediment and wood in many mountainous basins of the PCE (Montgomery and Buffington 1998). The relative importance of the widespread debris flows in small to medium-sized streams across much of the PCE, as agents of sediment movement and delivery to channels, varies according to geology, topography, soils, and hydrologic characteristics of a watershed. Debris flows occur when exceptionally heavy rainfall results in the breaching of a landslide-created dam or, more commonly, with sudden movement of materials from channel heads or hillslopes. The torrent of water, large wood, and sediment quickly scours the channel. The effects on riparian vegetation may be severe and long-term (Figure 5).

Channel gradient and spatial position in the drainage network influence the effects of debris flows and the rates of recovery from them. Steep, high-energy channels recover quickly from sediment deposition because of their high

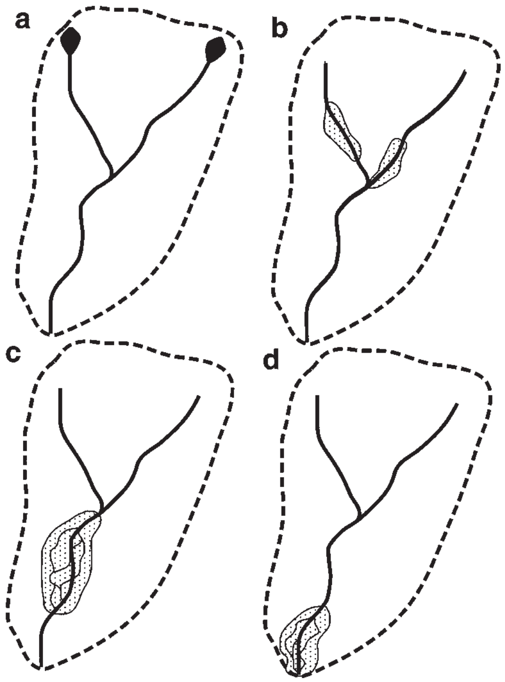

Figure 6. Sediment wave propagation through a channel network. Landslides originating at the head of the channel network (a) deliver sediment that rapidly propagates (b) through steep headwater channels to lower-gradient reaches (c) where deposition may trigger channel braiding, which eventually (d) recovers to a single thread morphology. From Montgomery and Buffington (1998).

Figure 7. Large woody debris (LWD) in the Queets River, Washington, illustrating the size and complexity of woody debris jams Photo: Robert J. Naiman.

transport capacities, and in contrast, lower gradient channels typically take longer to recover. Channel slope and tributary junction angles also exert important controls on debris flow routing (Benda and Cundy 1990). Debris flows originating at the heads of long, straight channels tend to scour long channel segments and deliver sediment to downstream alluvial channels. Debris flows originating in obliquely oriented tributaries tend to deposit materials at channel confluences. Subsequent movement of the accumulated material has important impacts on downstream alluvial channels and the riparian vegetation.

Massive inputs of sediment, such as from synchronous landslides within a single basin, may cause local bed aggradation. If enough sediment is introduced into a channel, the channel type may be altered: Bedrock channels may become alluvial, and pool-riffle channels may become braided. There is evidence that these sediment deposits are transported downstream as a wave, altering channel form and riparian characteristics as it travels (Figure 6). Frequent debris flows set up oscillations in channel type, the frequency varying with position in the network and debris flow frequency (Benda 1994). Such channel type changes can substantially affect community composition and ecological processes associated with riparian vegetation.

Origin, role, and residence time of large woody debris (LWD). Once LWD enters the channel, it exerts significant controls on the physical characteristics of streams, influencing channel type, sediment storage, and bedform roughness (Bilby and Bisson 1998). The advances of the last decade relate largely to the role of LWD in larger channels, its longevity there, and the processes responsible for its delivery to the channel.

Community characteristics of riparian vegetation determine the age and species of wood entering the fluvial system, and the variability in wood size and species has important ecological implications in terms of the persistence of LWD in the channel and subsequent successional processes associated with riparian forests. In the Queets River, Washington, hardwood species (*Alnus rubra*, *Populus trichocarpa*, *Acer macrophyllum*) are better represented among the riparian forests than among instream LWD; conversely, conifers (*Picea sitchensis*, *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Thuja plicata*) are better represented among LWD than in the adjacent riparian forest (Figure 7). These findings suggest that hardwoods are depleted from the channel faster than conifers. The depletion rate for a population of LWD pieces follows an exponential decay curve, whereby half the original LWD will be on the channel surface for only 10 years, and 80% of the LWD will be there for less than 50 years. Various processes are responsible for LWD depletion. Some of the wood decomposes in situ while other pieces either are deposited on the terrestrial portion of the floodplain, exported to the ocean, or buried by sediments until being exhumed by erosion centuries later. These latter pieces have ages up to 1400 years (Hyatt and Naiman in press).

The persistence of LWD is of fundamental ecological importance because of its influence on channel dynamics and the subsequent succession of riparian vegetation (Fetherston et al. 1995, Abbe and Montgomery 1996). Woody debris jams control local channel hydraulics and provide refugia against flood scour for vegetation development lasting decades or even centuries. The deposition of unusually large logs, with intact root wads, initiates the formation of stable woody debris jams that alter the local hydraulics and thereby control the spatial pattern of scour and deposition (Figure 8). Even though LWD accumulations may appear to form at random, there are distinctive structural patterns. Individual jams may be remarkably stable over the long term, allowing mature riparian forest patches to form and persist within a riverine environment that is characterized by rapid channel migration and frequent disturbance.

Recently, considerable effort has been devoted to better understanding the processes regulating wood delivery to streams. LWD enters streams when riparian trees fall or when trees are transported from upstream or upslope by floods, landslides, or snow avalanches. The relative importance of these input mechanisms relates to process domains within watersheds. Where landslides or avalanches are rare, nearly all LWD originates from riparian trees (Murphy and Koski 1989). In unstable landscapes, however, LWD is often transported to the channel over considerable distances. For example, nearly half the LWD in Cummins Creek, Oregon, originates upstream as opposed to being deposited from the adjacent riparian forest (McGarry 1994). The processes responsible for wood recruitment vary with channel form as well. For instance, windthrow is often the primary mechanism of wood delivery to channels with erosion-resistant banks (Andrus 1998) whereas erosive undercutting of trees is an important mechanism of LWD delivery to channels with erosion-prone banks (Murphy and Koski 1989).

