14

Origins, Patterns, and Importance of Heterogeneity in Riparian Systems

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Abstract

Riparian systems epitomize heterogeneity. As transitional semiterrestrial areas influenced by water, they usually extend from the edges of water bodies to the edges of upland terraces. Riparian systems often exhibit strong biophysical gradients, which control energy and elemental fluxes, and are highly variable in time and space. These attributes contribute to substantial biodiversity, elevated biomass and productivity, and an array of habitats and refugia. Focusing on riparian systems of medium-sized floodplain rivers, we describe heterogeneity at multiple space and time scales, illustrate interactions among scales, and propose a conceptual model integrating major system components. We show how climatic and geologic processes shape an array of physical templates, describe how disturbances redistribute materials, and illustrate how soils and subsurface processes form and are sustained. Collectively, these processes strongly influence plant productivity and fluxes of channel-shaping large woody debris (LWD). Ultimately, riparian ecosystem function integrates climate (past and present), geologic materials and processes, soil development and attendant microbial transformations, subsurface characteristics, plant productivity, animal activities, and LWD—and the active, continuous and variable feedbacks between the individual components.

Introduction

Riparian communities respond continuously in time and space to a complex array of hydrologic (e.g., water regimes, hydraulic shear stress, sediment deposition, erosion, deposition of large woody debris) and biotic (e.g., animal activities, plant production, microbially mediated nutrient cycling) influences. The resulting mosaic of riparian subcommunities are composed of species with contrasting life history strategies that moderate downstream fluxes of water, materials and energy —and fundamentally influence nutrient and organic matter dynamics. Collectively, the biophysical processes support numerous types of aquatic, semiaquatic, and terrestrial food webs, resulting in high biodiversity. Indeed, riparian systems appear to be sites of focused storage and dissipation of materials and energy within the larger, regional landscape. They are likely "hotspots" for regional heterogeneity owing to the inherently dynamic and nonlinear processes linking the flux and retention of water and materials to interactive landscapeforming processes (Benda et al. 1998; Naiman et al. 1998).

Riparian systems provide an unusually rich array of lessons on the origins, patterns, and ecological importance of biophysical heterogeneity. Heterogeneity is manifested in a diverse array of landscape elements and processes operating on several spatial and temporal scales. These include longitudinal, lateral, and vertical gradients in geomorphic features (e.g., gravel bars, terraces, islands), surface and subsurface flows of water and nutrients, and disturbance regimes (e.g., floods, drought, fire, wind). Fluvial actions (e.g., erosion, transport, deposition) are the dominant agents of riparian change and constitute one suite of the natural disturbance processes primarily responsible for sustaining the high level of heterogeneity (Poff et al. 1997; Ward et al. 2002). It is the hydrologic connectivity—the flux of matter, energy, and biota via water—in combination with animal activities (Naiman and Rogers 1997), microbial processes, and vegetation dynamics that largely sustain riparian heterogeneity. Although individual features such as a specific vegetative patch type may exhibit dynamic transitions fueled by interactions between fluvial dynamics and plant succession, their relative abundance within a catchment tends to remain in quasiequilibrium over decades to centuries. In general, riparian systems are highly heterogeneous, as well as central nodes for biodiversity, for energy and elemental fluxes, and for elevated biomass and productivity. Throughout a catchment, riparian systems exhibit strong biophysical gradients, high variability in time and space, and provide a diversity of habitats and refugia (Naiman and Décamps 1997; Naiman et al. 2005).

This chapter describes riparian heterogeneity at multiple scales of space and time, illustrates interactions among the scales, and offers a conceptual model integrating the major ecosystem components. We accomplish our objectives by showing how climatic and geologic processes shape physical templates, and by illustrating how soils and subsurface processes form and are sustained on the major physical templates. We then discuss how the latter processes influence biodiversity and plant productivity and, ultimately, the generation of channel-shaping large woody debris (LWD) and the disturbances driving fluxes of LWD from the forest to streams. Integration at the ecosystem scale is accomplished through a conceptual model relating climate, geology, soils, subsurface characteristics, plant productivity, and LWD with the active, continuous, and variable feedbacks between the individual components. Examples herein draw heavily on lessons we have learned from mid-sized alluvial rivers draining the rainforests of the North American

Pacific Coastal Ecoregion. Riparian heterogeneity in other regions may differ from our examples, at least in form and function. Likewise, examples presented here may not accurately represent the nature of riparian areas transformed by human activities. Nevertheless, we believe that fundamental principles governing the vitality and heterogeneity of riparian systems are similar.

Setting the Stage: Geologic and Climatic Processes

Riparian heterogeneity is a product of history. Geology, topography, climate, vegetation, and animals interact to create and maintain physical and biological heterogeneity over the full spectrum of time and space. Geological and biological legacies of long-term climate cycles persist at many scales and have lagged effects. For example, lithotopography (geological parent material and landforms) is a legacy of the distant past, while disturbances such as floods and fires produce effects that have immediate impacts but also may be expressed for centuries. The legacies of geology, climate, and biogeography shape riparian heterogeneity—including soil processes, subsurface flows, forest biodiversity and productivity, and the dynamics of LWD.

Geologic History

Coarse-scale heterogeneity is produced in riparian systems by parent material and landforms. Lithotopography places basic constraints on riparian assemblages and their heterogeneity: elevation, exposure, slope, groundwater dynamics, and parent material fundamentally shape system processes. The geology of tectonically active regions is especially complex, resulting in patchy distributions of parent material that strongly influence development of soils and biota (Figure 14.1A)—and the resulting topography interacts strongly with climate to influence weather patterns (Figure 14.1B). Ultimately, geologically driven heterogeneity is expressed in the character of stream corridors and their biota, as disturbance regimes change with channel geomorphology and climate (Vannote et al. 1980; Benda et al. 1998). These patterns are fully reflected in the biophysical heterogeneity of riparian zones (Figure 14.2) and are easily illustrated in large river basins such as the Amazon where the geology of mountainous headwaters exerts strong controls on downstream environments (e.g., McClain and Naiman 2005).

Although many geological processes operate over long time periods and large scales (e.g., formation of floodplains), important examples of decadal-scale geomorphic processes include sediment accumulations and avulsions, landslides, vertical channel adjustments, and debris flows (Montgomery and Buffington 1998). Medium to large river corridors are generally long-lived geologic features that exist in a quasiequilibrium where the lateral channel movements within floodplains maintain successional and geofluvial

