

An Ecosystem Perspective of Riparian Zones

Focus on links between land and water

Stanley V. Gregory, Frederick J. Swanson, W. Arthur McKee, and Kenneth W. Cummins

Riparian zones are the interfaces between terrestrial and aquatic ecosystems. As ecotones, they encompass sharp gradients of environmental factors, ecological processes, and plant communities. Riparian zones are not easily delineated but are comprised of mosaics of landforms, communities, and environments within the larger landscape. We propose a conceptual model of riparian zones that integrates the physical processes that shape valley-floor landscapes, the succession of terrestrial plant communities on these geomorphic surfaces, the formation of habitat, and the production of nutritional resources for aquatic ecosystems.

Riparian zones have been investigated from many perspectives, creating a diverse and often confusing array of definitions based on hydrologic, topographic, edaphic, and vegetative criteria (see reviews in Karr and Schlosser 1978, Swanson et al. 1982). Most riparian classification systems focus on a few selected at-

Perspectives based on isolated components are ecologically incomplete

tributes of riparian areas, such as hydric soil or hydrophylic plant associations (Cowardin et al. 1979). Although these perspectives adequately characterize terrestrial plant communities, they provide little understanding of the wide array of ecological processes and communities associated with the land-water interface, and they encourage an inappropriately rigid delineation of riparian boundaries.

The importance of landscape perspectives for understanding the structure and function of stream ecosystems was eloquently described by H. B. N. Hynes (1975). Recent concepts in stream ecology emphasize the importance of the land-water interface (Newbold et al. 1981, Vannote et al. 1980), but primarily as sources of organic and inorganic material for aquatic ecosystems. Historically, aquatic research on major rivers of the world has focused on the strong interactions between the rivers and their floodplains in lowland fluvial landscapes (Amoros et al. 1987, Décampes et al. 1988, Junk et al. 1989, Sioli 1984, Welcomme 1985). The ecotonal nature of riverine boundaries has served as a framework for understanding the organization, diversity,

and stability of aquatic communities in fluvial ecosystems (Naiman et al. 1988). In this article, we present an ecosystem perspective of riparian zones that focuses on the ecological linkages between terrestrial and aquatic ecosystems within the context of fluvial landforms and the geomorphic processes that create them.

We define riparian zones functionally as three-dimensional zones of direct interaction between terrestrial and aquatic ecosystems (Meehan et al. 1977, Swanson et al. 1982). Boundaries of riparian zones extend outward to the limits of flooding and upward into the canopy of streamside vegetation. Dimensions of the zone of influence for a specific ecological process are determined by its unique spatial patterns and temporal dynamics.

Extending this concept in time and space, riparian zones can be viewed in terms of the spatial and temporal patterns of hydrologic and geomorphic processes, terrestrial plant succession, and aquatic ecosystems (Figure 1). This ecosystem model is based on the premise that geomorphic processes create a mosaic of stream channels and floodplains within the valley floor. Geomorphic and other disturbance processes of both upland and fluvial origin affect riparian zones, determining the spatial pattern and successional development of riparian vegetation. Valley floor landforms and associated riparian vegetation form the array of physical habitats within the active channels and floodplains, and the streamside plant communities are major determinants of the abundance and quality of nutri-

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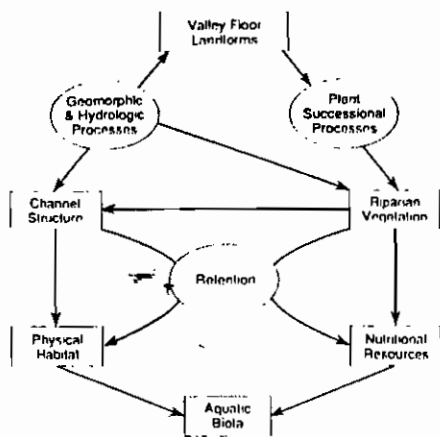


Figure 1. Diagrammatic representation of relationships among geomorphic processes, terrestrial plant succession, and aquatic ecosystems in riparian zones. Directions of arrows indicate predominant influences of geomorphic and biological components (rectangles) and physical and ecological processes (circles).

tional resources for stream ecosystems.

This ecosystem perspective of riparian zones emphasizes lotic ecosystems and the geomorphic organization of fluvial landforms. This perspective draws heavily on examples from the Pacific Northwest, but the conceptual framework can be applied to the land-water interfaces of other ecosystems (e.g., lakes, wetlands, estuaries, and marine intertidal areas) and other geographic regions. Although the importance of specific links in other ecosystems may vary because of different geomorphic and hydrologic patterns or different ecological characteristics, this general ecosystem perspective of riparian zones is applicable to any land-water interface.

Geomorphology

Studies of fluvial geomorphology examine both valley floor landforms and fluvial processes, which may be considered disturbances from an ecosystem perspective (Swanson et al. 1988). Geomorphic structure of valley floors results from the interaction of basin geology, hydrology, and inputs of inorganic and organic material from adjacent hillslopes and vegetation. Geomorphic surfaces along river valleys create physical patterns that are reflected in the development of riparian plant communities and

distributions of aquatic biota.

Past research on relations among geomorphic surfaces, vegetation, and channel hydraulics concentrated in lowland, floodplain rivers where lateral channel migration is a dominant process of valley floor landform development (Leopold et al. 1964, Osterkamp and Hupp 1984). In steeper montane landscapes, valley floor landforms are sculpted by fluvial processes and a variety of mass soil movement processes from tributaries and adjacent hillslopes. Geomorphic processes that modify riparian zones operate on time scales ranging from chronic (months to years) to episodic (decades to centuries) and on spatial scales ranging from localized shifts in channel position involving a few square meters to basin-wide flooding (Table 1). In addition to fluvial or erosional events that create new geomorphic surfaces, sediment deposition and battering during floods cause less severe but more frequent damage, which may influence the course and rate of vegetation succession.

Hierarchical structure of valley floor landforms

Valley floors are mosaics of geomorphic surfaces, which include active channels, floodplains, terraces, and alluvial fans (Figure 2). Active channels carry channelized streamflow and are modified by frequent flood events. Boundaries, or banks, of active channels commonly are topographically abrupt and mark the lower extension of perennial terrestrial vegetation (Hedman and Osterkamp 1982). During floods, fluvial

deposition of mainstem sediments adjacent to active channels create floodplains. These floodplain surfaces may extend great distances across valley floors, and several floodplains with successively higher surfaces can occur along a single transect across a valley. Remnants of old valley floors also may occur between hillslopes and the active channel or floodplain at elevations too high to be flooded under modern hydrologic and geomorphic conditions. Alluvial fans form where sediment and debris-flow deposits from the tributary streams accumulate on terrace and floodplain surfaces.

