

Stream and Riparian Ecology

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INTRODUCTION

Water is a valuable resource for humans (direct consumption, power, irrigation, industry) and provides essential habitat for many organisms, including highly valued fish species such as salmonids. Aquatic habitat is influenced by processes active not only in the near-stream (riparian) zone (e.g., provision of shade) but also over the entire watershed (e.g., hillslope hydrologic processes that control the supply of water or the generation of landslides). Processes at both of these scales, and others, can be profoundly influenced by forestry activities, as described in more detail in Chapter 7 ("The Effects of Forest Disturbance on Hydrologic Processes and Watershed Response"), Chapter 9 ("Forest Management Effects on Hillslope Processes"), and Chapter 10 ("Channel Geomorphology: Fluvial Forms, Processes, and Forest Management Effects").

The purpose of this chapter is to provide an overview of stream and riparian ecology in British Columbia. It describes the ecological structure and function of streams and the associated riparian zones, and the interactions between them. Several topics in this chapter are integrative; therefore, some topics are addressed only briefly but references are provided for more in-depth coverage. For additional information on stream and riparian ecology, see Giller and Malmqvist (1998), Naiman and Bilby (editors, 1998), Naiman et al. (2005), Allan and Castillo (2007), and Richardson and Danehy (2007).

STREAMS

Definitions

The word "stream" is a generic term used to describe watercourses of all sizes that have channels of running water and which show evidence of fluvial processes, even if it is only the erosion of organic materials during peak runoff events. The term "river" is generally used to describe a large stream (e.g., Richardson and Milner 2005). No specific scale distinguishes a river from a stream, creek, or brook; hence, the term stream is used to mean all running waters. Stream channels include the active channel (or open channel), as well as relict channels that may be disconnected from the active channel or are connected only at high flow. The active channel is characterized by open water interacting with its bed materials (mineral substrate, wood). Below and adjacent to the active channel is the hyporheic zone—a zone of saturated sediments where infiltration of stream water via the streambed and banks

has a strong influence on water quality. It is typically the interface between stream water and groundwater and, as such, is often characterized as an ecotone spanning the boundaries of the surface and subsurface environments. The riparian zone is the terrestrial area adjacent to the stream. It is influenced by the water in the stream and (or) has an influence on the aquatic system (see below). A more comprehensive discussion of the classification of streams, channel types, and morphology, and the processes that shape stream environments is provided in Chapter 10 ("Channel Geomorphology: Fluvial Forms, Processes, and Forest Management Effects").

The duration of surface flow throughout the year in a given stream will vary from year to year, depending on weather patterns. It will also vary among streams, and along streams, with smaller streams more likely to have lower flow duration than bigger streams. In perennial streams, flow over the streambed is usually maintained throughout the year, although the entire active channel does not have to be inundated (Feminella 1996). In general, perennial streams are considered distinct from intermittent and ephemeral streams along a continuum of flow duration (Feminella 1996; Halwas et al. 2005). Intermittent and ephemeral channels differ in the duration of surface flow. Intermittent channels carry water through an extended portion of the year and may support populations of some benthic invertebrates with adaptations to this environment. Ephemeral channels show evidence of fluvial processes but have flows only during and shortly after precipitation events (Halwas et al. 2005).

During extended periods of low flow, the water table may drop below the streambed because of a combination of reduced runoff generation from upslope areas and transpiration by riparian vegetation. Under these conditions, sections of streams dry up wherever stream discharge is insufficient to maintain continuous surface flow and to satisfy water losses through the streambed and banks. Stream drying may occur frequently in the upper portions of the channel network, which can interrupt connectivity (Hunter et al. 2005). For example, Story et al. (2003) found that dewatering of an intermediate segment of stream channel effectively decoupled a lower reach from the warming effects of harvesting and road construction on an upper reach of a small stream in the central interior of British Columbia.