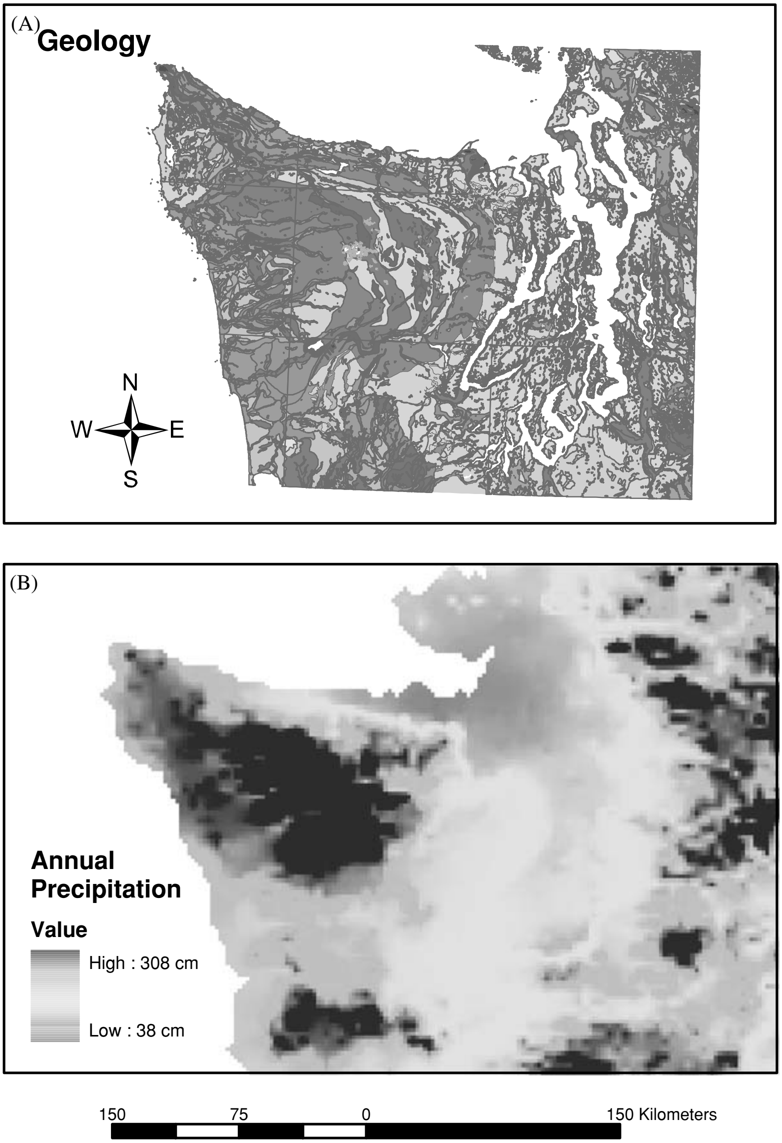


FIGURE 14.1. (A) The underlying geology of Washington's Olympic Peninsula illustrates the complexity of parent materials over macro and meso spatial scales. More than 600 geological formations are present (only a few major formations are represented here; color image available at (http://www.fish.washington.edu/people/naiman/cv/reprints/naiman_2004_cc/02_geology_precip_map.pdf). Adapted from Washington State Geospatial Archive (http://wagda.lib.washington.edu). (B) Total annual precipitation on the Olympic Peninsula is strongly influenced by topography, varying from only 38 cm/yr in the rainshadow of the northeastern peninsula to 308 cm/yr on the Pacific Coast (© 2000–2003 The Climate Source, http://www.climatesource.com).

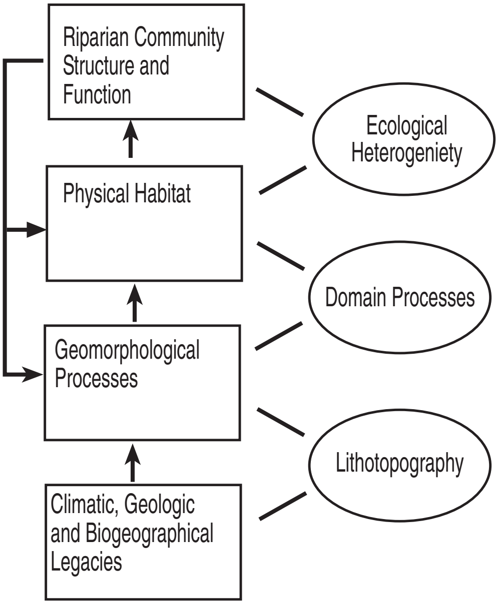


FIGURE 14.2. Schematic representation of relationships between drivers of ecological heterogeneity in riparian forests (from Naiman et al. 2000 Copyright, American Institute of Biological Sciences).

heterogeneity. However, at the catchment scale, riparian community structure and dynamics reflect the nature of catchment-scale variation in discrete disturbance regimes, or *process domains* (Montgomery and Buffington 1998).

Climate

It is well-known that large-scale climate fluctuations during the Quaternary drove the development of modern geomorphic features and plant assemblages (Davis 1981). In North America, at least 15 glaciations carved high-latitude landscapes, lowered sea levels, and dramatically altered the distributions of plants and animals. Conspicuous glacial features of modern riparian systems include terminal and lateral moraines, glacially carved river valleys filled with outwash, lake systems, and distinctive fluvial topographies caused by catastrophic glacial floods (e.g., the Red River Valley of Minnesota and the Channeled Scablands of eastern Washington). Lower latitude landscapes were also shaped by the cooler and wetter climate of Pleistocene glacial periods (e.g., the basin-and-range province of southwestern North America).

However, climate cycles also operate at relatively high frequencies. Examples include the El Niño Southern Oscillation (ENSO) with a 5–7 year period (Philander 1990), the Pacific Decadal Oscillation (PDO) which operates on an ~60-year period (Mantua et al. 1997), and the North Atlantic

Oscillation (NAO) at shorter than decadal timescales (Ottersen et al. 2001). These climate cycles influence precipitation patterns, temperature, stream flow, and storm frequency over relatively short scales, which in turn influence the frequency and scale of mass wasting, windthrow, and flooding—which are important drivers of heterogeneity in riparian forests.

Hydrologic regimes vary considerably even with relatively subtle climatic changes; for example, in the Pacific Northwest, average winter El Niño surface temperature are 0.4 °C to 0.7 °C higher than La Niña temperatures. Warmer winter temperatures result in lower snowpack and earlier hydrographic peak flows in El Niño years (University of Washington, Joint Institute for Study of the Atmosphere and Ocean, Climate Data; http://tao.atmos.washington.edu/PNWimpacts). Collectively, the physical drivers, along with temperature-regulated biological processes (e.g., decay rates and plant growth) shape the ecological properties of riparian systems, clearly demonstrating the strong influences of climate and climate change on heterogeneity.

Climate gradients and fire regimes are additional sources of riparian heterogeneity. Climate-driven heterogeneity resulting from sharp precipitation gradients are seen where dominant weather patterns intercept elevated landforms. For example, precipitation on Washington's Olympic Peninsula (Figure 14.1B) varies from 308 cm/yr of largely orographic precipitation on the west side of the Olympic Mountains to only ~38 cm/yr in the rainshadow of the Olympics—a linear distance of 130 km. Fire regimes are correlated with climate-related heterogeneity in riparian systems (Agee 1993). But fire, which can dictate nutrient cycling and forest succession dynamics, also affects erosion and sedimentation processes (Wondzell and King 2003). Wildfires burn even in very wet coastal temperate rainforests, albeit not at a high frequency. In British Columbia's Clayoquot River catchment (~554 cm/yr of precipitation) nearly all exposed, south-facing slopes within 1 km of the river burned in the past 800 years with only ~20% of all sites remaining unburned over the 6000-year history (Gavin et al. 2003). At small scales, fire can result in decreased habitat heterogeneity (e.g., as seen in substrate embeddedness and near-bed velocities; Minshall et al. 1989, 1997), whereas at larger scales, fire is an important natural source of heterogeneity playing a crucial role in creating and maintaining aquatic diversity (Bisson et al. 2003).

Biotic Responses to Geologic and Climatic History

Perceptions of heterogeneity are frequently based on vegetation, which is easily observed, sessile, and has an air of permanence. In reality, plant distributions are plastic and respond to geomorphic substrate (e.g., Gregory et al. 1991), changes in climate (Davis 1986), pressure from herbivores (e.g., Naiman and Rogers 1997), distributions of pollinators (e.g., Cox and Elmqvist 2000), and competition from other plants (e.g., DiTomasco 1998). Early successional riparian plants, in particular, are generally adapted to flooding, which facilitates reestablishment after disturbance (Naiman et al.

2005); succession after flooding illustrates a familiar manifestation of vegetative heterogeneity. As the riparian assemblage develops, it affects soil formation and fertility and helps control erosion. This is well illustrated in a recently deglaciated river valley in Glacier Bay, Alaska, where it took only ~100 years for woody vegetation to stabilize stream banks and provide points for LWD accumulation. The increased LWD retention and bank stabilization led to pool formation and improvement of fish habitat within 150 years (Sidle and Milner 1989).

Life history traits such as long-term seed dormancy, N-fixation in some early successional species, physiological adaptations to inundation, and water-borne dispersal of propagules allow riparian plants to thrive in heterogeneous and frequently disturbed environments (Naiman et al. 2005). Many riparian plants are specifically adapted to cope with flooding, sediment deposition, physical abrasion, and stem breakage (Blom et al. 1990; Mitsch and Gosselink 1993; Naiman et al. 1998). By the nature of their heterogeneity, riparian systems may support a greater diversity of organisms and life-history strategies than surrounding upland forests.