The hierarchical organization of drainage basins is based on functional relationships between valley landforms and the processes that create them (Frissell et al. 1986, Grant et al. 1990). Processes operating at one scale can affect geomorphic dynamics and structure at other scales. The network of valley floor landforms within a basin extends from headwaters to large rivers or estuaries and includes drainage segments, reach types, channel units, and channel subunits. Within this hierarchical system, spatial scales are consistent with the physical mechanisms responsible for landform change.

Segments of a drainage network are defined by regional landform patterns that reflect different agents of landscape formation (scale of 10 km to more than 100 km). Segments frequently are delineated by major topographic discontinuities such as high-gradient montane rivers or low-gradient lowland rivers in broad valleys.

Table 1. Spatial dimensions and temporal scales of stability of channel features and factors that influence stability. Stability is considered to be persistence of individual geomorphic features at a location within the drainage.

| Feature | Spatial dimensions (channel widths) | Time scale of stability (years) | Factors related to stability |
|----------------------|-------------------------------------|---------------------------------|--------------------------------------------------------------|
| Particle composition | 10^{-3} – 10^{-2} | 10^0 | Shear stress, bed |
| Subunit composition | 10^{-1} | 10^0 | Shear stress, bed composition, organic debris |
| Channel unit | 10^0 | 10^1 – 10^2 | Hydraulics, bed composition, organic debris |
| Reach | 10^1 – 10^2 | 10^3 – 10^4 | Basin-wide aggradation/degradation, local base-level control |
| Section | 10^3 – 10^4 | 10^4 – 10^5 | Tectonic and/or sea level change, climate |
| Network | 10^4 | 10^6 + | Geology |

Drainage segments are composed of reaches of various types. Reaches are distinguished by the type and degree of local constraint imposed on the channel and valley floor by geomorphic features such as bedrock, landslide deposits, and alluvial fans. Degree of local constraint controls fluvial development of geomorphic surfaces within river valleys and therefore influences both terrestrial and aquatic communities through topographic, edaphic, and disturbance mechanisms. Constrained reaches tend to have relatively straight, single channels (e.g., the lower reach in Figure 3). During flood flow, the position of the stream channel is relatively fixed within narrow floodplains; stream depth and velocity increase rapidly with increasing discharge. Valley floors in constrained reaches are narrow and include few geomorphic surfaces within the valley floor. Vegetation on adjacent hillslopes is likely to be similar in composition to plant communities located further upslope. In studies of Cascade Mountain streams, we operationally defined constrained reaches as valleys floors less than twice the width of the active channel.

Unconstrained reaches lack significant lateral constraint and are characterized by complex, commonly braided channels and extensive floodplains (e.g., upper reach in Figure 3). At high flow, the stream spreads across the broad valley floor, dissipating much of the energy of the current.

Unconstrained reaches are common in low-gradient, lowland rivers, but these reaches also are important components of valley floors in mountainous topography. Riparian zones in unconstrained reaches are broad and complex, with a diverse array of geomorphic surfaces and plant communities of various ages. Riparian stands include components of hillslope communities but are composed largely of species adapted to valley floor environments. Effects of fluvial disturbance are widespread, including numerous patches of early-successional-age vegetation.

Reaches are composed of sequences of channel units, whose distinct hydraulic and geomorphic structures reflect different processes of formation (Grant et al. 1990). Different types of channel units are distinguished on the basis of water-surface slope, width:depth ratio of the channel, and extent of turbulent, high-velocity flow. Classical studies of fluvial geomorphology in low-gradient, sand- and gravel-dominated streams typically classify channel units as pools and riffles (Leopold et al. 1964). Riffles are found in steep montane streams with stepped streambed morphology, but additional types of higher-gradient channel units may occur—rapids, cascades, and falls (Grant 1986, Grant et al. 1990). Channel units are a major scale of variation in the structure of stream ecosystems and are major determinants of the physical habitat for aquatic organisms.

At flows lower than those required to fill the active channel, boulders, logs, or gravel bars may create local hydraulic features at scales less than the active channel width, which are termed subunits. Subunits are transitory hydraulic features over annual hydrological cycles, changing rapidly with rising or falling water levels. As flow increases and the active channel is completely inundated, channel units attain uniform surfaces and delineations between subunits become less distinct. Like the larger channel units that contain them, channel subunits within the main channel axis are classified as riffles, pools, rapids, or cascades based on local hydraulic conditions. Geomorphic features lateral to the main axis of flow (i.e., thalweg), such as backwaters, eddies, and side channels, are also included as subunits and play distinctly different ecological roles similar to hydraulic features within the main channel (Moore and Gregory 1988a, Tschaplinski and Hartman 1983). Habitat types described in studies of stream communities frequently correspond to channel subunits.

Valley-floor landforms also are organized hierarchically in a temporal sense because the force required to modify geomorphic surfaces at different spatial scales is directly linked to the recurrence intervals for floods or other geological events of such magnitude (Frissell et al. 1986, Swanson 1980, Swanson et al. 1988). Long-term geomorphic processes (e.g., volcanism, glaciation, and tectonic uplift) modify landscapes over tens of thousands to hundreds of thousands of years (Figure 4). More localized geomorphic processes (e.g., landslides) extending over many square kilometers and occurring over hundreds to thousands of years may constrain valley development within stream reaches. Smaller channel features (10^{-3} – 10^{-2} m²) are altered by high-flow events that recur over several years to several decades, and small patches of sediment particles or hydraulic features (<10 m²) may be reshaped several times each year.