Numerous models of wood delivery from riparian zones to stream channels have been developed (e.g., McDade et al. 1990, Andrus 1998). Most of these attempt to predict the amount of wood delivered from riparian zones of varying widths, a topic of considerable controversy because of its potential significance for formulating forest practice and other land use regulations. However, many of the models' assumptions clearly indicate a need to interpret the predictions carefully (Kennard et al. 1999).

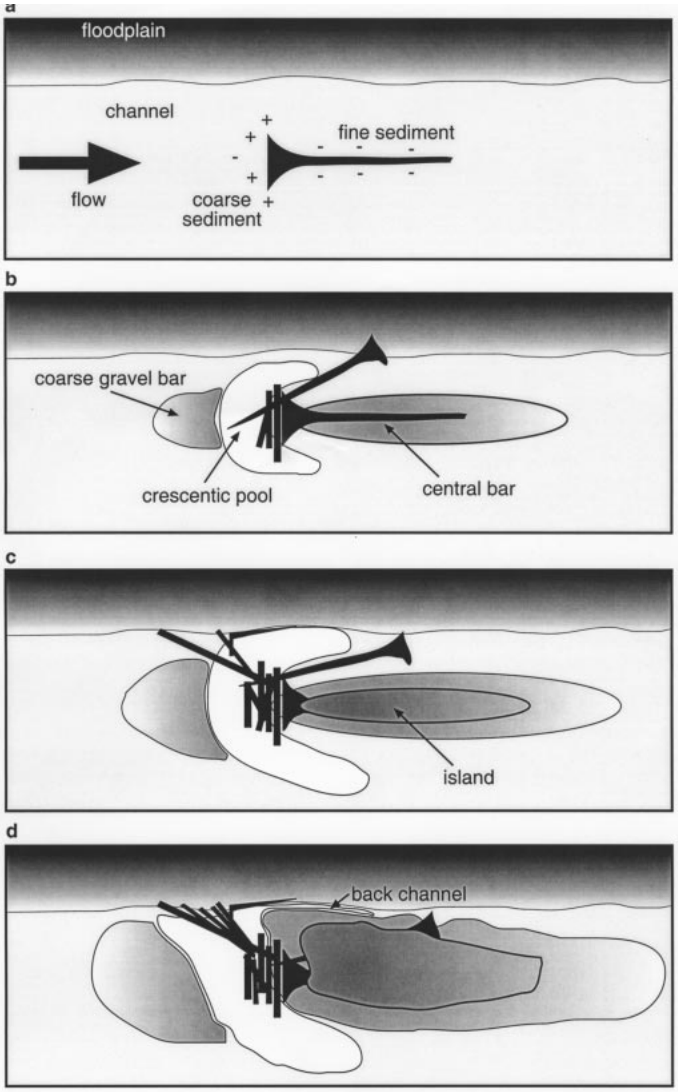

Figure 8. Morphological stages in alluvial topography associated with construction of a woody debris (bar-apex) jam. (a) Deposition of an especially large tree with the root wad intact. (b) Formation of a coarse gravel bar upstream, a crescent-shaped pool immediately upstream of the root wad, and a downstream central bar of finer sediments along the axis of the tree. (c) Island development along the central bar. (d) Integration into the broader floodplain. Modified from Abbe and Montgomery (1996).

All the wood input models include assumptions about tree growth and mortality, longevity of wood in the channel, and direction of tree fall, which greatly influence estimates of future LWD abundance. Tree fall and depletion of wood from the channel are often treated as constant processes, and the projected mortality rate of riparian trees because of growth suppression is generally assumed to be an adequate surrogate for tree fall rate. However, these assumptions ignore the fact that wood input and output tend to be episodic, not constant. Most tree fall and wood delivery is caused by relatively rare disturbances such as windstorms, floods, fires, or landslides. Similarly, wood removal from a stream is greatly influenced by floods. All models acknowledge that the probability of a fallen tree intersecting a channel decreases with distance from the channel edge; however, many assume that the probability of direction of fall for a tree is random. Empirical data on probability of fall direction indicate that it is strongly influenced by local topography, and that the chance of a tree's falling toward the channel is considerably greater than of its falling in another direction (McDade et al. 1990, Andrus