In summary, patterns of geology and climate interact with biological components of riparian systems to produce characteristic patterns and feedbacks in soils, hyporheic zones, plant communities, and woody debris processes. We now turn to a discussion of riparian system patterns and processes and their relationships to heterogeneity, drawing primarily on themes and examples from our research on forested small- to mid-sized rivers while fully recognizing that every river has a unique combination of processes, organisms, and conditions.

Heterogeneity in Floodplain Soils

Salient characteristics of riparian floodplains include spatial and temporal heterogeneity resulting from fluvial redistribution of sediments, organic matter, and other materials, as well as temporal heterogeneity in the form of cumulative soil alterations by vegetation. As the primary reservoir of nutrients and carbon, and as a growth medium for plants, soil heterogeneity is reflected in patterns of production, community composition and terrestrial-aquatic transfers of carbon and nutrients.

Complexity in Sediment Distribution

Differences in the mobility of eroded materials lead to depositional patterns observable at multiple scales. Within an overall longitudinal pattern of decreasing particle size with distance downstream, floodplain soils form where hydrologic energy is dispersed in lateral directions, and landforms reflect the energies of stream flows at the time of deposition. Coarse sediments form levees, abandoned and secondary channels, and a variety of bar forms in areas of intense stream flows (Leopold et al. 1964), especially when coincident with roughness elements, such as riparian vegetation or LWD. Elevation of floodplain surfaces occurs in areas subjected to less intense flows. At macro- and mesoscales, depositional patterns are controlled by channel morphology, while at the microscale resistance to flow created by emergent vegetation and LWD can be especially effective at trapping fine sediments (Walling et al. 1996). This sorting also affects the distribution of organic matter and various chemical compounds that become associated with mineral sediments. Both iron and phosphorus are transported in microaggregates of organic matter, silt and clay particles, and tend to concentrate in overbank deposits in alluvial soils (Walling et al. 2000; Rhoton et al. 2002).

The size distributions of sediments in fluvial landforms influence soil nutrient and moisture dynamics in two important ways. First, the complex surfaces of fine sediments provide large amounts of surface area for adsorption of organic and inorganic materials, including organic matter and bioavailable nutrients. Adsorption to mineral surfaces and incorporation within stable aggregates reduces leaching losses (Sollins et al. 1996) and inhibits decomposition (Christensen 1996), contributing to short and long-term organic matter (OM) retention (Raich and Schlesinger 1992; Trumbore 1993). Strong correlations between OM and soil clay and/or silt concentration (Burke et al. 1989; Schimel et al. 1994; Epstein et al. 1997; Hook and Burke 2000) have been measured in a variety of well drained soils. The contribution of this to floodplain heterogeneity is well illustrated by the distribution of silt, clay, and OM in Washington's Queets River soils (Figure 14.3). Soil OM is strongly related to silt and clay concentration in both young and old soils despite large changes in plant production and community composition, suggesting that fluvial deposition of fine particles plays a primary role in the rapid development of OM-rich, productive soils that are characteristic of floodplains.

Soil particle size also affects nutrient and moisture dynamics by determining the size of pore spaces between sediment particles. This influences the movement of liquids and gases—most importantly water and oxygen—through the soil. Coarse soils tend to be droughty and are especially prone to leaching of nitrate (Vitousek et al. 1982) and dissolved organic carbon (Nelson et al. 1993). Anoxic conditions in poorly drained, fine-textured soils reduce decomposition of organic matter, facilitate anaerobic microbial processes, and can lead to accumulation of toxic chemicals (Mitsch and Gosselink 1993). On the Garonne River (France) floodplain, denitrification increases linearly with soil silt and clay content in fine-textured (>65% silt and clay) soils but is not measurable in medium and coarse soils (Pinay et al. 2000). Denitrification may occur more broadly in coarse-textured soils in "microsites," especially where buried wood supports high rates of microbial activity (Jacinthe et al. 1998). A better understanding of the distribution of buried wood in floodplains may be useful in predicting where denitrification is likely to occur.

Spatial variation in soil texture has important implications for growth rates and species compositions of floodplain forests. Fine-textured soils tend to

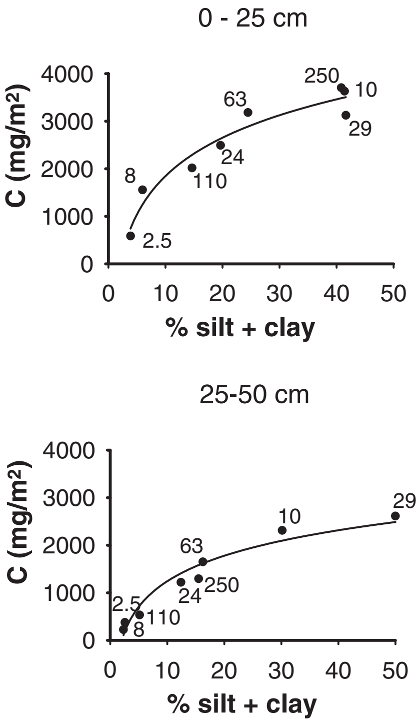


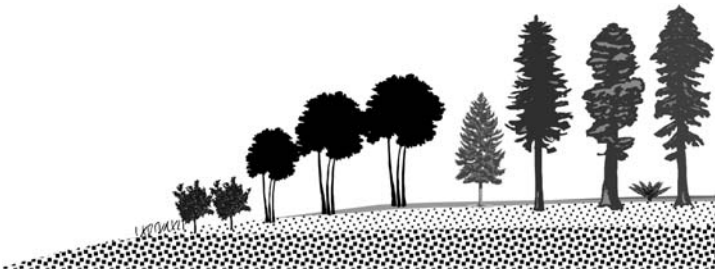
FIGURE 14.3. Correlation of soil C with silt and clay concentration in Queets River floodplain soils ($C = 1163.7 * \ln(\% \text{ silt} + \text{clay}) - 831$; $r^2 = 0.94$, $p < 0.01$). Silt and clay range from 4% to 42% of total soil volume and are well correlated with soil OM throughout the 250-year chronosequence despite large changes in plant production and community composition, suggesting that particle size rather than plant production is the primary factor controlling soil OM retention. Numbers indicate soil patch ages and are not correlated with C or % silt and clay (S. Bechtold and R.J. Naiman, unpublished data).

have higher rates of net N mineralization and primary productivity, which may be reflected in faster within-species growth rates (Reich et al. 1997; Prescott et al. 2000) or species replacements to faster growing species (Pastor et al. 1984). Although the complexity of contributing factors makes it difficult to distinguish causal relations, correlations suggest that primary production is fundamentally influenced by interactions with sedimentary templates (Reich et al. 1997; Prescott et al. 2000); buffering of nutrient and water exchange conferred by fine sediments and associated OM may lead to more efficient cycling through soil-plant pathways and reduced leaching losses.

Landform heterogeneity subsumes many potential influences on soil biogeochemistry besides sediment size. Because floodplain topography is shaped by interactions between water flows, sediments, vegetation, and LWD across a low-gradient environment, fine-scale topographic variation often results in large contrasts in soil properties and access to water. Interaction with ground/hyporheic water is frequently an important influence on soil dynamics. Water table depth in combination with soil/subsoil texture can influence soil moisture and organic matter regimes. Saturated soils in swales and other wetland areas not subjected to scour can become sinks for river-borne OM (Johnston et al. 2001) and phosphorus (Stoeckel and Miller-Goodman 2001) and are often hotspots for denitrification (Groffman and Tiedje 1989; Farrell et al. 1996). In arid environments, evaporation from the surface of bare sediments in areas of shallow ground water may initiate a capillary pump leading to the formation of a salt crust at the sediment surface, inhibiting plant colonization of sediments (Van Cleve et al. 1993). Even where soil moisture is not influenced by ground/hyporheic water, enhanced plant production resulting from root exploitation of subsurface water can enhance soil organic matter inputs (Décamps 1996). The thickness of a soil cap overlying coarse bed sediments can also influence plant production through modification of moisture and nutrient regimes (Binkley et al. 1995).