Riparian vegetation

Riparian vegetation occupies one of the most dynamic areas of the landscape. Distribution and composition

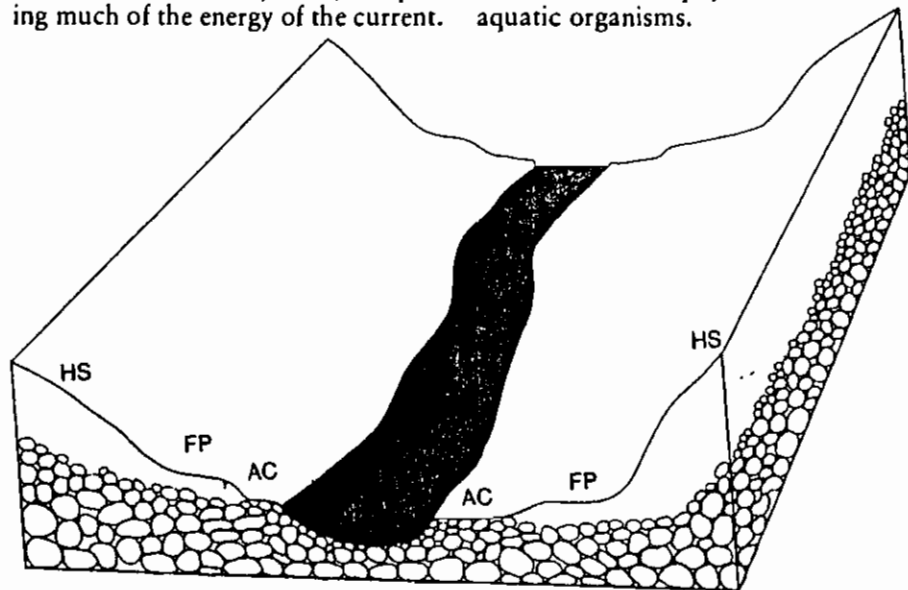


Figure 2. Geomorphic landforms associated with river valleys. The active channel includes the wetted channel (WC) and channel surface exposed during low flow (AC). Floodplains (FP) are located between the active channel and hillslope (HS).

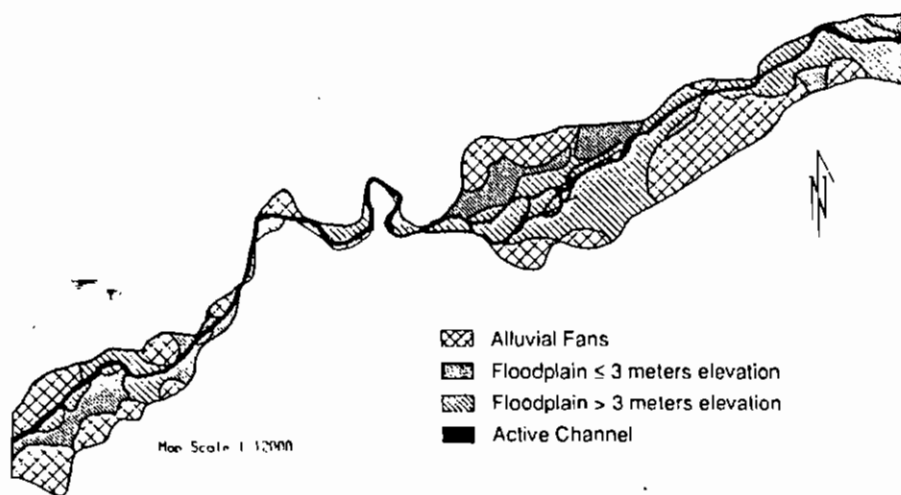


Figure 3. Map of the valley floor of Lookout Creek, a tributary in the McKenzie River basin in Oregon. In the upstream section in the upper right corner, width of the valley is more than four times the active channel width and is considered an unconstrained reach. Note the secondary channels and complex floodplains of the unconstrained reach. The downstream section is a constrained reach, with a valley width less than twice the active channel width.

of riparian plant communities reflect histories of both fluvial disturbance from floods and the nonfluvial disturbance regimes of adjacent upland areas, such as fire, wind, plant disease, and insect outbreaks. Soil properties and topography of valley floors are extremely varied, ranging from perennially wet to well-drained soils over short distances (Hawk and Zobel 1974). Consequently, riparian plant communities exhibit a high degree of structural and compositional diversity.

Geomorphic surfaces of the valley floor and lower hillslopes adjacent to the channel provide a physical template for development of riparian plant communities (Figure 5). During periods of low discharge in most streams, the exposed active channel is colonized by herbs and seedlings of shrubs and trees. Frequent flooding within this zone discourages establishment of terrestrial vegetation both by surface erosion and physiological effects of periodic inundation. Floodplains, terraces, or hillslopes immediately adjacent to active channels may be occupied by herbs, shrubs, and trees, often with a mixture of age classes reflecting the history of flooding.

Magnitude, frequency, and duration of floods diminish laterally away from the active channel. Development of riparian vegetation reflects distur-

bance regimes on these lateral surfaces. Riparian vegetation on surfaces closer to the active channel is characterized by younger stands, commonly composed of deciduous shrubs and trees. Floodplains farther from the active channel may contain older plant communities composed of either typical riparian species (e.g., alder, cottonwood, and willow) or up-

land species extending down onto the floodplain (Hawk and Zobel 1974). Lateral meandering of stream channels tends to modify this pattern by cutting into older riparian plant communities along the outer edge of a meander and creating depositional surfaces for development of younger stands along the inner margin of meanders (Everitt 1968, Fonda 1974).

Spatial dimensions of riparian vegetation patches reflect the heterogeneity of geomorphic surfaces within the river valley. In streams and rivers flowing through conifer forests, fluvial processes commonly create narrow bands of early successional or seral stages, predominantly deciduous, bordered by the stream on one side and much taller conifers on the other. Vegetation within such early seral patches commonly are asymmetrical, with young, shorter stands bordering one stream bank and older, taller forests along the other. In constrained reaches, riparian plant communities are narrow and closely resemble those of upslope forests. In contrast, riparian plant communities in unconstrained reaches are complex, heterogeneous patches of different successional stages, including herbs and grasses, deciduous trees, and coniferous stands of many ages.