The use of various terms to define streams can cause confusion. For example, "headwaters" is sometimes used to refer to the sources of any stream, regardless of its size (Gomi et al. 2002; Moore and Richardson 2003). In this chapter, headwater streams are defined as having no perennially flowing tributaries (Gomi et al. 2002; Moore and Richardson 2003; Richardson and Danehy 2007). This narrow definition distinguishes headwaters from networks of streams (Gomi et al. 2002), placing the focus instead on the different processes governing headwaters versus non-headwaters and on the different management strategies available for these two channel types (see Gomi et al. 2002; Richardson and Danehy 2007).

Influence of Channel Type on Habitat

Channel components such as pools, riffles, steps, cascades, and plane beds provide important habitat for many organisms (Chapter 10, "Channel Geomorphology: Fluvial Forms, Processes, and Forest Management Effects"). Variations in the hydraulic characteristics of different reaches and channel sub-units create distinctive habitat characteristics that influence the spatial distributions of aquatic organisms (Hawkins et al. 1993). For example, riffles, a common channel feature, are characterized by relatively high flow velocities. This channel feature is favoured habitat for a diversity of aquatic organisms that filter fine particles of organic matter or prey from the water column and that require sufficient flow to bring these materials to them. Larval blackflies and net-spinning caddisflies, for example, can filter large masses of particles from passing water (Wallace and Merritt 1980), removing this load of organic material from water supplies and thus providing an important ecosystem service. Fish often require particular channel features during different life cycle stages. Adult salmonids (Pacific salmon, trout, char) generally use riffles for spawning redds, whereas juvenile salmonids usually inhabit pools. Within these pools, young salmon take advantage of cover behind boulders or logs, finding refuge from the full hydraulic force of the channel flow but still having ready access to prey carried along in the current (i.e., "drift").

Hydrology

Hyporheic exchange flow refers to the transfer of stream water through the streambed and banks (recharge), the down-valley transport of this water within the saturated zone surrounding the stream channel, and the subsequent discharge from the subsurface back into the channel (Figure 13.1). Hyporheic exchange flow occurs in response to variations in hydraulic potential along the streambed and banks and takes place at a range of spatial and temporal scales. For example, at a small scale, water pressure is often higher on the upstream side of bedforms than on the downstream side; the resulting hydraulic gradient induces infiltration of stream water on the upstream side of the bedform and discharge on the downstream side. This type of exchange flow is important for salmon redds, where the through-flow of surface water maintains high dissolved oxygen. This topic is covered in more detail in Chapter 14 ("Salmonids and the Hydrologic and Geomorphic Features of Their Spawning Streams in British Columbia").

Hyporheic exchange flow is controlled primarily by the morphology of the valley floor and stream channel (Harvey and Bencala 1993; Wroblicky et al. 1998; Kasahara and Wondzell 2003; Gooseff et al. 2006; Wondzell 2006). In steep headwater streams, hyporheic exchange flow can be controlled by boulder or log steps in the longitudinal profile of the stream (Kasahara and Wondzell 2003; Anderson et al. 2005). The volume of sediment stored above these steps largely determines the extent of the hyporheic zone. Downwelling stream water seeps into the