Stages of Floodplain Evolution

Temporal heterogeneity is illustrated by manifold changes in physical, chemical, and biological properties accompanying riparian system development (Figure 14.4). Evolution of the floodplain landscape begins with the formation of depositional landforms, such as bars and terraces. Terraces form as floodplain elevation increases through aggradation or channel incision, isolating sediments on terraces from surface flows. Terrace formation can occur



	Channel (0-15 yrs)	Floodplain (5-40 yrs)	Terrace (25-500 yrs)
Sediments	Scour/ deposition	Sand/silt/clay deposition	Little or no deposition
Soil OM	Very low	Rapid increase in mineral soil OM	Slow increase in organic layer
Nutrient availability	Low N, Low P	High N, P	Decreasing N, P
pH	High	Low	Low
Export	Low export	High N, Ca, K Low C	Low N, Ca, K

FIGURE 14.4. Idealized floodplain evolution of mid-sized rivers in the Pacific Northwest. Deposition of progressively finer sand, silt, and clay over coarse bed sediments leads to rapid formation of floodplain soils. P-rich silt and clay deposits, N-fixation by red alder, and rapid mineral soil OM accumulation contribute to soil fertility. However, high leaching losses of N and base cations and reduced availability of P moderates nutrient dynamics in older conifer soils on terraces. Organic layer OM accumulates in older conifer patches.

within a few decades in small- to medium-sized rivers with a large sediment supply (Schumm 1977; Richards et al. 1993) and may be especially rapid in forested catchments where LWD contributes to localized aggradation/degradation of the river channel (Montgomery et al. 1996). Isolation of terraces from flooding forms a crucial juncture in the evolution of soils. Although soils continue to undergo gradual pedological alteration relative to the rapid changes that result from fluvial deposition, the distribution of sediments in terraces can be considered a fixed physical template relative to its subsequent influence on soil dynamics. The legacy of channel movement across its floodplain is manifested in a complex mosaic of sedimentary landforms of varying ages. This mosaic includes both highly dynamic components continuously altered by interaction with surface waters and components that have become isolated from surface waters but bear the legacies of past disturbances.

Following deposition, soils undergo alteration via interactions with riparian vegetation. On-site production of soil OM inputs increases rapidly in seral forests, usually reaching a maximum when the canopy achieves full leaf area. N-fixing plants are common colonizers of early successional ecosystems (Walker 1993). In the Pacific Northwest, red alder (*Alnus rubra*) has a profound effect on soils during the first 60–80 years of floodplain development (Bormann et al. 1994). In addition to providing a rich source of N to terrestrial vegetation, large amounts of nitrate are often leached to streams (Bechtold et al. 2003). Soil acidification results from formation of organic acids during decomposition, and is especially strong in conifer forests or where there is a vigorous N-fixer (Johnson 1992). In addition to weathering of primary minerals, this results in displacement of cations from soil exchange sites (Foster et al. 1989; Homann et al. 1994). Although large amounts of P are frequently deposited on floodplains, little is known of its availability for uptake. N-fixation is frequently P-limited (Crews 1993; Vitousek 1999). Although high P availability in new sediments may initially enable high rates of N-fixation, subsequent complexation of P with hydrous Fe and Al oxides as pH decreases could have important influences on both P and N availability.

The end point for floodplain soils is disintegration by erosion. Relative to most upland soils, riparian floodplain soils have limited—and variable—life spans. Estimated 200–2000 year turnover rates of Washington's western Olympic Peninsula river floodplains (O'Connor et al. 2003) maintain soils in early states of pedogenic development. Channel migration is an important control on soil development even in very large rivers. For example, >26% of the lowland Amazon forest is maintained in early successional stages by river migration (Salo et al. 1986).

Interactions Between Patches

Exchange of nutrients across patch boundaries is often an important influence on the biogeochemistry of adjacent areas. Although some exchange may occur between adjoining soil patches, by far the most significant fluxes are from soils to subsurface (hyporheic/ground) waters and between soils and surface waters. Overall, leaching of lithogenic nutrients tends to reduce the productive capacity of soils, and leaching of atmospherically fixed C and N leads to increases in aquatic productivity. As noted above, base cation leaching is driven by soil acidification and is highly responsive to vegetation type. The mobility of many chemical species is influenced by redox reactions. Fluxes of Fe, Mg, S, P, and other elements tend to occur where fine soils, high OM, and/or shallow water tables facilitate the formation of reducing conditions.

Relative to subsurface water, soils are usually rich in C and N. There are large differences in the mobility of different chemical species in soils affecting their transfer to aquatic systems. The physical, chemical, and biological factors controlling these exchanges often vary dramatically between adjacent soil patches. Nitrate will freely move through soils, as well as subsurface and surface waters, where it exists in excess of biotic demand. For example, in Oregon forests, nitrate export is more strongly related to the proportion of entire watershed with red alder cover than to the amount of riparian alder (Compton et al. 2003). Carbon is of particular interest as its availability usually limits groundwater/hyporheic microbial activity and is, by comparison, very abundant in soils (Findlay and Sinsabaugh 2003). Soils tend to be efficient at retaining dissolved organic matter. Sorption dynamics and hydrology play important roles in controlling dissolved organic carbon (DOC) export (Neff and Asner 2001), with coarse soils high in organic content more likely to leach DOC into subsurface hyporheic waters. Direct lateral transfer of DOC from soils immediately bordering streams frequently occurs during elevated stream flows (Boyer et al. 2000).

Many biogeochemical transformations occur primarily along well defined boundaries. The vertical boundary between soils, subsoil sediments, and ground/hyporheic water is of particular interest. Convergence of deeper nitrate-bearing flow paths with a C source, which frequently occurs as groundwater upwells into soils near stream edges, may lead to greatly increased denitrification (Hedin et al. 1998). Where the water table is deeper and does not directly interact with soils, soil leaching leaves an imprint but does not determine hyporheic/ground water productivity.

Hidden Heterogeneity: Hyporheic Processes

The hyporheic zone encompasses saturated sediment below and adjacent to the river channel and represents an interface where surface water mixes with groundwater (Stanford and Ward 1993; Edwards 1998). The hyporheic zone is thus a three-dimensional subsurface component of the riparian landscape, connected to the stream channel (Figure 14.5) and is important because of its large interstitial volume and surface area. Inputs of carbon

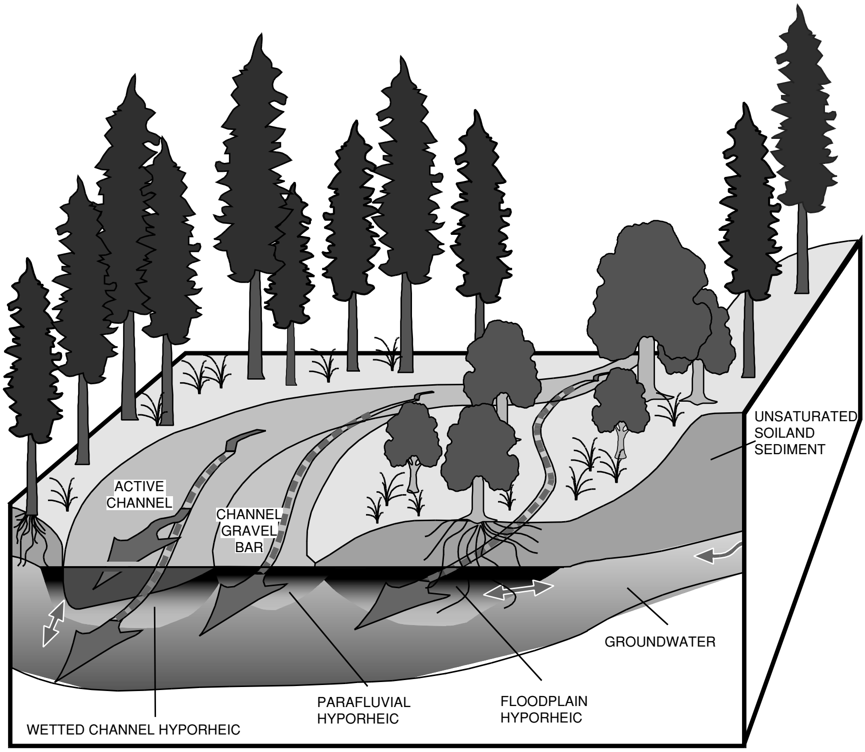


FIGURE 14.5. The hyporheic zone forms the subsurface interface between the river channel and the riparian forest and, in many cases, it modulates the fluxes of water, nutrients, and energy between the river and the riparian soils and vegetation (from Naiman et al. 2000. Copyright, American Institute of Biological Sciences).

and nutrients from upriver, groundwater, and from the overlying riparian soils, along with variable concentrations of oxygen and microbial diversity in the saturated sediments, drive the important microbial and physical processes responsible for nutrient transformations.