Abundance and composition of terrestrial vegetation differ greatly among

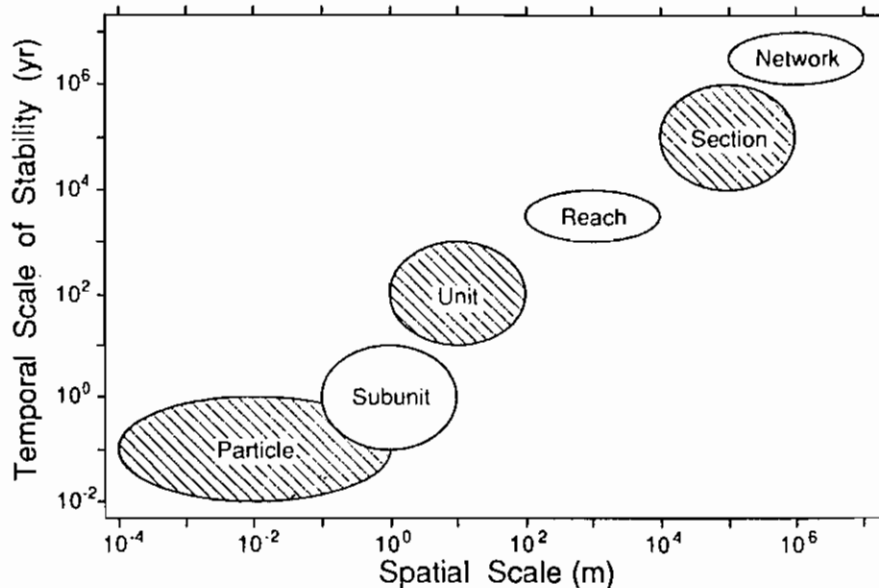


Figure 4. Temporal and spatial scales of hierarchical organization of valley landforms (modified from Frissell et al. 1986 and Swanson 1980). Spatial scale represents the longitudinal dimensions of geomorphic features and landforms created by different geomorphic processes. Temporal scale of stability is the period over which these geomorphic features persist without major change in dimensions or locations.

riparian successional stages. Forested riparian zones, both deciduous and coniferous, contain much greater biomass of total plant material than do zones of nonforested vegetation. In the McKenzie River drainage of Oregon, old-growth conifer riparian stands support approximately five times more biomass, mostly in the form of wood, than do deciduous stands (Table 2). Foliar biomass is also greatest in the conifer riparian zone. Quantity and composition of this plant matter greatly influence both the terrestrial and aquatic ecology of riparian areas.

The high diversity of microsites and complex, high-frequency disturbance regimes along river valleys leads to a greater species diversity in riparian zones than in upslope habitats. In stands of vegetation in Oregon ranging in age from recent clearcuts to old-growth forests in excess of 500 years, riparian communities contained approximately twice the number of species observed in upslope communities (Figure 6a). Similar patterns of total species richness in hillslope and riparian areas occur in comparisons of plant communities in

Table 2. Total above-ground plant biomass and leaf biomass by vegetation stratum in coniferous, deciduous, and herb and shrub-dominated riparian zones (kg/ha), estimated from maps of vegetation within 100 meters of the active channel. Litterfall values are based on annual means of ten litterfall traps at each stream.

| Vegetation component | Stratum | Shrub | Deciduous | Coniferous |
|----------------------|---------------|-------|-----------|------------|
| Total plant | Moss | 9 | 44 | 31 |
| | Herb | 436 | 315 | 357 |
| | Shrub | 1173 | 1807 | 2199 |
| | Tree | 202 | 172,876 | 1,100,736 |
| | Total | 1820 | 175,042 | 1,103,323 |
| Foliar | Moss | 9 | 44 | 31 |
| | Herb | 368 | 314 | 267 |
| | Shrub | 148 | 165 | 194 |
| | Tree | 23 | 3902 | 15,675 |
| | Total | 548 | 4425 | 16,167 |
| Litterfall | Herb and moss | 377 | 358 | 298 |
| | Shrub | 148 | 150 | 193 |
| | Tree | 5 | 1853 | 3171 |
| | Total | 530 | 2361 | 3662 |

the Cascade Range in Oregon and the Sierra Nevada in California (Figure 7). The sharpness of gradients in species richness reflects patterns in environmental gradients from the stream to the hillslope, as indicated in the comparison of Cascades and Sierran riparian zones.

Though species richness was much greater in riparian areas within the total areas sampled, species diversity indices (Shannon-Weiner H') were only slightly higher in riparian forests than in similar sampling areas (0.25 m²) of hillslope plant communities (Figure 6b). This observation indicates that many of the species contained within riparian plant communities in Oregon are rare. The patchy nature of the frequently disturbed riparian zones may account for the high number of species in riparian areas, but patterns of local diversity that are not substantially greater than those found in hillslope habitats.

Riparian zones are commonly recognized as corridors for movement of animals within drainages, but they also play a potentially important role within landscapes as corridors for dispersal of plants. Because of their persistence as open habitats, floodplains have been suggested as one of the original habitats of weedy plants (i.e., grasses and forbs) before human modification of North American forests (Marks 1983). Streamside habitats commonly include most hillslope species as well as plants associated with hydric soils; therefore riparian zones may be major sources of most plant colonists throughout the landscape. The importance of riparian zones in plant dispersal increases during periods of rapid climatic change because of the ameliorated microclimates along river valleys.

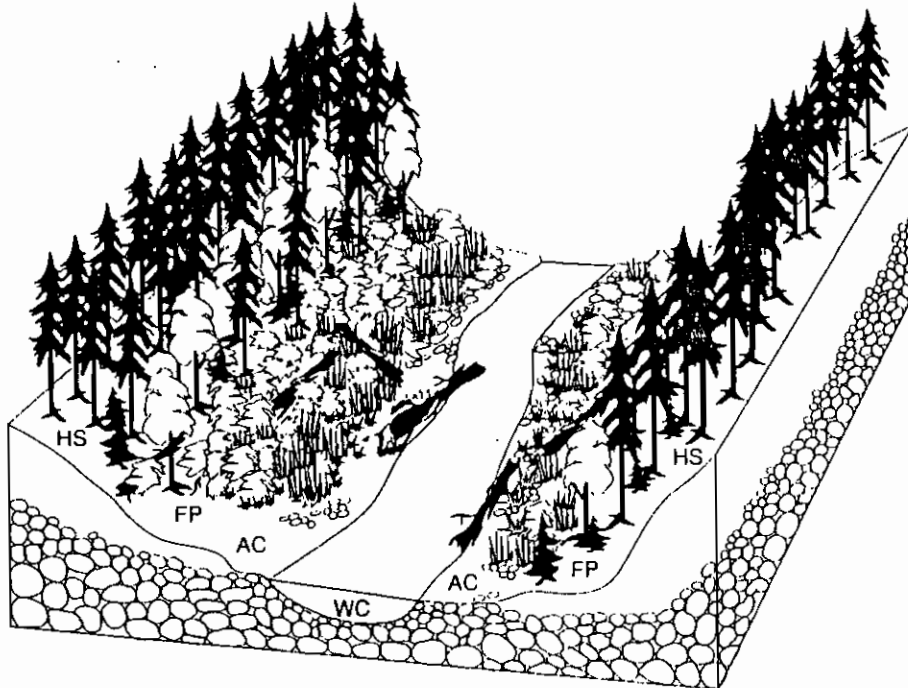


Figure 5. Typical patterns of riparian plant communities associated with different geomorphic surfaces of river valleys in the Pacific Northwest. Scattered patches of grasses and herbs occur on exposed portions of the active channel (AC), but little terrestrial vegetation is found within the low-flow wetted channel (WC). Floodplains (FP) include mosaics of herbs, shrubs, and deciduous trees. Conifers are scattered along floodplains and dominate older surfaces. The overstory species in riparian forests on lower hillslopes (HS) consist primarily of conifers.