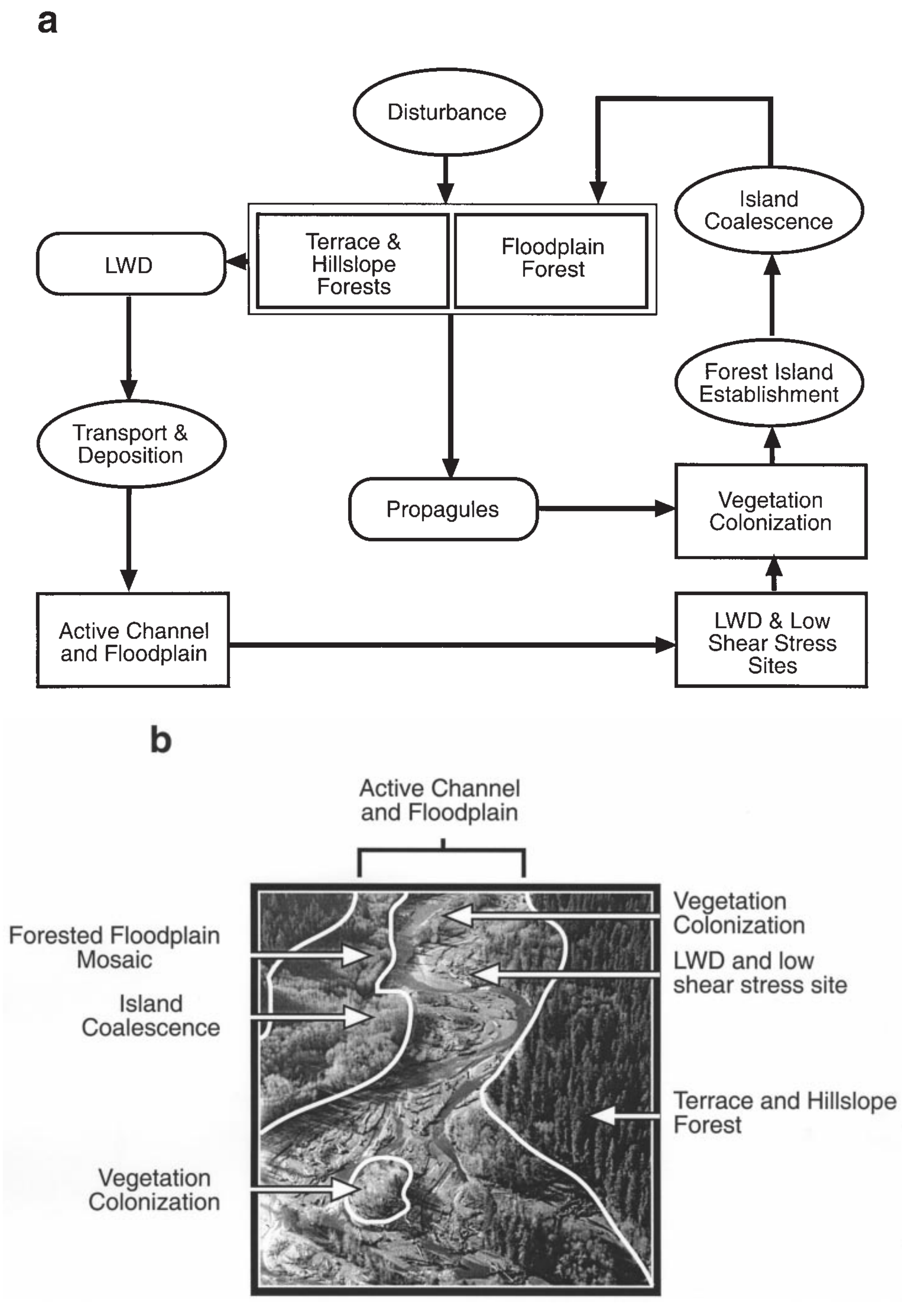

Figure 9. There is an intimate relationship among disturbance regimes, production of large woody debris, and riparian forest development. (a) Conceptual model of riparian forest development in alluvial rivers showing how LWD plays a key role in the formation of vegetated islands that eventually coalesce to form the riparian forest (from Fetherston et al. 1995). (b) Photo of the Queets River riparian forest and floodplain illustrating model components described in the text. Photo: T. Hyatt.

1998). Finally, none of the wood input models addresses delivery from upstream or upslope. Overall, these assumptions make the models computationally simple but render their projections of wood abundance somewhat unrealistic. Nevertheless, the models have proven useful in comparing the wood delivery to streams among various riparian management approaches, and they are being continually improved (Kennard et al. 1999).

Riparian plants and the environment. Vegetative communities in the riparian zone are dynamic, reflecting a dynamic landscape. Heterogeneity in landform, microclimate gradient, site productivity, and disturbance regime all play important roles in influencing forest structure, species richness, and colonization by exotic plants.

Alluvial landform and riparian forest structure. Integrating interactions among landform and vegetation provides insights into understanding the biotic dynamics of riparian zones. In small to medium PCE streams, the arrangement of the physical environment and the characteristics of the riparian forest vary with spatial and temporal scale (Rot et al. 2000). At the largest scales, valley form influences alluvial landform development and pattern (i.e., floodplain, low terrace, high terrace, hill slope). At the next smallest scale, alluvial landforms of varying height above the channel mediate the impact of fluvial disturbance on riparian zones, influencing the vegetative composition and the production of LWD. Integration of these biophysical factors across all scales, with the disturbance regime, determines channel type and channel configuration.

The same interactions operate in larger streams but, as was briefly described earlier, LWD becomes uniquely important in creating suitable sites for colonization by riparian plants in alluvial rivers. Riparian forest "islands" become established in association with accumulations of LWD, which act as refugia for plant propagules and protect against scour. As the vegetation grows over time, the islands increase in size and coalesce with other LWD-associated islands, forming a forest mosaic on the floodplain (Fetherston et al. 1995). Individual forest islands can grow rapidly at more than 500 m^2/year. What appears to be a large, homogeneous riparian forest patch formed at one time may actually consist of numerous smaller patches that coalesced over a relatively short time.

The interaction among the riparian forest, the channel, and the initiation of new riparian forest patches involves several steps (Figure 9). These include the deposition of one or more pieces of LWD of sufficient size and durability to establish debris jams, the colonization of vegetation either on the wood or on sediment deposited immediately downstream from the jams, and the growth of "islands" as additional sediment accumulates and plants colonize. In low-gradient, alluvial PCE rivers, there is abundant LWD, often more than 160 jams/km having a minimum size of 3 m^2 each (Steel et al. 1999).

Determination of species richness. Disturbance, productivity, and spatial heterogeneity of microenvironments regulate species richness in all plant communities, including PCE riparian zones (Huston 1994, Pollock 1998, Pollock et al. 1998). The high diversity of PCE riparian corridors is related to disturbances caused by floods, to spatial heterogeneity created by debris flows, to lateral river migration, to LWD input, to animal activities, to site productivity and landform, and to variation in local climate as a function of elevation. Collectively, these factors create a mosaic of nonequilibrium habitats of various physical conditions that allow a large number of species to coexist.

Disturbance frequency and moisture gradients play key roles in determining the vegetative composition of riparian areas, and are associated with riparian landform. Distinctive communities occupy floodplain, low-terrace, and high-terrace landforms along smaller channels (Rot et al. 2000). However, no physical factors can explain the vegetative differences between these landforms and adjacent hill slopes, suggesting that biological factors (e.g., competition, herbivory, disease) become increasingly important with small increases in elevation (and decreases in disturbance frequency) from the channel.

Flood frequency and spatial heterogeneity (in the form of topography) are particularly good predictors of plant species richness and even better predictors of plant species composition. Floods destroy habitat patches and create new patches as well as altering competitive interactions in patches that are disturbed but not destroyed. Topographic heterogeneity creates spatial variation in the frequency and duration of flooding. Such differences enable plants requiring different conditions to exist in close proximity. For example, along the Kadashan River, Alaska, interactions between flood frequency and topography explain 80% of vascular plant species richness (SR), 73% of forb SR, 66% of moss SR, and 38% of grass SR (Pollock et al. 1998). Site productivity, in combination with flood disturbances, also results in a variety of riparian communities with different suites of species, explaining 78% of the total SR. Animal activities (e.g., grazing by ungulates, dam-building by beaver) also increase site diversity. Finally, temperature and precipitation limit the distribution of plant species. Riparian corridors pass through most elevations within a watershed, thus encompassing a range of temperatures and precipitation suitable to the needs of the regional plant community.