This subsurface component of the riparian landscape displays considerable spatial and temporal heterogeneity at catchment, individual reach, and sediment interface levels. Heterogeneity in the hyporheic zone may be manifested in extent and biophysical characteristics, as dictated by agents like parent geology, variation in stream flow, groundwater recharge, and channel changes. Interactions between floods, sediment, LWD, and historical legacies serve as controllers to create heterogeneous patterns of subsurface flow.

To understand what controls spatial heterogeneity in the physical and functional attributes of hyporheic zones, the river's geomorphology must be examined through an historic lens where parent geology and past glaciations play important roles. The amount and rate of exchange between the surface water and groundwater is dependent on local geology, as this establishes the degree of hydraulic conductivity and the water residence time (Valett et al. 1996). In alluvial rivers such as Montana's Flathead River this translates to ~3×10^8 m^3 of hyporheic habitat compared to ~1×10^5 m^3 of channel habitat, with the hyporheic area demonstrating significant heterogeneity relative to the river channel as measured by biophysical characteristics (Stanford and Ward 1988).

The shape and extent of the hyporheic zone exhibits strong heterogeneity over space and time in response to channel movement and alluvial deposition, which control the formation, evolution, and blockage of hyporheic flowpaths. Sediment sorting through fluvial processes stimulated by LWD and other roughness elements and subsequent channel movement results in paleo-channels (i.e., abandoned channels) that become preferential flowpaths for hyporheic flow (Stanford and Ward 1988). As new preferential flowpaths are formed, previous areas of hyporheic activity become increasingly isolated from the active channel. These processes have important functional significance for stream biota—when the proportion of surface water decreases in the hyporheic zone, there is a concurrent change in the interstitial invertebrate community (Marmonier and Chatelliers 1991). Seasonal variation in surface flow is also important in driving the temporal and spatial heterogeneity in the shape and extent of the hyporheic zone. With increasing discharge in winter, the primary flow of water shifts from focused flowpaths to sheet flows throughout the terrace (Clinton et al. 2002). This triggers spatial and temporal heterogeneity in the delivery of nutrients and C, and the oxygen regime (i.e., redox environment) by affecting residence time and interaction with sediment surfaces. These changes in redox play a major role in determining nutrient transformations and subsequently affect microbial production and associated nutrient processing.

Spatial and temporal variability in biogeochemical and physical processes within the hyporheic zone creates heterogeneity in nutrient concentrations, which has important implications for system productivity. Nitrate leaching from overlying soils, delivery to the hyporheic zone, and subsequent emergence of nitrate-rich water from focused subsurface flow paths results in patchy "hotspots" of aquatic primary production (see Fevold 1998; Dent and Grimm 1999). Heterogeneity in nutrient sources, microbial assemblages, and inherent physical characteristics may cause the hyporheic zone to act as either a source or sink for nutrients. The process of denitrification is particularly important because it results in a loss of available N and illustrates the interaction among nutrients, microbes, and physical characteristics of the hyporheic zone. Specifically, hot spots of denitrification arise where overlying soils or an influx of organic-rich stream water provide ample carbon and nitrogen while microbial respiration depletes oxygen resulting in anoxic conditions (Figure 14.6). Rates of biogeochemical transformations are greatest in the boundary layers, which are found at the interfaces between upland areas, riparian zones, and the active channel. These form steep gradients between nutrients (particularly N and P), C, and oxygen (Hedin et al. 1998),

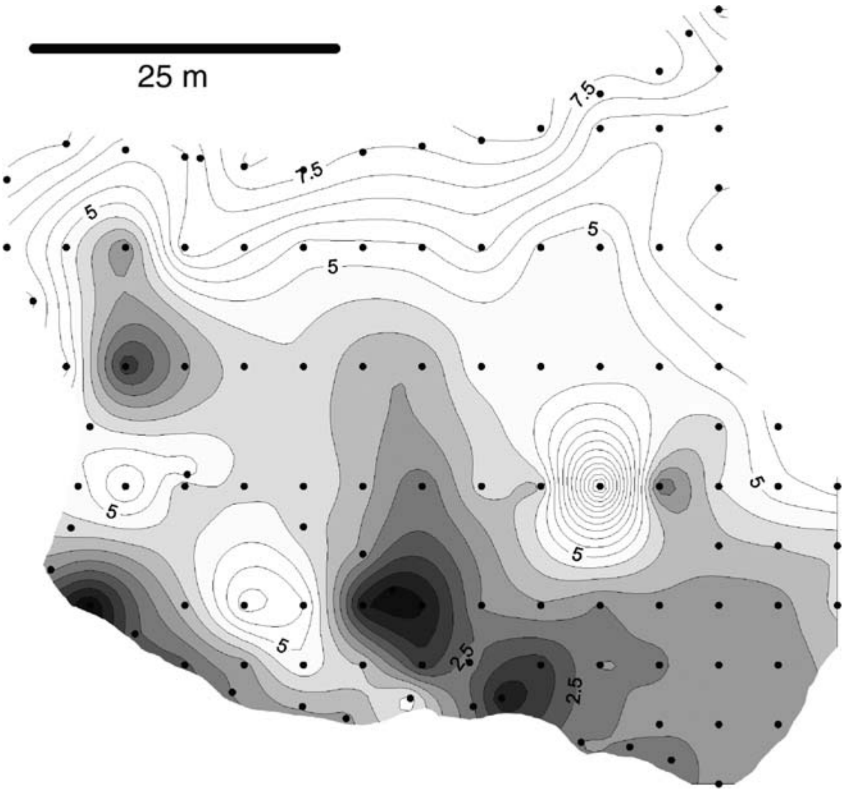


FIGURE 14.6. Concentrations of dissolved oxygen (DO) are highly heterogeneous within hyporheic zones. This figure illustrates DO (mg O_2/L) variability in two dimensions with darker shading illustrating areas of low oxygen, although DO also varies with depth (a third dimension). Biochemical processes such as denitrification exhibit high spatial variability relative to gradients in DO.

and these interfaces thus serve as functionally important locations for nutrient processing. Strong chemical gradients generally occur at the heads, intersections, and tails of flowpaths but may be heterogeneously distributed across the riparian landscape. Flowpath heads occur where surface water enters the hyporheic zone while the tails of flow paths are found where hyporheic water emerges in the main channel and throughout side channels. Heterogeneity in the rate of biogeochemical transformations that occur along these chemical or flow gradients is controlled by variation in the particle size of the substrate, which plays an important role in determining hydraulic conductivity. Gradients tend to be strong in areas with fine substrate and low hydraulic conductivity as these sites are characterized by slower moving water, which preserves anoxic conditions. In contrast, water chemistry in hyporheic zones is most similar to surface water in reaches that are relatively unstable (i.e., high levels of bed movement). These areas are dominated by larger substrate with greater hydraulic conductivity (Fowler and Death 2001).

Variability in C flux, driven by variation in seasons, discharge, and overlying vegetation (Clinton et al. 2002), creates strong heterogeneity in the hyporheic zone and has important consequences for microbial communities. Dissolved organic carbon (DOC) concentrations are controlled by the levels of surface water input, leaching from the overlying forest soil patches, metabolic uptake, and adsorption to sediments. Leaching of C from soils is seasonal and highly dependent on soil characteristics. The discharge regime helps determine both the direction of dominant flow paths and residence time of water in the hyporheic zone. Attributes of the overlying riparian forest are largely responsible for the quantity and quality of C and associated nutrients that leach through overlying soils. The patchwork of vegetation and soils is thus a controller of microbial production. Spatial variability in hydraulic conductivity creates additional heterogeneity in flow rates that lead to diverse redox conditions. Buried wood is likely an additional source of C in these environments (Nanson et al. 1995), although its relative importance remains difficult to quantify.