Mosaics of landforms strongly influence spatial patterns of riparian plant communities, but riparian vegetation also influences the evolution of geomorphic surfaces. Root networks of riparian stands increase resistance to erosion. Aboveground stems of streamside vegetation increase channel roughness during overbank flow, thereby decreasing the erosive action of floods and retaining material in transport.

Riparian plant communities also contribute large woody debris to channels, a major geomorphic feature in streams and rivers (Bilby 1981, Keller and Swanson 1979, Swanson et al. 1976). Relative influences of large woody debris on development of geomorphic surfaces decrease from headwaters to large rivers (Harmon et al. 1986, Swanson et al. 1982). Woody debris can influence both floodplains and channels in headwater streams; but channel-spanning de-

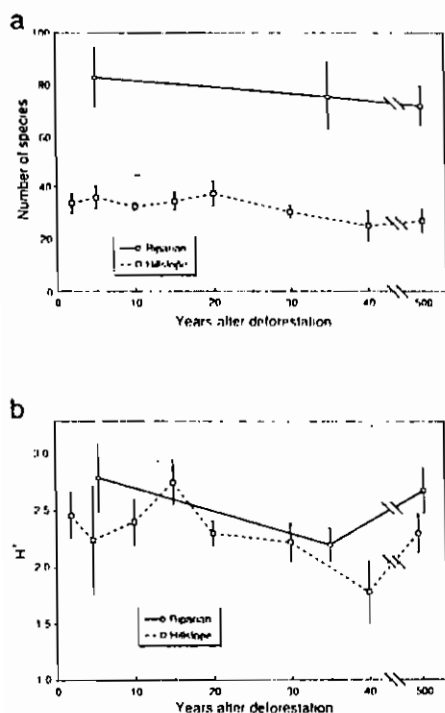


Figure 6. (a) Species richness of plant communities per 300-square-meter belt transect and (b) species heterogeneity (H' : Shannon-Wiener index) of plant communities in hillslope and riparian habitats in the McKenzie River valley, Oregon (hillslope data modified from Schoonmaker and McKee 1988). Points represent means for riparian and hillslope habitats for three sites for each stand age (total of 23 sites; only 2 sites for 10-year stands); bars represent standard deviations.

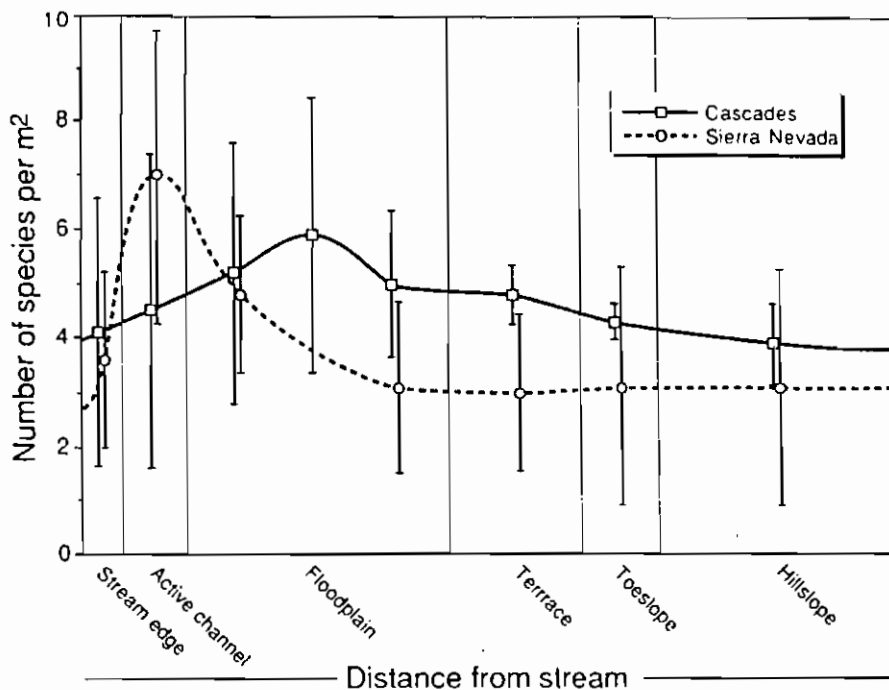


Figure 7. Gradients of species richness along lateral transects from the stream channel to upper hillslopes along three streams on the west slope of the Cascade Mountains of Oregon and three streams in the Sierra Nevada of California (from unpublished data). Richness is expressed as number of species in one-square-meter plots sampled in longitudinal, one-meter \times five-meter belt transects. Points represent means for more than 45 transects per surface; bars represent standard deviations.

bris accumulations are less common in larger rivers, where woody debris accumulates on streambanks, heads of islands, and floodplains. Historically, large rivers contained numerous islands and secondary channels before forest clearing, log removal, and channelization by man (Sedell and Froggatt 1984).

Riparian interactions: links between forest and stream

The importance of riparian zones far exceeds their minor proportion of the land base because of their prominent location within the landscape and the intricate linkages between terrestrial and aquatic ecosystems. Fluxes of water, air masses, dissolved and particulate matter, and organisms across a landscape are channeled into and along valley floors. Interactions between terrestrial and aquatic ecosystems include modification of microclimate (e.g., light, temperature, and humidity), alteration of nutrient inputs from hillslopes, contribution of organic matter to streams and floodplains, and retention of inputs.