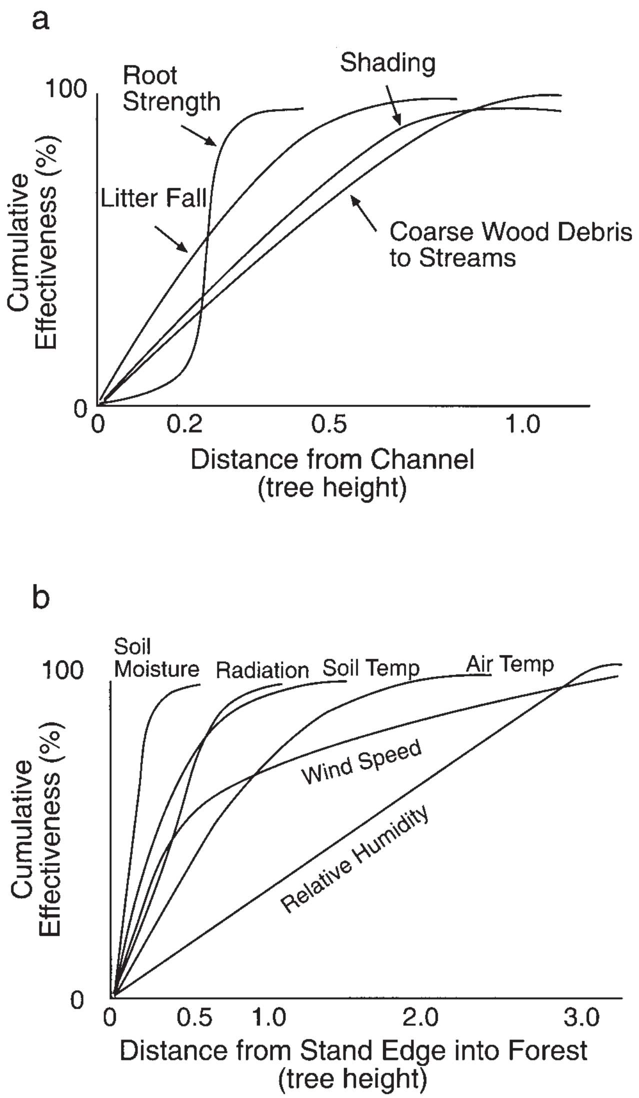

Figure 10. The effectiveness of riparian vegetation in supplying ecological services to the river corridor depends on the height of the vegetation and its distance from the stream edge. (a) Cumulative effectiveness of four riparian processes as a function of relative distance from the edge of a stream, in fractions of a dominant tree height. (b) Cumulative effectiveness is shown for six microclimate factors as a function of relative distance from the stream edge. Modified from FEMAT (1993).

Aquatic and riparian habitat recovery options (NRC 1996)

Strategy		Description
Protection		Preserve riparian areas that are ecologically intact and fully functional. Human activities that significantly impact aquatic and riparian ecological functions are restricted. The strategy is intended to protect aquatic and riparian ecosystems that are in good condition so that naturally regenerative processes can operate.
Restoration		
	A. Passive	Remove anthropogenic disturbances from altered aquatic and riparian ecosystems to allow natural processes to be the primary agents of recovery. Allow the natural disturbance regime to dictate the speed of recovery in areas with a high probability of returning to a fully functional state without human intervention.
	B. Active	Return functionally impaired aquatic-riparian ecosystems to a state that would occur naturally at the site by actively managing certain aspects of habitat recovery. Combine elements of natural recovery with management activities directed at accelerating development of self-sustaining, ecologically healthy riparian ecosystems. Many riparian restoration projects fall into this category.
Rehabilitation		Reestablish naturally self-sustaining riparian ecosystems to the extent possible, while acknowledging that irreversible changes such as dams, permanent channel changes caused by urbanization and roads, stream channel incision, and floodplain and estuary development permit only partial restoration of ecological functions. Combine natural and active management approaches where ecological self-sufficiency cannot occur.
Substitution		
	A. Enhancement	Deliberately increase the abundance or functional importance of selected riparian characteristics as desired. Such modifications may be outside the range of conditions that would occur naturally at a site. The strategy involves technological intervention and substitution of artificial for natural habitat elements. In using this strategy, there is some risk that enhancement may shift riparian ecosystems to another state in which neither restoration nor rehabilitation can be achieved.
	B. Mitigation	Offset habitat losses by improving or creating riparian habitats elsewhere or by replacement of lost habitat on-site. The strategy involves extensive use of technological intervention and replacement of natural habitats with artificially created habitats, and is often employed in highly altered urban/industrial settings.

Microclimate considerations. Riparian forests exert strong controls on stream microclimate, and these considerations have already been incorporated into watershed management plans (Figure 10; FEMAT 1993). However, microclimatic gradients in the riparian forest for air, soil, and surface temperatures, relative humidity, and solar radiation also have important implications for the plant community (Brosofske et al. 1997). Streams significantly influence air temperature in the riparian forest laterally for up to 60 m in summer, either through direct cooling or by supplying water for evaporative cooling by vegetation. Average air temperatures for riparian zones can be several degrees cooler than in adjacent forests. In warmer PCE climates and seasons, an indirect consequence of temperature is the modification of stream discharge through evapotranspiration. Gradual changes in soil temperature and relative humidity from streams to uplands in the PCE also can be detected. Overall, the ecological consequences of many of these important microclimatic gradients and processes represent new research opportunities for understanding observed patterns in biodiversity, biogeochemical cycles, and other system-level processes.

Exotic plant invasions via riparian corridors. The abundance of non-native plants in riparian areas suggests that PCE rivers serve as corridors for exotic species to move through the landscape. More than 50 non-native species are encountered on Washington's Olympic Peninsula, including perennial ryegrass (*Lolium perenne*), buttercup (*Ranunculus* spp.), common sowthistle (*Sonchus oleraceus*), and sheep sorrel (*Rumex acetosella*). Exotic plants provide 25–30% of the species richness in riparian forests of the southern portion of the PCE, but the vegetative cover of exotic plants is often greater than 75% (DeFerrari and Naiman 1994, Planty-Tabacchi et al. 1996).