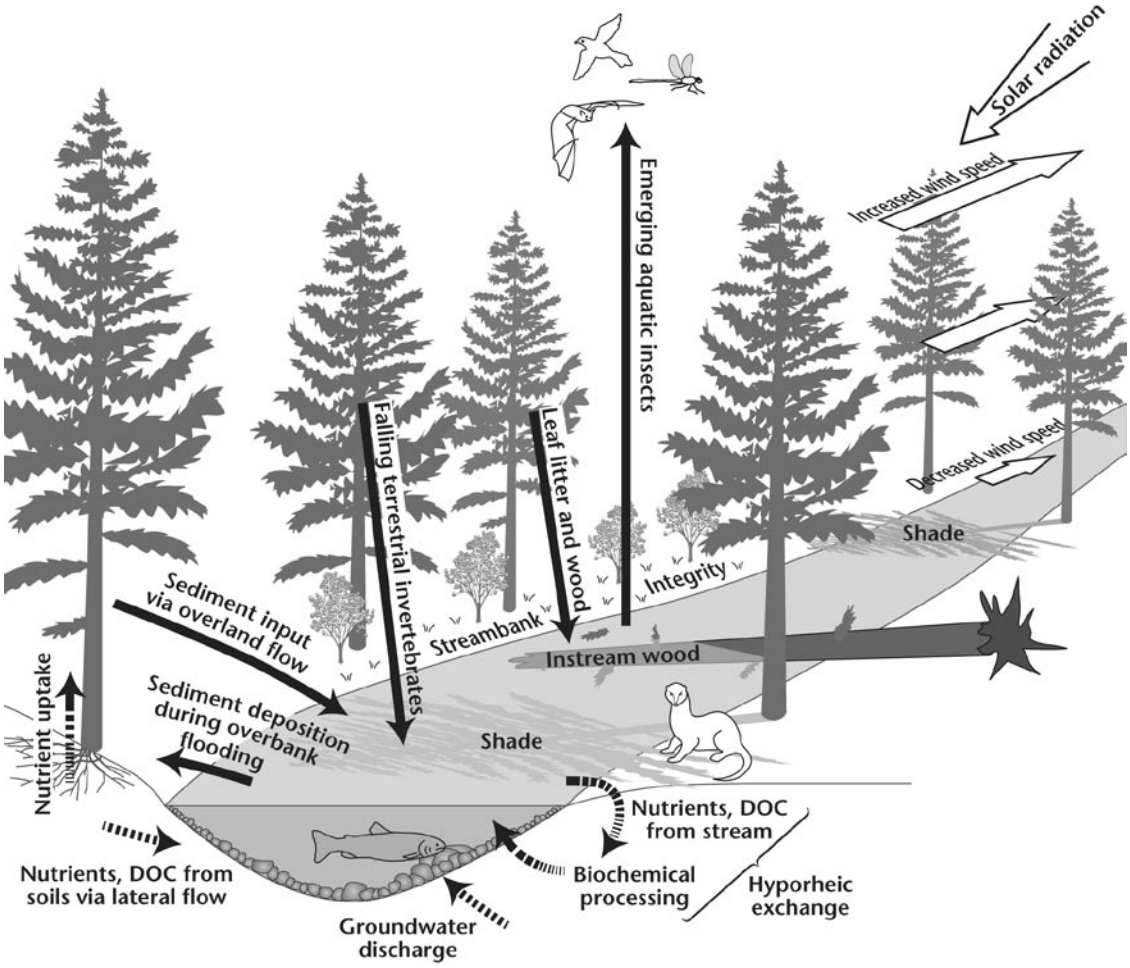


FIGURE 13.1 *A stream reach showing many of the elements and processes that link streams and riparian areas (E. Leinberger, University of British Columbia).*

streambed upstream of the steps and returns to the stream channel below the steps, where it upwells through the streambed (Harvey and Bencala 1993; Moore et al. 2005b; Scordo and Moore 2009).

In streams with riffle-pool morphology, channel water tends to flow into the streambed and banks at the riffle heads and discharge back into the stream in the downstream pools (Harvey and Bencala 1993; Kasahara and Wondzell 2003; Anderson et al. 2005). In larger, unconstrained streams with relatively wide and flat floodplains, exchange flows occur through mid-channel bars. Stream water flows into the bars through the streambed and bank on the upstream side, and returns to the stream channel on the downstream side (Vervier and Naiman 1992; Kasahara and Wondzell 2003). Exchange flows across gravel bars also support upwelling of stream water into floodplain springbrooks where abandoned channels are incised below the water table (Wondzell and Swanson 1996, 1999). Where streams meander through a floodplain, hyporheic flow paths typically shortcut the meander bends; water infiltrates across the downstream bank of one bend and re-emerges at the upstream bank of the following meander segment.

In wide, gravel-filled glaciated valleys, the bedrock underlying the alluvium often has sills that rise toward the alluvial surface alternating with over-deepened basins. In these situations, water typically leaves the stream near the head of a basin, flows down-valley near the base of the alluvium, and then is forced to emerge at the downstream end of the basin by the confining effect of the bedrock sill (Malard et al. 2002).