Solar radiation. Solar radiation is selectively absorbed and reflected as it passes through the riparian canopy adjacent to streams, thus the quantity and quality of light available for aquatic primary producers is altered. Degree of shading of streams is a function of the structure and composition of riparian vegetation. Dense, low, overhanging canopies greatly reduce light intensity at the water's surface, but high, relatively open canopies allow greater amounts of light to reach the stream. Deciduous riparian vegetation shades streams during summer, but it only slightly modifies light conditions after leaf fall, and evergreen riparian zones shade stream channels continuously. Degree of shading is a function of channel size relative to the lateral and vertical dimensions of the streamside vegetation. As channel width increases, the canopy opening over the stream increases and the influence of streamside vegetation on solar inputs to the stream channel decreases.

Solar radiation striking the water's surface also contributes energy in the form of heat. Riparian vegetation

plays a major role in modifying solar inputs and influencing stream temperatures (Barton et al. 1985). Density of the riparian canopy is one of the most critical factors in determining the heat input in a given reach of stream. The upstream length of forested channel, riparian vegetation width and density, canopy opening, and groundwater influence the contribution of heat to a reach.

Dissolved nutrient inputs. Dissolved nutrients are transported from terrestrial ecosystems into streams primarily in the form of material in groundwater. Riparian zones are uniquely situated within watersheds to intercept soil solution as it passes through the riparian rooting zone before entering the stream channel. Riparian plant communities also deliver seasonal pulses of dissolved leachates derived from terrestrial litter into streams and rivers (Fisher and Likens 1973). As a result, riparian zones may significantly modify the amount, form, and timing of nutrient export from watersheds.

Nutrient concentrations in riparian soils exhibit patterns related to composition of streamside plant communities and to the history of fluvial disturbance. In riparian zone soils in the Pacific Northwest, concentration of available nitrogen is higher in alder-dominated stands than in coniferous riparian zones, a reflection of the nitrogen-fixing ability of alder. This influence of alder on nitrogen availability also has been observed in the surface water chemistry of aquatic ecosystems (Goldman 1961, Thut and Haydu 1971).

Microbial transformations of nitrogen alter relationships between soil dynamics and nitrogen content in stream water. In alder-dominated riparian zones in the Cascade Mountains of Oregon, elevated concentrations of nitrate in stream water are

not observed. Rates of denitrification were higher in the alder-dominated stand than in the conifer- or herb- and shrub-dominated stands (Table 3), an observation that may account for the similarity in nitrogen concentration in the stream reaches. In both deciduous and coniferous riparian sites, rates of denitrification were greater in riparian soils near the stream than in toeslope or hillslope soils, presumably a reflection of the soil moisture content and the availability of organic substrates for denitrifiers. Although soils in the active channel and floodplain are disturbed more frequently than soils in upslope areas, high moisture levels and abundance of organic matter deposited by floods enhance microbial activity.

As soil solution passes through riparian zones before entering streams, vegetative demand for dissolved nutrients may greatly reduce nutrient loads. Riparian forests were found to be responsible for removal of more than three-quarters of the dissolved nitrate transported from croplands into a Maryland river (Peterjohn and Correll 1984). In coastal plains of Georgia, riparian forests retained more than 65% of the nitrogen and 30% of the phosphorus contributed in soil solution from surrounding agricultural lands (Lowrance et al. 1984). Because of their central location at the base of terrestrial ecosystems, riparian zones play a critical role in controlling the flux of nutrients from watersheds.

Particulate terrestrial inputs. Riparian plant communities offer an abundant and diverse array of food resources for both aquatic and terrestrial consumers. Much of the food base for stream ecosystems is derived from adjacent terrestrial ecosystems. In Bear Brook, New Hampshire, more than 98% of the organic matter was supplied by the surrounding forest (Fish-

er and Likens 1973). Gallery forests along a prairie stream in Kansas contribute greater quantities of organic matter than do the grasslands in upstream reaches (Gurtz et al. 1988).

Although total plant biomass differs by several orders of magnitude among the different stages of succession in riparian zones (Table 2), foliar biomass is only 5 to 20 times greater in deciduous and coniferous stands, respectively, than in herb- and shrub-dominated stands. Most studies of terrestrial litter inputs have focused on leaves and needles of trees, but herbaceous and shrub litter represent a significant input of litter in many riparian zones. In herb- and shrub-dominated riparian zones in the McKenzie River drainage, herbaceous plants can account for up to 75% of the foliar production. Although conifer stands contain greater foliar biomass, only a fraction of that biomass is lost as litterfall in any given year. As a result, litterfall in deciduous stands may exceed that of coniferous stands and exhibit more pronounced seasonal patterns of input. Timing of leaf abscission of trees and shrubs is species specific and more constant from year to year than is herb senescence. Senescence of herbs is strongly influenced by the timing of frost, but herbaceous material primarily enters the stream during floods. Thus the contribution of herbaceous plants to the food base of streams is influenced largely by the spatial distribution of herbs and by temporal patterns of flooding.

In recent years, stream ecologists have investigated organic-matter sources for stream ecosystems, but generally they have overlooked the contribution of terrestrial soils to stream channels. In floodplain soils, most of the fine sediments are high-density material that is most probably composed of soil particles or mineral sediments that became coated with organics while in the stream (Dahm 1981, Rounick and Winterbourn 1983). Proportions of fine sediments in different density fractions of soils differ by location within a riparian zone (Sollins et al. 1985). Foliage and wood fragments are found primarily in the light- and intermediate-density fractions.

The large proportion of high-density material in floodplain soils

Table 3. Potential rates of denitrification in soils of riparian zones and hillslopes in a 40-year-old deciduous and a 450-year-old coniferous forest (means expressed as $\text{ng N} \cdot \text{g}^{-1}$ dry weight of soil $\cdot \text{hr}^{-1}$ with standard errors in parentheses).

| Site | Soil depth (cm) | Geomorphic surface | | |
|------------|-----------------|--------------------|-----------|-----------|
| | | Floodplain | Toeslope | Hillslope |
| Coniferous | 0-15 | 6.3 (2.2) | 4.2 (4.2) | 1.2 (1.2) |
| | 15-30 | 0.4 (0.3) | 0.2 (0.1) | 0 (0) |
| Deciduous | 0-15 | 15.0 (2.9) | 8.2 (4.3) | 3.2 (1.2) |
| | 15-30 | 11.3 (2.6) | 1.4 (1.0) | 1.2 (0.7) |

reflects the hydraulic sorting and deposition of these materials during floods. Floodplain soils of major world rivers, such as the Amazon, frequently contain large percentages of highly weathered clay minerals resulting from extensive processing during erosion, transport, and storage (Sombroek 1984). Erosion and deposition within valley floors create complex patterns of soil development and mineralogy, which strongly influence riparian plant communities.