Surprisingly, some spatial characteristics of the rivers (e.g., proximity to population centers, major highways, or river mouths, or the size of adjacent forest clearcuts) and some environmental variables (slope, aspect, and elevation) are not correlated with the number or cover of exotics in the PCE (DeFerrari and Naiman 1994). What is important is the place where the plant propagules are deposited—that is, whether it is a cobble bar, alder flat, upland forest, or another patch type. However, the large variation in the number and cover of exotics for individual habitats may obscure important factors related to understanding why invasions of exotic plants succeed. Nevertheless, highly disturbed areas, such as riparian zones, forest clearcuts, farm fields, and roadsides, harbor the greatest number and cover of exotics. Where succession is allowed to proceed to a coniferous forest (as opposed to a deciduous forest that receives more light in winter), the number and cover of exotic plants decrease upon canopy closure (at about 10–15 years), although a few exotic species may persist.

Hyporheic dynamics linked to riparian processes. The hyporheic zone, a critical component of streams that has strong links to riparian vegetation, is the saturated sediment beneath a river channel and under the riparian zone that contains some proportion of water from the surface channel (Figure 11). In the hyporheic zone, groundwater and surface water mix, blending properties of both. The mixing of these water masses, which differ significantly in origin and chemical composition, stimulates biological activity (Bencala 1984, Edwards 1998). For example, streams with extensive hyporheic zones retain and process dissolved nutrients more efficiently than those without. Moreover, decomposition in hyporheic habitats easily can double the ability of streams to eliminate organic wastes.

Fundamental characteristics. Hyporheic zones are important to PCE rivers because of their relatively large interstitial volume and surface area, as compared with the overlying stream. Hyporheic interstitial volume (habitat volume) estimated from sediment porosity—the proportion of a given sediment volume occupied by air or water—ranges from 25% to 70%, providing a potentially large habitat for hyporheic organisms. A typical stream channel 20 cm deep and flowing over 100 cm of sediment could have 2.5 times as much habitat volume (per unit channel area) in the hyporheic zone as in the surface water itself. In floodplain rivers, where lateral hyporheic zones under the riparian vegetation are large compared with the surface channel area, interstitial volume differences are even greater. For example, the hyporheic area of Montana's Flathead River extends 3 km from the channel (Stanford and Ward 1988). For this system, the estimated hyporheic volume is 2400 times greater than the channel habitat volume. Contrasts in the relative sediment surface areas are equally dramatic. For example, the surface area available for colonization by organisms such as bacteria, fungi, and protozoa is at least 2000 times greater in the hyporheic zone than on surface sediments in a stream 20 cm deep with a bed composed of 2-mm-diameter sand. The large hyporheic surface area is responsible, in part, for the significant microbial influences on water quality.

The intensity of riparian-hyporheic interactions is influenced by factors operating at scales ranging from major geologic factors (i.e., bedrock geology, valley form) to characteristics of individual stream reaches (alluvial, colluvial, bedrock) and channel units (pools, riffles). For example, topography at the reach scale can create extensive subsurface flows parallel to the wetted channel (Triska et al. 1993) or in adjacent floodplains (Wondzell and Swanson 1996a). Flow paths can travel through relic channels (buried paleochannels) underneath the riparian vegetation, sometimes even passing under the wetted channel. At this scale, hyporheic water easily contacts the root zones and soils associated with riparian plants.

On the surface, riparian plants and their products (e.g., LWD) also act as roughness elements that enhance flow into the hyporheic zone as well as trap and store alluvium, effectively increasing the size of the zone. In addition, alterations in riparian LWD inputs change the number of pieces of LWD that are eventually buried, thus affecting the number and distribution of short hyporheic flow paths. Such alterations also affect larger-scale hyporheic flows by changing sediment storage in the reach. Basin-wide changes in sediment supply and retention affect hyporheic zones at a variety of scales by influencing channel morphology and the total volume of saturated sediment. When hyporheic flow paths and water residence times are altered, key biophysical variables such as oxygen concentration, water chemistry, and the quality and quantity of food supplies change.

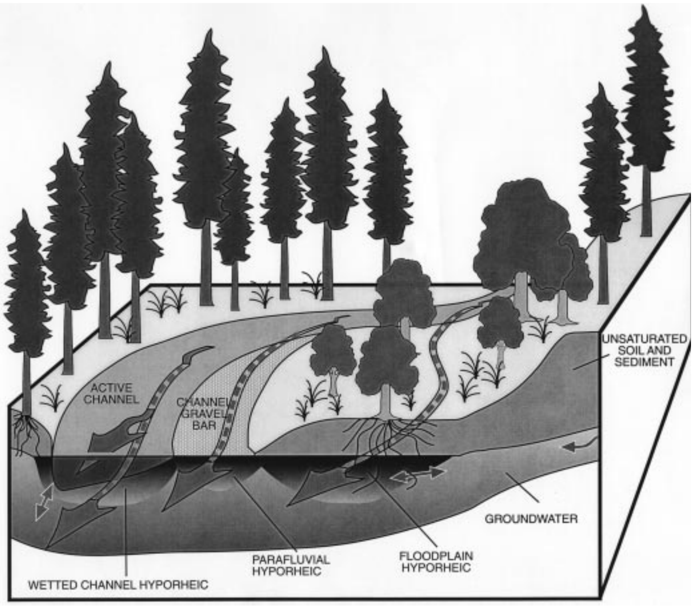

Figure 11. Location of three major types of hyporheic zones beneath and adjacent to a river. Single-ended arrows symbolize subsurface flowpaths. Double-ended arrows indicate mixing with adjacent water masses. Although the three zones are shown as distinct regions, in any catchment, they are connected to varying degrees depending on sediment and hydraulic head characteristics.

Linked hyporheic-riparian biogeochemical processes. In the PCE, nitrogen often limits primary production. In general, riparian zones are thought to be important in regulating nitrogen availability because they effectively remove nitrogen from water entering streams through either direct uptake or denitrification by bacteria (Peterjohn and Correll 1984). However, some PCE riparian forests may act as nitrogen sources rather than nitrogen sinks. Bacteria (*Rhizobium* spp.) growing in the roots of red alder fix large amounts of nitrogen in excess of the tree's growth needs (Cole et al. 1990). Consequently, large pools of organic and inorganic nitrogen accumulate in the associated riparian soils. Increased hyporheic nitrogen concentrations and hyporheic-stream nitrogen transfers have been reported from three PCE streams (Triska et al. 1989, Wondzell and Swanson 1996b, Bechtold 2000). However, some soil nitrogen may be lost via denitrification in the hyporheic zone.