Water Chemistry and Temperature

Sources of hyporheic water include shallow subsurface flow from hillslopes, upwelling of deeper groundwater, and infiltration of channel water through the streambed and banks. Consequently, hyporheic zone water chemistry varies in both time and space due to variations in chemistry of the different water sources, and the associated rates of supply, flow paths, and mixing within the hyporheic zone. Because of the contributions of channel and hillslope water, hyporheic zones are biogeochemically distinct from groundwater. For example, the hyporheic zone tends to have enhanced dissolved oxygen, particularly near the recharge zones where oxygenated channel water infiltrates the streambed and banks (Ward et al. 1998). The contrasts in biogeochemistry between groundwater and the hyporheic zone are particularly important in relation to nitrogen processing. Information on nitrogen cycling in terrestrial and aquatic ecosystems is provided in Chapter 12 ("Water Quality and Forest Management").

The hyporheic zone is often thermally intermediate between surface water and groundwater. The water temperature in shallow sediments in hyporheic recharge zones usually follows diurnal and seasonal fluctuations in stream temperature but with a lag and attenuation that increases with depth (Moore et al. 2005b; Arrigoni et al. 2008).

Biology

Biologically, hyporheic zones provide habitat for a set of aquatic species that includes some not found in surface waters, and most of which are microscopic. Some of these taxa are rarely seen other than by people who expressly look for them; consequently, very little work has been done in British Columbia on these species. These taxa include a variety of rotifers, copepods and other crustaceans, nematodes, and gastrotrichs (Ward et al. 1998). Increasing evidence shows that some macro-invertebrate species (e.g., Capniidae stoneflies) live much of their life in the hyporheic zone and come to the bed surface only when nearing completion of the larval stages before emergence as a flying adult. These organisms feed on biofilm, the thin microbial layer growing on wet surfaces supported by dissolved organic carbon (DOC), and on particulate organic matter in the interstitial spaces in the hyporheic zone. These tiny invertebrates can move easily through the small interstitial spaces and may find refuge from predators and the forces associated with flowing waters.

Definition

The riparian zone has been defined in various ways, and the definition applied depends on the context in which it is used. The riparian zone has been referred to as the ecotone between aquatic and terrestrial realms (Naiman and Décamps 1997). The zone is often defined based on diagnostic plant communities; however, the applicability of this approach differs according to climatic context. In xeric (or seasonally xeric) landscapes, a strong gradient often exists from the vegetation associated with riparian areas to that of upslope areas. In mesic landscapes, such as those found in coastal areas, the contrast between upslope forest and riparian zones may be subtle or non-existent (Hibbs and Bower 2001).

From a functional perspective, the riparian zone is considered to be the portion of the terrestrial environment that exerts influence on a stream and (or) that is influenced by the water body (Gregory et al. 1991; Richardson et al. 2005b, Figure 13.1). The influences of streams on riparian areas are frequently expressed through differences in microclimate (e.g., Moore et al. 2005a; Rambo and North 2009). In addition, riparian soils often differ owing to periodic inundation by groundwater or overbank flows, which directly influence soil-forming processes and can lead to the development of Gleysols.

Management guidelines commonly define the riparian zone in terms of the width of a riparian buffer (Gregory et al. 1991; Forest Ecosystem Management Assessment Team 1993; Richardson et al. 2005b). The management guideline is the most arbitrary definition, but it is also the most pragmatic because it captures many of the functions of riparian–stream interactions and is simple to measure. A comprehensive review of the methods used to define and delineate riparian management areas (or zones) is provided in Forest Ecosystem Management Assessment Team (1993) and Chapter 15 ("Riparian Management and Effects on Function").