Retention. Geomorphic and hydraulic processes, riparian vegetation, and aquatic biota are linked functionally through processes of retention. Organic material and inorganic sediment must be retained within a stream to serve as either nutritional resources or habitats for most aquatic organisms. Boulders, logs, and branches trap material in transport, and low-velocity zones are depositional areas where particles drop out of suspension. These features of channel complexity also slow the transport of water and dissolved solutes, increasing the potential for biological uptake or physical adsorption of dissolved materials.

Retentive characteristics of stream channels are closely linked to the structure and composition of adjacent riparian zones. Channels with greater relative streambed roughness (i.e., height of streambed sediments relative to water depth) retain inputs more efficiently. Woody debris also creates major obstructions that alter flow patterns and remove both dissolved and particulate material from transport in forest streams (Bilby 1981). Stream reaches with debris dams in Oregon are four times more retentive than are reaches without debris dams (Speaker et al. 1984). Smaller woody debris, such as branches, sticks, and twigs, create sievelike accumulations, which are the most efficient structures for retaining leaves (Speaker et al. 1988). Complex arrays of different sizes of woody debris enhance the ability of streams to retain organic matter.

Valley landforms and location along a drainage also influence the ability of a stream to physically retain particulate inputs. Retention efficiency for particulate organic matter decreases from headwaters to large

rivers (Minshall et al. 1983), reflecting the decrease in relative streambed roughness and longitudinal bed relief and the influence of adjacent riparian vegetation. After high flows, storage of litter on streambanks in a prairie stream in Kansas was greater in a forested reach than in upstream reaches in grassland (Gurtz et al. 1988). In Lookout Creek, a tributary of the McKenzie River in Oregon, travel distances of leaves in unconstrained reach types (37 meters for the average leaf) were less than a third those in constrained reaches (127 meters), reflecting the more retentive nature of streams associated with broad floodplains.

Physical and biological factors that influence the process of retention are defined explicitly in the nutrient spiraling concept (Newbold et al. 1981). Longitudinal patterns of dissolved nutrient concentrations are functions of flux and uptake and can be expressed quantitatively as spiraling length (i.e., distance the average molecule travels as dissolved ions in transport, particles, or consumers). Increases in either algal production or inputs of leaves from the riparian forest decreased spiraling lengths for phosphorus in Walker Branch, Tennessee, where some spiraling lengths were as short as 10 m (Mulholland et al. 1985).

Valley landforms also influence longitudinal patterns of nutrient transport. In unconstrained reaches of Lookout Creek, Oregon, retention of ammonium was more than double that observed in constrained reaches (Lamberti et al. 1989). In this study, rates of leaf retention in the broad floodplain reaches were more than three times those measured in the more narrow valleys.

As stream channels pass from montane segments into broader stream valleys with lower channel gradients, they meander across the valley and form complex, braided channels. The longitudinal pattern of decreasing retention efficiency is reversed in this portion of river basins because the braided rivers create smaller channel dimensions and increased channel roughness. Modification of large rivers through practices such as channelization, levee construction, and land drainage has reduced the ability of these rivers to retain dissolved and particulate inputs.

Primary producers. Riparian vegetation strongly influences primary production in lotic ecosystems through attenuation of light energy (Minshall 1978). Riparian control of aquatic primary production is a cornerstone of the river continuum concept (Vannote et al. 1980). The influence of vegetation is most pronounced in forested headwater streams, where a small fraction of total solar radiation reaches the stream. Larger streams receive more solar radiation, and the production by aquatic plants increases accordingly (Minshall et al. 1983, Naiman and Sedell 1980).

Successional stage of riparian plant communities also determines the amount of light energy available for photosynthesis (Bott et al. 1985, Naiman 1983). In streams of comparable size but differing forest structure in Oregon, we observed that light intensities in summer rarely exceed 5% of full solar radiation in an old-growth coniferous stand and 7–15% of full sun in a 40-year-old deciduous stand. However, light intensities are 30–100% of total solar radiation in a recently clearcut stand. Net primary production was greatest in the open reach, averaging $210 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. Significantly less primary production occurred in the forested reaches, though primary production in the deciduous site ($58 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) was approximately double that in the coniferous site ($26 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$).

Processing of organic matter. Composition and abundance of riparian plant communities are major determinants of litter processing rates and consumer community structure (Cummins 1974, Cummins et al. 1989). Riparian vegetation controls the quantity and type of terrestrially derived organic matter delivered into streams. Vegetational composition also determines seasonal patterns of litter inputs. This organic material is decomposed by heterotrophic microorganisms, consumed or fragmented by aquatic macroinvertebrates, physically abraded into smaller particles, or leached and released as dissolved organic matter.

Leaf structure and chemical composition control the time required for processing of common riparian plants in streams, which ranges from several weeks to more than one year (see review in Webster and Benfield

1986). In general, leaves of herbaceous plants and many shrubs are processed quickly (30–50 days). Tree leaves that are high in nutrients or are not structurally resistant to breakdown require four to six months for complete processing. Leaves of other tree species (e.g., oak and aspen) and conifer needles may persist in streams for one to two years. A few shrubs and herbs with thick waxy cuticles, such as willow and sword fern, also require more than a year for complete decomposition. Although the quantity of litter contributed by forest stands is greater than that of herb- and shrub-dominated communities, food availability to aquatic consumers in different riparian settings differs far less than total litter inputs would suggest because the material from herbs and shrubs has a higher nutritional quality.

Aquatic invertebrates. Influences of streamside vegetation on allochthonous (produced outside the stream ecosystem) and autochthonous (produced within the stream ecosystem) food resources for aquatic invertebrates are potentially reflected in the trophic structure of invertebrate assemblages and relative composition of feeding functional-groups (i.e., classification based on method of food acquisition). These links may be manifested in the growth rates, abundance, and community structure of macroinvertebrate consumers in streams. Abundance and composition of detritivore assemblages in streams are determined in large part by the plant composition of riparian zones (Vannote et al. 1980).

Trophic groups of consumers are based on the type of food consumed, but aquatic macroinvertebrates also have been classified into functional groups by the mode of food acquisition (Cummins and Merritt 1984). Shredders, which break apart and consume larger food particles, frequently comprise more than 30% of the invertebrate densities in forested stream reaches (Hawkins and Sedell 1981, Minshall et al. 1983). Even in relatively open streams bordered by herbs and shrubs, shredders may be locally numerous in response to the less-abundant but higher-quality allochthonous food resources. Aquatic detritivores generally feed in deposi-

tional areas where organic matter accumulates, so riparian influence on the retention efficiency of a stream may affect the spatial distribution of stream detritivores (Anderson and Sedell 1979, Cummins et al. 1989).