Where stream communities are limited by nitrogen availability, inputs from hyporheic zones significantly influence primary and secondary production. However, the spatial distribution of enhanced production is patchy, and it, too, may be controlled by riparian forest characteristics. In the Queets River, Washington, hyporheic transfers of alder-derived nitrogen are spatially variable because of the pattern of alder colonization in the floodplain forests (Fevold 1998). The interaction between the patchy distributions of alder, soil nutrients, and variable hyporheic flows beneath the floodplain forest creates a spatially complex three-dimensional pattern of hyporheic nutrients flowing laterally into the channel (Ritzenthaler 1998, Bechtold 2000). Visible algal mats are concentrated at sites of hyporheic water inputs, which have up to seven times the mass of algae at other stream sites.

In alluvial rivers, hyporheic flow paths more than 10 m long frequently occur beneath the floodplains, which are overlain by productive riparian forests. Preliminary data suggest that the downward transport of dissolved organic matter leached from overlying soils may be more important to hyporheic microbes than material entrained within downwelling river water (Bechtold 2000). Movement of riparian soils into the hyporheic zone is influenced by vegetation type, soil decomposition dynamics, and chemical partitioning along the flow path. Organic matter supply may be seasonal where the overlying vegetation is deciduous. Thus, hyporheic microbial communities appear to be sensitive to changes in riparian forest vegetation resulting from successional dynamics, floods, or riparian land use where the composition of the vegetation is altered.

Animals use and shape riparian corridors. Riparian zones exhibit high diversity of wildlife species because of habitat they provide for obligate riparian species, species seeking edge habitat, and species associated with early successional plant communities. Approximately 29% of PCE wildlife species are riparian obligates (depending on riparian and aquatic resources and experiencing severe population declines when riparian forests are removed; Table 1). Riparian communities also support riparian generalists (species that use both riparian and upland habitats) and exotic species, provide refuge for upland species whose habitat experiences major disturbances such as clear-cutting or fire, and function as topographic landmarks to visually cue species during migration or dispersal (Kelsey and West 1998).

The composition of riparian wildlife communities is influenced by two important gradients. First, riparian obligates depend on certain habitat characteristics associated with stream size: The riparian communities that large rivers support differ greatly from those associated with small streams. Second, wildlife species respond to habitat characteristics associated with forest successional stage that is largely determined by the type, frequency, duration, and severity of disturbance. For example, species richness and abundance of spring breeding birds are significantly greater on larger rivers than on small rivers of the Olympic Peninsula, Washington. The pattern is positively correlated with the percentage of deciduous trees at a site or with the juxtaposition of hardwood and coniferous species (Lock and Naiman 1998). Likewise, the presence and distribution of LWD piles in riparian zones has a positive influence on avian community diversity as well as on the species richness and abundance of small mammals (Steel et al. 1999).

Historically, animals have been viewed as passive components of riparian ecosystems, merely responding to the local conditions. In many cases, however, animals are responsible for biogeochemical, successional, and landscape alterations that may persist for centuries (Butler 1995, Naiman and Rogers 1997). For example, in riparian zones, the numbers of animals and the abundance and quality of food vary constantly but irregularly in time and space. These variations are connected with variations in abundance of some animals and have indirect effects on the abundance of others, thereby affecting system-level characteristics. For example, selective foraging by some large mammals (e.g., beaver, *Castor canadensis*, and elk, *Cervus canadensis*) changes plant species composition, nutrient cycling rates, and soil fertility. Selective browsing by deer and elk on hardwood species and certain conifers (e.g., western redcedar, *Thuja plicata*) allows unbrowsed or lightly browsed conifers (e.g., Sitka spruce, *P. sitchensis*, and western hemlock, *T. heterophylla*) to dominate the PCE landscape (Schreiner et al. 1996). The ecosystem-level consequence of this browsing is an increase in the relative abundance of conifer litter, which depresses the availability of soil nitrogen—often the limiting nutrient in coastal rain forest ecosystems. Furthermore, the foraging strategies of browsers may result in the creation of riparian and terrestrial vegetative communities distinct in composition, density, and distribution that, over the long term, affect browser population density and survival.

An interesting example is provided by Pacific salmon (*Oncorhynchus* spp.), which traditionally have been viewed primarily as products of their aquatic habitats. However, anadromous salmon play a key role in the nutrient and trophic dynamics of both aquatic and riparian ecosystems (Kline et al. 1994, Bilby et al. 1996, Ben-David et al. 1998). More than 95% of the body mass of Pacific salmon is acquired in the ocean, but this material is transported and deposited in the freshwater habitats in which salmon spawn and die. The significance of this nutrient and organic matter subsidy has long been recognized in sockeye salmon lakes (Juday et al. 1932). However, until recently, little quantitative information was available on the contribution of salmon-derived nutrients to riparian corridors.

Transfer of salmon-derived nutrients from the stream to riparian areas occurs by three processes (Ben-David et al. 1998). First, elevated flows transport and deposit carcasses in the riparian area where they decompose and make their nutrients available to plants. Floods are common when salmon are spawning in many streams in the PCE. Second, dissolved nutrients from the carcasses carried in stream

Table 1.[a] Numbers, by taxonomic class, of native riparian obligate and upland species compared with the total number of native species in the Pacific Coastal Ecoregion.

Riparian obligates	Upland specialists	All species	Riparian obligates	(%)[b]
Amphibians	18	7	30	60
Reptiles	3	12	19	16
Birds	78	93	231	34
Mammals	13	31	107	12
Total	112	143	387	29

[a] From Kelsey and West (1998).

[b] The proportion of riparian obligates to all species is shown in this column.

water may enter the hyporheic zone beneath the riparian area. This makes the salmon-derived nutrients available to riparian vegetation via root uptake. Third, piscivorous predators or scavengers may remove salmon from the stream and carry them to the riparian area, where they are consumed or cached for later use. Subsequent deposition of waste products by these animals can distribute salmon-derived nutrients at great distances from the channel.

Stable isotope analysis has permitted direct quantification of the proportion of salmon-derived nutrients in stream and riparian ecosystems. Spawning salmon are enriched with the heavier isotopic forms of nitrogen and carbon (15N and 13C) acquired in the marine environment relative to nitrogen and carbon from other sources. As a result, the proportion of nitrogen or carbon from salmon in aquatic and riparian plants and animals can be determined.