Riparian areas associated with lakes, wetlands, estuaries, and the ocean have special characteristics. Soils at the edges of these water bodies may remain saturated for most of the year if the surrounding area has little elevational gradient compared to areas with steeper gradients. This contrast in soil moisture condition can be an important determinant of riparian plant communities. Vegetation communities at the edge of lakes, wetlands, estuaries, and the ocean may show evidence of greater specialization than communities that border flowing waters; for instance, these communities may include extensive areas of rushes (e.g., *Juncus* spp.) and cattails (e.g., *Typha* spp.) that grade into partially submerged species (e.g., *Potamogeton* spp., *Nuphar*).

Functions of Riparian Vegetation

Riparian vegetation strongly influences both stream and riparian zone processes (Gregory et al. 1991). The magnitude or degree of coupling of instream processes with riparian vegetation partly depends on stream size (Richardson and Danehy 2007). For example, the forest canopy can cover the entire width of a small stream, shading the streambed from most light input. A larger stream, by creating a wider gap in the vegetation, may be exposed to direct sunlight over part of its area. This in turn affects the microclimate, thermal regime, and primary productivity of the stream (Figure 13.1).

Forest canopies can intercept 95% or more of the light reaching the canopy. The amount of light actually reaching the level of the stream depends on latitude, time of year, time of day, cloud cover and type, stream width, overstorey canopy characteristics, and shading by the streambanks and surrounding topography (Figure 13.2). The effect of the canopy on light infiltration can vary seasonally where deciduous trees are an important component of the riparian community (Hill et al. 2001). It can also vary over decadal and longer time scales in association with the state of forest development (second-growth forests typically intercept more light than old forests) and disturbance history (e.g., fires, blowdown). Increased light levels reaching the stream surface after disturbance can result in enhanced rates of primary production (Kiffney et al. 2003; Melody and Richardson 2007), depending on whether nutrients or other factors are limiting. Photosynthetically active radiation (PAR) and ultraviolet (UV) radiation can be intercepted by canopy vegetation, and can increase after the canopy has been opened by forest harvesting, fire, or insect damage. Light inputs (including UV, especially UVB, radiation) can negatively affect many organisms (Kelly et al. 2003). Ultraviolet



FIGURE 13.2 *Small stream at the University of British Columbia's Malcolm Knapp Research Forest (Stream G); note that with a 10-m riparian reserve on each side the stream channel is still mostly shaded from incoming solar radiation by canopy and shrub-layer vegetation. (Photo: J. Richardson)*

inputs can be attenuated by water depth or by high concentrations of DOC, which tends to increase following forest harvesting.

Riparian forests contribute to bank stability (Eaton et al. 2004) and strongly influence the rate and kind of organic matter inputs. The influence of vegetation also varies with the sizes of plants. In general, a closed tree canopy shades a stream more effectively than the herb or shrub layer, although small streams can be shaded effectively by understorey vegetation (e.g., Macdonald et al. 2003; Teti 2006).

Riparian vegetation influences microclimate by affecting solar radiation, longwave radiation, air temperature, humidity, and wind speed. Relative to an open site, forest cover tends to decrease solar radiation, increase incident longwave radiation, decrease wind speed, and moderate diurnal air temperature variations (Moore et al. 2005a). Decreased wind speed limits ventilation above and near streams; consequently, riparian zones are usually more humid than upslope areas (e.g., Danehy and Kirpes 2000) because the stream is a source of moisture.

Hydrology of the Riparian Zone

Hydrologically, the riparian zone functions to transmit groundwater and hillslope water to the stream channel. In addition, when the riparian water table rises to the ground surface, infiltration of rainfall and snowmelt is impeded, producing saturation overland flow (Hewlett and Hibbert 1967; Troendle 1985; Burns et al. 2001; McDonnell 2003; Buttle et al. 2004). Two-way exchanges of water between

the stream and the riparian aquifer (i.e., hyporheic exchange) can also occur.

Transpiration by riparian vegetation can extract water from the riparian zone, drawing down the riparian water table and producing a diurnal decrease in streamflow followed by recovery at night (Dunford and Fletcher 1947; Hewlett 1982; Bond et al. 2002). However, the timing and magnitude of these streamflow fluctuations vary with discharge, likely caused by changes in travel time and the downstream routing of streamflow fluctuations from different parts of the catchment (Wondzell et al. 2007). The magnitude of this process is also strongly affected by temperature, soil moisture regime, and vegetation types.