Heterogeneity in the Diversity and Productivity of Riparian Vegetation

Physical heterogeneity in riparian systems sustains high levels of biodiversity and creates spatial heterogeneity in productivity of riparian vegetation. Various landforms, from micro- to macroscales, provide physical templates for vegetation with differing species-specific life history characteristics (Walker et al. 1986; Pollock et al. 1998). It is the interrelation of disturbance regimes, soil characteristics, biological processes, and life-histories variation that is responsible for the high degree of heterogeneity observed in riparian vegetation at the reach and catchment scale (Figure 14.7).

Heterogeneity in microclimate, particularly temperature and humidity (Chen et al. 1999), soil characteristics (see earlier), and microtopography in riparian landscapes has important habitat implications for a wide range of taxa and drives variability in rates of microbially mediated processes. For example, in riparian wetlands, sites with intermediate flood frequencies and high spatial variation in flood frequency are species-rich in plant life, whereas sites that are frequently, rarely, or permanently flooded are species-poor (Pollock et al. 1998). These data suggest that small-scale spatial variation in physical processes, which is characteristic of riparian zones, can dramatically alter the ecological consequences of disturbances. In southeast Alaska, 78% of the variability in plant species richness (vascular plants and mosses) in riparian forests can be explained by the interaction between flood level and microtopography, with high species richness occurring at sites subject to

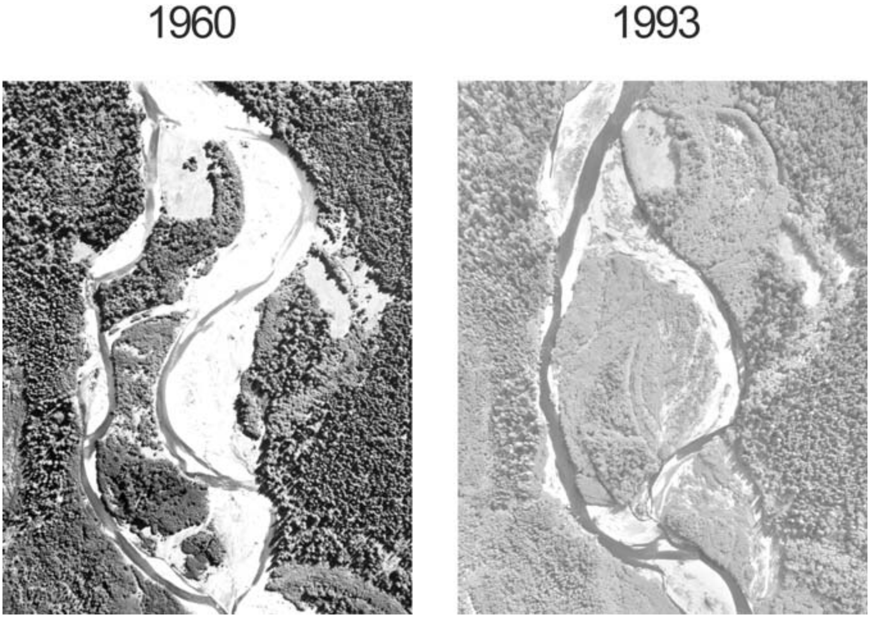


FIGURE 14.7. Dramatic shifts in the Queets River over the past 30 years illustrate the ability of the river to drive spatial and temporal heterogeneity in its riparian system.

intermediate flood duration and having the most diverse microtopography. This variability in local environmental conditions also influences development of different vegetative communities on same-age surfaces in floodplains that comprise patchworks of species composition and productivity rates (Balian 2001; Bartz and Naiman 2005).

In addition to forming patchworks of landforms, the natural flow regime also creates templates with a variable range of biophysical characteristics that are important factors for vegetative production and composition—which in turn favor high levels of biodiversity. Heterogeneity in flood frequency and magnitude creates gradients of disturbance and soil moisture that favor variety in the spatial arrangement of riparian species. In periodically flooded riparian systems, for example, the physiological responses of some plants allow them to maintain sufficient aeration when roots are flooded while other species survive by adjusting their timing of reproduction (e.g., Blom et al. 1990). These hydrologic controllers create a concentrated and highly diverse assemblage of plant species, including trees, shrubs, forbs, grasses, and epiphytes. In some cases up to 90% of the plant species within a catchment are represented in riparian areas (Naiman et al. 2005). Riparian plant species typically exhibit a spectrum of life-history strategies that are either tolerant of flooding and associated sedimentation, only found on surfaces no longer receiving overbank flows, or those that are adapted to some intermediate condition (Nanson and Beach 1977). The flow regime thus plays an important role in driving the structure of riparian vegetation patches, illustrated by declines in diversity where flow regimes are transformed by dams (Nilsson et al. 2002).

Limited data exist on tree production in riparian areas. Forest productivity in upland forests and the characteristics of individual species have been studied extensively. However, understanding riparian forest productivity and assemblages of riparian species is important in quantifying organic matter production and the rate at which riparian trees attain sufficient sizes to initiate the formation of stable LWD jams when they fall into rivers. The generation of LWD triggers feedbacks that create high levels of landscape heterogeneity (described below). Our data from Washington's Queets River indicate that productivity on floodplain terraces is within the range found in upland forests (Balian 2001), but considerable spatial and temporal variability, often more than an order of magnitude, exists within patches of approximately the same age at adjacent sites.

Successional processes associated with disturbance events and subsequent recolonization are responsible for much of the heterogeneity observed in riparian tree production, with annual rates closely related to dominant tree species and their associated understory communities. On the Queets River, the first stage is often a fast growing community of willow (*Salix* spp.) that reaches maximum productivity (4.3 Mg/ha/year) at approximately 10 years of age (Balian 2001). Willow is soon replaced by red alder (*Alnus rubra*) that reaches maximum productivity (7.9 Mg/ha/year) ~40 years after stand initiation. Finally, Sitka spruce (*Picea sitchensis*) out-competes red alder with a continuous increase in production (~13.9 Mg/ha/year) between 40 and 150 years. The first 40–60 years in the development of the riparian forest are thus the most dynamic. This is significant because fluvial disturbance resets stand development at scattered locations throughout the floodplain. These heterogeneous patterns of disturbance create high spatial variability in production relative to upland stands though the range of observed values may be similar. As a result of the episodic nature of disturbance, riparian vegetation patches can be found at different states of succession at the reach scale (Figure 14.8). Even with patches at similar states of succession, productivity can vary by an order of magnitude due to local soil characteristics, driven by deposition and the local accumulation of organic material. The lateral channel movement eventually captures riparian trees, where they continue to play important roles in shaping the dynamics of the system.

Large Woody Debris and Riparian Heterogeneity

The ruins of riparian forests form the prominent LWD jams that shape the next generation of riparian forest. Depending on the scale of examination, LWD jams may simultaneously create, exhibit, control, or respond to ecological heterogeneity. Within forested floodplain rivers, at mesoscales of space (e.g., stream reaches) and time (e.g., decades to centuries), stable LWD jams

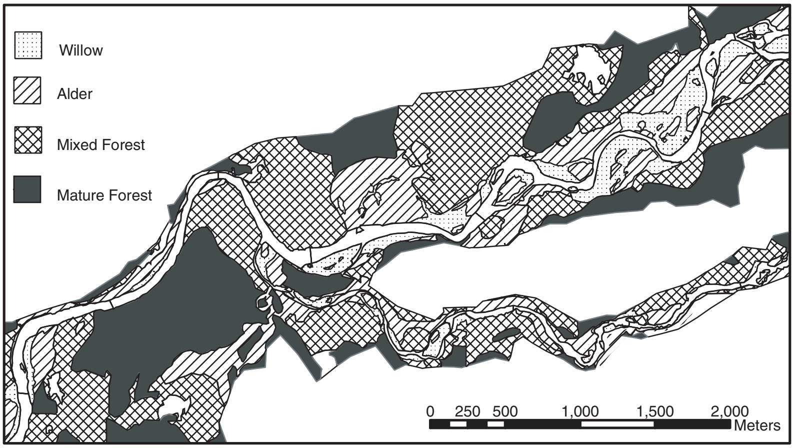


FIGURE 14.8. The migrating river channel is responsible for the establishment of a heterogeneous assemblage of vegetative patches within the channel migration zone. The patches shown represent young willow, mixed mid-age alder and young spruce, and old-growth spruce-dominated forests.

play key ecological roles in creating heterogeneity. At these scales, differentiation in form and dispersion of LWD jams strongly influences the availability of resources (e.g., habitat quantity and quality) for aquatic organisms and riparian vegetation, and subsequently riparian system function.