In western Washington and southeastern Alaska, nitrogen derived from the carcasses of salmon often constitutes a substantial proportion of the nitrogen in the foliage of riparian plants. Bilby et al. (1996) report that 18% of the nitrogen in the foliage of western hemlock (*T. heterophylla*), devil's club (*Oplopanax horridum*), and salmonberry (*Rubus spectabilis*) growing within 5 m of a small stream in Washington is derived from spawning coho salmon (*O. kitusch*). Examination of the spatial distribution of salmon-derived nitrogen in riparian ecosystems on Chichagof Island, Alaska, also reveals that 18%–25% of the nitrogen is of marine origin (Ben-David et al. 1998, James Helfield and Robert J. Naiman, University of Washington, unpublished data). The lateral extent of nitrogen deposition varies by site and plant species and is influenced by the presence of piscivorous predators and carcass scavengers. Blueberry fruit (*Vaccinium* spp.) and Sitka spruce (*P. sitchensis*) seeds found more than 50 m from the channel exhibit a lower nitrogen isotope ratio than samples found closer to the stream, indicating lower levels of salmon-derived nitrogen. Devil's club fruit contains elevated levels of salmon-derived nitrogen up to 200 m from the channel.

A large number of riparian vertebrates use salmon as a food resource. Cederholm et al. (1989) found over 22 species of mammals and birds consuming salmon carcasses along streams on Washington's Olympic Peninsula, and over 40 species have been found to forage on salmon in southeast Alaska (Willson and Halupka 1995). In Alaska, plants near sites with evidence of fish-eating predators or scavengers exhibit nitrogen-stable isotope values comparable to those seen at the stream edge for all plant species except skunk cabbage (*Lysichitum americanum*; Ben-David et al. 1998). This indicates that animals play an important role in the lateral transport of salmon-derived nutrients. The net result of the increased nitrogen availability is that riparian trees grow faster and reach larger sizes at a given age than their upslope counterparts, and thereby contribute larger pieces of woody debris to the stream channel at an earlier age. Along salmon streams, it takes Sitka spruce 86 years to reach 0.5 m diameter, whereas it takes 307 years along nonsalmon streams (James Helfield and Robert J. Naiman, University of Washington, unpublished data).

Management implications for riparian zones

Recent discoveries about the structure and dynamic of riparian zones have extended the scope of understanding about this portion of the landscape and have important implications for stream and watershed management. The last decade has witnessed dramatic changes in the management of riparian zones in the PCE that have been driven by new understandings of riparian processes. The condition of riverine habitat is closely linked with the integrity of riparian zones, and stream habitat restoration proposals are beginning to take into account many of the dynamic processes discussed in this paper (Reeves et al. 1995, Bisson et al. 1997). This example illustrates the recognition of the role of periodic natural disturbances in the establishment of desired future conditions within watersheds.

The administrative paralysis accompanying the 1991 and 1992 court injunctions against logging federal forests in the range of the northern spotted owl (*Strix occidentalis*) prompted the President's Forest Conference in 1993. A major outcome was the formation of an interdisciplinary scientific group, the Forest Ecosystem Management Assessment Team (FEMAT), charged with helping to develop plans for both the long-term health of PCE ecosystems and human socioeconomic systems. The plans were to be scientifically sound, ecologically credible, and legally responsible, and to yield sustainable timber harvests while incorporating habitat protection for salmon, spotted owl, and other important species. One outcome of this effort was an aquatic conservation strategy (Sedell et al. 1994).

This strategy established interim buffer requirements intended to ensure the long-term viability of aquatic and riparian species on federal lands within the range of the spotted owl. The interim buffer width was set at the height of a dominant riparian tree. However, implementation of such a system of streamside buffers in landscapes with high drainage densities would, in practice, create a spaghetti-like network of riparian reserves that would not resemble natural forest landscapes and in which other activities, such as timber harvest, would be operationally difficult. The understanding that developed over the last decade of natural watershed processes creating a mosaic of riparian conditions (Benda et al. 1998) provided the basis for applying a novel management paradigm. The FEMAT scientists therefore recommended that watershed assessments be carried out as part of the management planning process and that their results be used to tailor management activities to the unique characteristics of individual watersheds.

Figure 12 illustrates, for example, how natural disturbance regimes were used to develop a landscape management plan for the 7600-ha Augusta Creek watershed, which drains to the McKenzie River in western Oregon (Cissel et al. 1998). Plant, soil, water, and fire specialists identified the locations and histories of the dominant disturbance agents in the watershed—fires and landslides (Figures 12a and 12b). Based on the frequency and extent of wildfires and landslides, a system of reserves was identified that would provide essential riparian functions for fish and wildlife while permitting extended timber rotations (prolonged periods between logging) in the remainder of the watershed. Tree retention levels were based on the natural disturbance regime (Figure 12c). Parts of the watershed prone to landslides were placed in reserves so that when landslides occur, LWD would be included with the coarse sediment delivered to stream channels, thereby creating complex fish habitat. Hillslope forests would be managed to simulate the effects of the historic size, frequency, and severity of wildfires. In areas with stable soils, riparian zones would be managed according to the prescriptions for adjacent hill slopes to promote development of plant communities that would occur at the sites naturally.

This approach illustrates how recent advances in understanding riparian processes and landscape dynamics can be applied to difficult management issues. Tailoring the buffers and timber management activities to the disturbance history of the watershed results in a landscape-based plan that is designed to promote development of natural forests and healthier riparian zones. Maintaining the natural disturbance regime is central to restoring diverse and productive aquatic ecosystems in the PCE (Reeves et al. 1995, Bisson et al. 1997). The use of disturbance history information during watershed assessment therefore facilitates a landscape plan that is compatible with both conservation objectives and human uses.

The improved understanding of riparian ecology also played a role in the development of the concept of the "normative" river. Stanford (1997) and Williams et al. (1999) emphasized the need to conserve, stabilize, enhance, and restore aquatic and riparian ecosystems to a "normative" condition. This does not necessarily imply pristine, since it is often impossible to restore watersheds to a state without anthropogenic disturbances, but does imply the restoration of ecosystem connections that permit as many natural processes as possible, given other social and economic objectives. The normative river approach has been suggested recently as an alternative to current measures to restore fish and riparian wildlife in the Columbia River basin (Williams et al. 1999)—a large, highly altered river system where salmon and other native aquatic animals and plants have declined steadily despite costly restoration efforts.