Influences of riparian vegetation on aquatic primary producers indirectly affect the production of herbivores in streams. Heavily shaded stream reaches support low densities and lower relative abundances of herbivores than do areas with open riparian canopies, which contain high densities of herbivores (Hawkins and Sedell 1981).

Woody debris from riparian zones provides important invertebrate habitat (Anderson and Sedell 1979), and it strongly influences the formation of pools and lateral habitats. In sand-dominated rivers, woody debris serves as the major substrate for invertebrate assemblages (Wallace and Benke 1984). In addition, wood is directly consumed by a few specialized aquatic insects, and it provides an abundant but low-quality source of organic matter for other detritivores.

Aquatic vertebrates. Riparian zones are major determinants of both the food resources and habitats of aquatic vertebrates in streams and rivers. In headwater segments of drainages, riparian zones control allochthonous and autochthonous food resources for invertebrate consumers, which are the food base for predaceous fish. Furthermore, riparian zones directly control the food resources of herbivorous and detritivorous fishes.

In response to greater availability of prey, production and abundance of fish may be greater in reaches that are relatively unshaded by the riparian canopy (Murphy et al. 1981, Tschaplinski and Hartman 1983). Prey availability is a function of increased abundance of invertebrate consumers (Gregory et al. 1987). Forested reaches offer lower abundances of prey, a reflection of the lower quality of allochthonous food resources for aquatic invertebrates. In addition, fish are able to capture prey more efficiently in areas of higher solar radiation (Wilzbach et al. 1986). As a result, food for fish in forested reaches is potentially less abundant

and captured less efficiently.

Productivity of aquatic biota is closely linked to the degree of geomorphic and biological complexity within riparian zones. Abundances of both juvenile and adult trout in unconstrained reaches of Lookout Creek, a tributary to the McKenzie River, were more than double those in constrained reaches (Moore and Gregory 1989). Even when trout densities were adjusted for wetted channel area (which was approximately 30% greater in unconstrained reaches), unconstrained reaches contained higher abundances than adjacent constrained reaches. In broad, complex, unconstrained reaches, diversity of habitats and availability of refuges during floods are much greater than in structurally simple, constrained reaches. Numerous patches of diverse riparian plant communities on the multiple geomorphic surfaces contribute greater amounts of allochthonous litter to the active channel and floodplain. Even if fish populations are equal on the basis of wetted channel area or volume, broad valleys of unconstrained reaches potentially contain greater abundances of fish within a river basin than unconstrained reaches are able to support.

Productivity of riverine fish communities is determined by both habitat and food resources, factors that are intricately linked to the structure and composition of riparian zones. Geomorphic processes within the valley floor and modification of those processes by riparian plant communities create the habitat for fish communities. Channel morphology is strongly influenced by streambank stabilization by riparian vegetation and large woody debris (Keller and Swanson 1979). Complex lateral habitats, such as backwaters, eddies, and side channels, are created by the interaction of streamflow and lateral roughness elements that include living vegetation and large woody debris. These areas provide critical refuge during floods and serve as rearing areas for juvenile fish (Moore and Gregory 1988a,b).

In large, lowland rivers, floodplains provide food and habitat for migratory and resident fish communities (Welcomme 1988). Much of the world's freshwater fish production occurs in large floodplain rivers. Pro-

ductivity in these rivers depends on the exchange of dissolved nutrients, particulate organic matter, and organisms between active channels and floodplains (Junk et al. 1989).

Although the spatial and temporal extent of flooding in small, headwater rivers differs from that in large floodplain rivers, the fundamental ecological links are functionally similar in the two systems. Throughout a drainage, lateral habitats exhibit lower velocities and shallower dimensions than main channels and serve as depositional zones and refugia during high flows. Flooding of riparian forests along large rivers occurs during predictable seasons, covers extensive areas, and persists for many months. Forest-river interactions in these productive, flood-pulsed ecosystems predominantly occur within the flooded forest. In steep, montane streams, floodplains comprise less of the valley floor; consequently, interactions between the forest and the stream occur predominantly along the active channel and narrow floodplains.

Ecosystem perspectives of riparian zones

More than any other ecosystem, the structure and processes of lotic ecosystems are determined by their interface with adjacent ecosystems. The narrow, ribbon-like networks of streams and rivers intricately dissect the landscape, accentuating the interaction between aquatic and surrounding terrestrial ecosystems. Along this interface, aquatic and terrestrial communities interact along steep gradients of ecosystem properties.

The linear nature of lotic ecosystems enhances the importance of riparian zones in landscape ecology. River valleys connect montane headwaters with lowland terrains, providing avenues for the transfer of water, nutrients, sediment, particulate organic matter, and organisms. These fluxes are not solely in a downstream direction. Nutrients, sediments, and organic matter move laterally and are deposited onto floodplains, as well as being transported off the land into the stream. River valleys are important routes for the dispersal of plants and animals, both upstream and downstream, and provide corridors for migratory species. The low topographic

position of valley floors within a basin makes them avenues for the headward movement of warm air masses and the descent of cold air masses.

Riparian zones are one of the most dynamic portions of the landscape (Swanson et al. 1988). Frequent disturbance events in riparian zones create complex mosaics of landforms and associated biological communities that often are more heterogeneous and diverse than those associated with upslope landscapes. Flooding is frequent, often annual or even more often, and a single flood may modify hundreds of square kilometers of river valley. Individual patches created by flooding in valley floors are small and discontinuous relative to the total area influenced by the disturbance within a river basin. In contrast, many common disturbance events on hillslopes are limited in total area to tens of hectares or less, but the area affected is relatively continuous.

Riparian zones contain valuable water resources, plant communities, fisheries, and wildlife. Perspectives of riparian zones based on isolated components of the terrestrial-aquatic interface are ecologically incomplete and have limited application to understanding of ecosystems. Management of riparian resources requires a conceptual framework integrating the physical processes that create valley floor landforms, patterns of terrestrial plant succession, and structural and functional attributes of stream ecosystems. An ecosystem perspective of riparian zones provides a rigorous ecological basis for identifying riparian management objectives, evaluating current land-use practices, and developing future resource alternatives.

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