In gently sloping floodplain rivers, most LWD originates from lateral channel movement through forested terraces, and stream power is often sufficient to redistribute the pieces into jams during high flows (Murphy and Koski 1989). LWD jams in floodplain rivers typically form along channel margins or mid-channel and may be composed of LWD from the adjacent riparian forest, upstream forests, or a combination of the two (Abbe and Montgomery 1996, 2003). Jams vary widely in size, stability, arrangement, and functional significance. The dynamic behavior of forested floodplain landscapes is stimulated, in part, by a web of small-scale feedbacks set in motion by the localized scour and deposition of sediments that result from alteration of flow hydraulics by stable LWD jams. By simultaneously creating localized areas of stability and instability, LWD jams are the infrastructure for a complex web of positive and negative feedbacks that mold the riparian landscape into a patchwork of LWD-rich landforms, forest patches, and channel features (Figure 14.9). This biologically generated heterogeneity builds upon the heterogeneity imposed by physical processes at larger scales.

Influence of LWD on Fluvial Landforms

Interactions between LWD jams and the stream channel (e.g., the physical substrate) stimulate structural heterogeneity in fluvial landforms. Acting

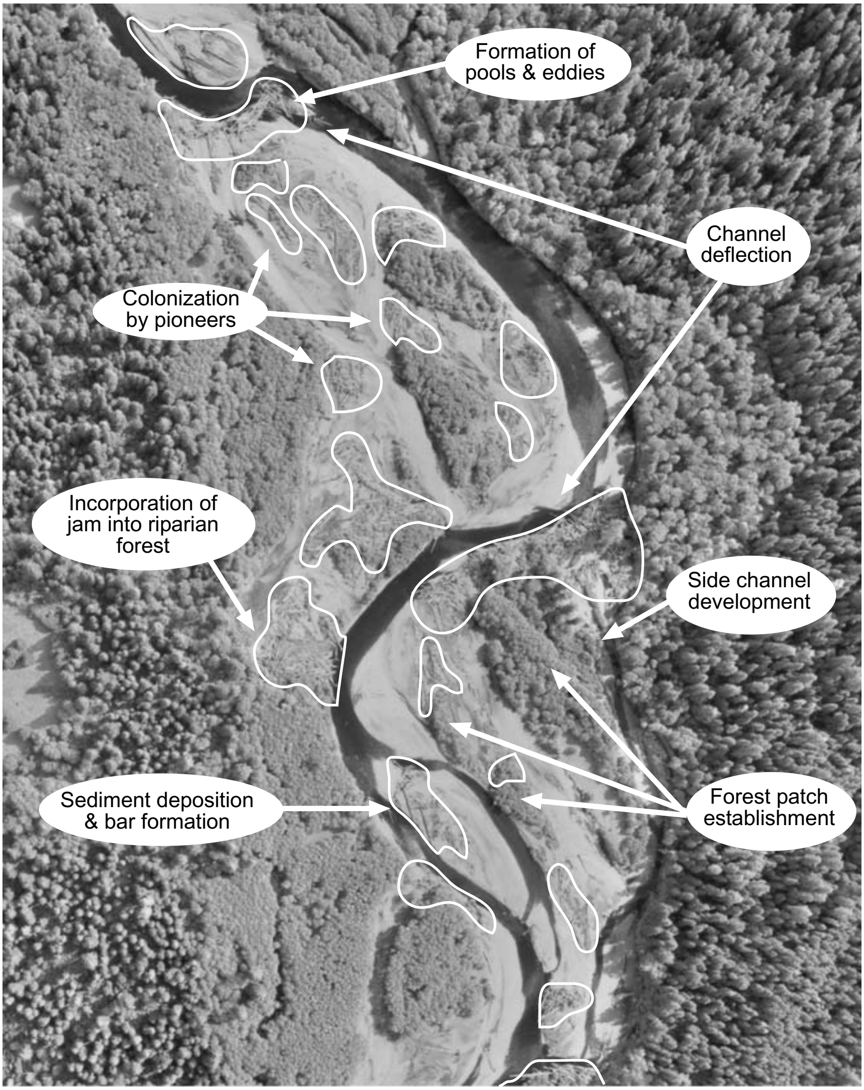


FIGURE 14.9. LWD jams (outlined) stimulate heterogeneity in structural and functional attributes of the flood plain of the Queets River, Washington. Only exposed jams are indicated, though LWD is also abundant within riparian forest patches.

alone, or synergistically, LWD jams cultivate new landforms, reinforce existing landforms, and transform or reconfigure existing landforms within stream reaches. In general, where LWD increases flow velocity and turbulence, channel stability is reduced. By redirecting flow and elevating shear stress, LWD jams create pools and side channels and promote bank erosion, channel avulsions, and channel switching (Nakamura and Swanson

1994; Abbe and Montgomery 1996). Where jams reduce flow velocity and turbulence, channel stability and resource availability for pioneering vegetation is enhanced. LWD jams may form backwaters and eddies and encourage deposition of sediments and organic matter in areas of enhanced stability. Over time, or in areas with high sediment supply, alluvial bars form downstream from stable LWD jams and may enlarge and coalesce into islands or extend from floodplain margins as terraces (Fetherston et al. 1995; Gurnell et al. 2001; Abbe and Montgomery 2003). In addition to triggering the formation of new fluvial landforms, LWD jams may armor landform margins against erosion, enabling the long-term persistence of some landforms within an otherwise volatile landscape (Abbe and Montgomery 1996). Floodplain terraces may arise from aggrading LWD-reinforced landforms adjacent to areas where the active channel is downcutting. As the relative elevation of the stream channel is lowered, patterns of sedimentation and disturbance on the floodplain terraces become less volatile and intense.

Biophysical Controls on Interactions Between LWD and Stream Channels

The outcome of interactions between LWD jams and stream channels (jam-channel interactions) is determined by a complex web of linkages between LWD, flow hydraulics, channel morphology, sediment supply, landforms, and riparian vegetation. The flow regime, the physical attributes of the valley, and the composition of riparian forest, though interwoven, each have strong and recognizable influences on the intensity and dispersion of interactions between LWD jams and stream channels.

Spatial and temporal variation in the incidence and intensity of jam-channel interactions result when natural fluctuations in flood magnitude, frequency, and duration are superimposed upon variable patterns of LWD jam distribution. For example, in a river where the seasonal hydrograph is driven by snowmelt, jams may form and dissipate relatively frequently in areas inundated on an annual basis—these jams may be engaged in sustained, relatively intense interactions with the stream channel throughout periods of snowmelt runoff. In contrast, jams higher on the floodplain may form infrequently and only interact with the stream channel during large, episodic intense floods (e.g., rain-on-snow events).

Channel gradient, confinement, and width control the intensity of jam-channel interactions and strongly influence jam dispersion. The intensity of jam-channel interactions increases with jam size and stability and depends on the orientation of the jam relative to the channel axis (Abbe and Montgomery 2003). LWD jams tend to be larger and more isolated as channel size increases and confinement is alleviated (Swanson et al. 1982) and as the capacity for fluvial transport of LWD is enhanced (Lienkaemper and Swanson 1986). The capacity for LWD jams to transform reach-scale channel bed morphology is also constrained by valley confinement (Montgomery and Buffington 1998). LWD jams strongly influence channel morphology at small scales within large, unconfined alluvial reaches. In addition, LWD jams may transform simple stream reaches underlain by coarse sediments or bedrock into complex reaches, rich with patchy sediment accumulations and pools (Montgomery et al. 1995, 1996).