Important principles essential to maintaining or restoring normative conditions (Stanford 1997, NRC 1999) are based in part on new insights into riparian processes:

- *Restoring biophysical properties of riparian zones improves all natural resource values.* This principle recognizes that riparian areas are linked longitudinally and, as a result, must be managed holistically. Active management of riparian zones is far greater in forested headwaters than in urban areas or agricultural floodplains (NRC 1996, 1999). Additional effort to improving riparian conservation over the entire landscape will provide many direct and indirect benefits for fish, wildlife, and water quality.
- *Protecting interactions between surface flows and groundwater is essential to aquatic-riparian ecosystem integrity.* As we have pointed out, recent findings have documented the importance of hyporheic areas to the productivity and community structure of riverine and riparian ecosystems (Edwards 1998). Removal of water from alluvium and locations where aquifers pass close to the surface, or disrupting the downwelling of surface water into hyporheic zones, truncates the exchange of water and nutrients between surface flows and groundwaters, with serious consequences for aquatic and riparian biota.
- *Allowing streams and rivers to migrate laterally is necessary for habitat development.* Lateral channel movements foster essential interactions between streams and their valley floor and create a biologically rich and diverse environmental mosaic. The importance of this process has been emphasized by recent research showing the important role channel migration plays in maintaining diversity and productivity in riparian forests (Fetherston et al. 1995, Pollock et al. 1998). Without the environmental heterogeneity created by river meandering, river and riparian habitats in alluvial valleys become highly simplified. Throughout the twentieth century, there has been a concerted effort to

straighten and simplify channels to improve river transportation, speed flood runoff, and prevent encroachment of rivers onto developed lands. Such efforts have resulted in the loss of many aquatic and riparian habitats in the PCE and elsewhere throughout the developed world. In several locations in the PCE, dikes and levees are being breached to facilitate reconnection between rivers and their floodplains and reclaim lost habitats, and partial or complete removal of several dams is being considered.

- *Incorporating natural flow regime characteristics in regulated rivers promotes aquatic and riparian diversity and resilience.* Water flows that more closely approximate the natural seasonal and daily cycles of flow provide the hydrologic pattern to which native plant and animal communities are adapted (Poff et al. 1997). River regulation is now beginning to include seasonal flooding that is essential to creating and maintaining healthy floodplains, to flushing accumulated sediment from channels, and to rebuilding gravel bars. Reduction or elimination of fluctuating base flows caused by hydroelectric "load following" or periodic dewatering for irrigation creates biologically sterile zones along the margins of streams and streambanks.
- *Control of exotic species depends on reestablishing natural land-water interactions in riparian areas.* Designation of reserves for remaining intact assemblages of native plants and animals (Moyle and Yoshiyama 1994, Sedell et al. 1994) and eradication of unwanted exotic species where feasible are valuable recovery strategies. But improvement of riparian ecosystem functions—including flooding, restoring surface and groundwater exchanges, and removal of anthropogenic disturbances such as grazing, timber harvesting, and roads—often reduces the need for frequent, expensive exotic species control measures or habitat substitution projects.

Conclusions

Riparian communities are now being managed for a wider variety of ecological functions than ever before, and their role in governing watershed "goods and services" has been given greater importance in regulatory frameworks. Four trends are emerging in riparian management: an emphasis on ecological function and natural riparian forest pattern, adoption of a landscape perspective of river networks, development of ecologically sound systems of restoring riparian ecosystem properties, and attention to social needs for riparian resources (Gregory 1997). As the need for riparian protection and restoration is increasingly accepted, these trends will become focal points around which conflicts among competing uses of riparian zones can be resolved.

Each of these trends has been integrated into the planning and implementing of riparian management in the PCE. Nevertheless, a large discrepancy remains in the application of riparian management strategies across different types of land use: Portions of the landscape subject to forest management receive the most riparian protection, whereas conservation of riparian zones in developing urban and industrial areas is usually limited to narrow borders along streambanks. Additionally, restoration of highly altered riparian communities in heavily urbanized environments is often constrained by pavement and other structures that prevent reestablishment of natural functions. Riparian zones in agricultural lands usually receive an intermediate level of protection between those given forested headwaters and urbanized floodplains. On a broad geographic scale, this situation has resulted in a highly fragmented condition in many PCE watersheds where islands of "healthy" riparian ecosystems are separated by long reaches of altered, dysfunctional river corridors. Building a network of functional, intact riparian zones to reconnect these remaining areas within ecologically healthy watersheds remains one of the most significant challenges for natural resource management in the twenty-first century.

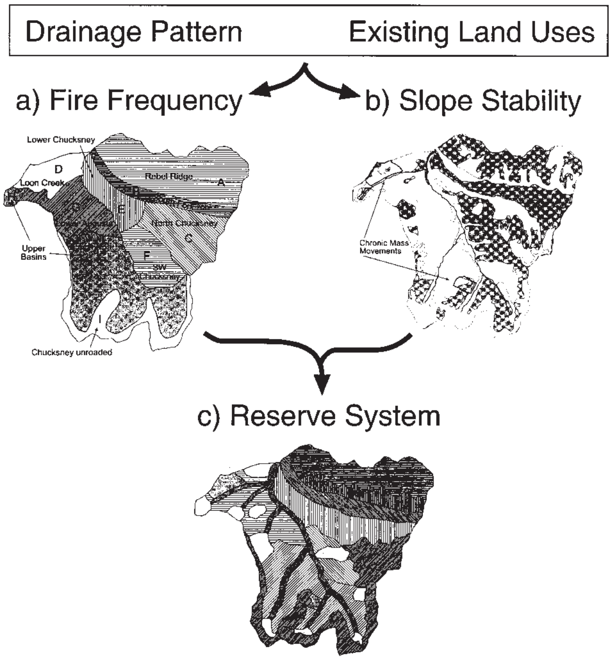

Figure 12. Landscape management plan for the Augusta Creek, Oregon, watershed. (a) The historical fire regime. (b) Vulnerability of the watershed to mass soil movements. (c) Suggested watershed management plan that simulates a natural disturbance regime yet accounts for existing land uses. Modified from Cissel et al. (1998).

Acknowledgments

We thank Estelle Balian, Mark Brinson, Rebecca Chasan, Henri Décamps, Scott R. Elliott, Jack A. Stanford, Fred Swanson, and Monica G. Turner for comments on the manuscript. Research support by the Andrew W. Mellon Foundation, Pacific Northwest Research Station of the US Forest Service, and the National Science Foundation is gratefully acknowledged.

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