The size, species composition, and density of floodplain forest communities control the intensity of interactions between LWD jams and the stream channel, as well as the dispersion of jams. These factors contribute to heterogeneity in the residence time of LWD, which limits the longevity of the ecological effects of LWD. The functional significance of LWD may rapidly diminish or extend for centuries, according to the rate at which LWD is depleted from the river corridor through decay, fragmentation, abrasion, and transport (see Hyatt and Naiman 2001). The longevity and stability of LWD in the stream channel is enhanced in trees of large dimensions and high decay resistance. For example, coniferous riparian forests typically produce larger LWD with greater longevity, whereas hardwoods produce smaller debris more susceptible to flushing, fragmentation, and decay (Harmon et al. 1986; Bilby and Wasserman 1989). Jams are likely to form adjacent to mature stands of trees that contribute LWD sufficiently large to initiate jams. Even though the amount of LWD in stream channels typically increases with riparian tree density (Bilby and Wasserman 1989), the capacity for LWD jams to transform reach-scale channel bed morphology is also constrained by riparian forests (Montgomery and Buffington 1998). Extensive riparian vegetation reduces the susceptibility of stream reaches to transformation by LWD jams, as vegetation enhances bank stability, particularly in unconfined reaches (Smith 1976).

Interplay Between LWD-Driven Heterogeneity and System Function

Spatial and temporal variation in LWD jams and related landforms result in a rich mosaic of aquatic habitats, forested landforms, and microclimates. LWD jams create heterogeneity in the low- to moderate-gradient streams by enhancing the variety and abundance of pools, riffles, and side-channels inhabited by aquatic organisms. Likewise, LWD jams enhance reach-scale heterogeneity in the variety, abundance, and spatial configuration of forest patches in various stages of initiation, establishment, growth, and destruction (Fetherston et al. 1995; Abbe and Montgomery 1996; Gurnell et al. 2001).

Interplay between LWD jams, organic matter, and stream substrates enhance the productivity of many stream organisms by creating resource-rich aquatic habitats. LWD encourages retention of particulate organic material, where it can be processed and used by aquatic invertebrates (Gregory et al. 1987; Bilby and Bisson 1998). Likewise, LWD can slow the downstream transport of spawning substrate, which can benefit fish production (House and Boehne 1989). Some fish benefit from the energetically profitable habitat (see Fausch 1984) within backwater pools, side channels, and eddies flanking marginal LWD jams (Moore and Gregory 1988). Pools created by LWD may contribute to fish productivity by providing refuge during climatic extremes, cover from predators, and encouraging habitat portioning among sympatric species (McMahon and Hartman 1989; Reeves et al. 1997). Fish and aquatic invertebrates often decline after LWD removal (Dolloff 1986; Elliott 1986; Fausch and Northcote 1992) and increase in response to LWD additions (House and Boehne 1989; Wallace et al. 1995; Cederholm et al. 1997). These contrasting responses underscore the functional importance of LWD, which extends beyond the margins of riparian forests to streams.

Patterns of LWD-related floodplain forest development follow predictable trajectories that differ according to the type of jam that initiated landform development (Fetherston et al. 1995; Abbe and Montgomery 1996, 2003) (Figure 14.10). Moisture-rich, sandy alluvial deposits in the lee of LWD jams may be colonized after floods by pioneering riparian vegetation such as red alder and willow. When LWD jams establish mid-channel, the establishment and growth of pioneering vegetation enhances local hydraulic roughness, encouraging additional sediment deposition. Persistent bars accumulate sediments with successive floods—burying most of the

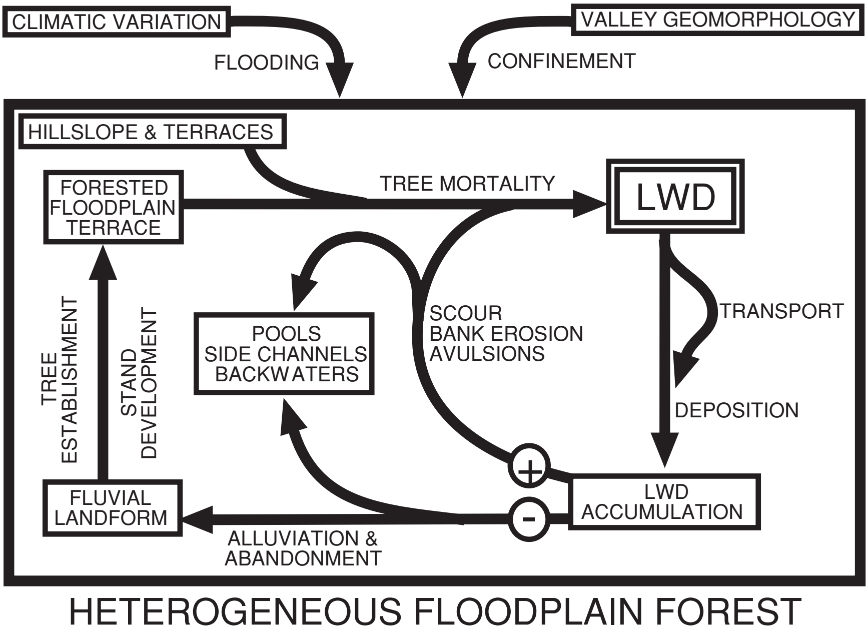


FIGURE 14.10. Linkages between LWD and heterogeneity in patterns and processes within a forested floodplain valley. Positive feedbacks stimulate instability, whereas negative feedbacks enhance stability.

original wood jam—and emerge as forested islands (Naiman et al. 2000). LWD jams may also form wedge-shaped bars along the floodplain margin (i.e., flow-deflection jams; Abbe and Montgomery 2003). These jams may form as bank erosion accelerates around large trees that have toppled into the channel—surrounding trees topple like dominoes as the river cuts deeper into the forest, gradually forming a jam that deflects flow from the previous channel axis. Patches of riparian forest establish on the resulting sediment accumulations, typically with the oldest trees located at the distal portion of the bar where the jam was initiated. Alternatively, swaths of even-aged floodplain forest may form as riparian vegetation establishes in abandoned channels created by LWD-related channel avulsions or channel switching. Eventually, exposed jams soften with decay and conifers (*Picea, Tsuga*) germinate the largest remaining of LWD, which provide moist microsites and refugia from competition and disturbance (McKee et al. 1982). Jams incorporated into riparian forest patches may strengthen the landform against further erosion, providing refuge for patches of mature forest within a highly dynamic corridor (Abbe and Montgomery 1996; Naiman et al. 2002). Ultimately, conifers overtop the alder and reach sufficient size to initiate new LWD jams upon their death and delivery to the channel. Many landforms are eventually eroded at various stages of development by channel movement, adding the living trees and accumulated LWD to the channel and starting the process of floodplain forest development anew.

Conclusions

Riparian forests are highly complex systems exhibiting substantial heterogeneity—and ecosystem linkages—over broad spatial and temporal scales. Geology and climate interact to set the physical template, and that template shapes subsequent riparian structure and processes, from soils to LWD. The concepts presented here represent a rudimentary beginning. The collective understanding of riparian corridors as dynamic biophysical systems increases substantially every few years—and there remain immediate uncertainties as well as great challenges to be met. The chief uncertainties relate to determining what aspects of heterogeneity are most ecologically meaningful as well as predicting how system heterogeneity will respond to changes in system components due to the nonlinearity and apparent stochasticity of complex interactions between components. Major challenges relate to setting meaningful spatial and temporal scales on heterogeneity and to focusing on multiple factors as drivers of heterogeneity. Identifying meaningful scales is important because intellectual paradigms or management guidelines are often based on acceptable minimums, which can lead to system simplification if operative scales are not clearly identified. Finally, heterogeneity and the responses of the riparian system arise from many factors, some of which may dominate at particular scales of space and time—and it is this perspective that needs quantification for achieving a predicable understanding.

Acknowledgments. We are grateful to the Andrew W. Mellon Foundation, Weyerhaeuser Company, Pacific Northwest Research Station of the U.S. Forest Service, National Science Foundation, and the Olympic National Park for support and cooperation. H. Décamps, M. McClain, J.F. Franklin, and two anonymous reviewers provided many useful comments on an earlier version.

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