Water Quality

Forested riparian areas are often characterized as filters, intercepting sediments and nutrients that would otherwise enter streams (Lowrance et al. 1997). Removal of nutrients, such as nitrogen, is accomplished by plant uptake of riparian groundwater as it flows from surrounding slopes toward the stream (Castelle et al. 1994). The riparian zone can also trap sediments because its lower gradient reduces the transport capacity of overland flows. In addition, riparian vegetation provides flow resistance.

These observed water-quality functions have been well demonstrated in agricultural settings, and have led to recommendations for retaining forested reserves along streams. However, these water quality functions have been less well studied in forested catchments, and may be less important than in agricultural catchments. For example, several studies in the Pacific Northwest and elsewhere have shown that infiltration excess overland flow in areas with severely disturbed soils and saturation excess overland flow in topographic convergence zones may transport significant amounts of sediment from hillslopes to a stream even though the stream has an intact riparian buffer (Belt and O'Laughlin 1994; Rivenbark and Jackson 2004; Gomi et al. 2005).

Wood

Wood, large and small, performs several functions in stream and riparian systems. It can function as a geomorphic structure, as a place for interception and storage of organic matter, as cover for organisms, as a substrate, and even as a source of nutrition (e.g., Richardson 2008). Large wood is well known for contributing to stream channel stability. This function is discussed in detail in Chapter 10 ("Channel Geomorphology: Fluvial Forms, Processes, and Forest Management Effects"). Large wood contributes to the diversification of channel sub-units, and is especially important in the formation of plunge and scour pools, which provide habitat for many instream species.

Wood provides important habitat elements for organisms in streams (and riparian areas). Single logs, debris jams, and other accumulations of wood provide security cover for organisms seeking refuge from predators. Small fish can hide from predators among wood accumulations (Roni and Quinn 2001; Boss and Richardson 2002). The signal crayfish (*Pacifastacus leniusculus*), the sole species of native, freshwater crayfish in British Columbia, is most often found in wood accumulations where it hides from predators, such as river otters and mink (Bondar et al. 2005). Wood provides shelter from the full force of the stream current. This can allow fish and other organisms to occupy the water column without having to struggle against strong flows. In addition, wood contributes to the storage of fine sediments by damming and locally reducing the bed slope. The stored fine sediments may provide important spawning substrate for some species.

Organic matter would be easily entrained from the streambed and washed downstream if it were not for the presence of instream wood. A large proportion of organic matter gets stored temporarily against wood. Small pieces of wood, a single large piece, or a debris jam can all trap organic matter. The retention of organic matter over an extended period allows it to be broken down and utilized by the local aquatic community.

Wood provides a substrate for attachment for some organisms. This has not been demonstrated in British Columbia or the Pacific Northwest but, in other parts of the world, a number of aquatic organisms use wood preferentially as an attachment site. This is especially true for "collectors"—organisms that filter fine particles of organic matter that passes by in the water column (e.g., Benke et al. 1984).

Finally, wood provides a source of food, particularly for biofilm (see further detail below), which can use the wood as a carbon source or extract dissolved carbon from the passing water. Examination of well-decayed wood in many streams in British Columbia frequently reveals the presence of many

small organisms, especially stonefly larvae (Nemouridae) and midge larvae (Chironomidae). The role of wood as a substrate versus a food source is not easily distinguished for many organisms. For example, numerous invertebrate species consume biofilm from the wood surface, and it may constitute the largest proportion of some species' diets (Bondar et al. 2005; Eggert and Wallace 2007). The stomachs of adult signal crayfish were shown to contain large amounts of wood, and a stable isotope signature of the crayfish body matches biofilms growing on wood (Bondar et al. 2005). Some species feed almost exclusively on wood (referred to as xylophagy), including larvae of the elmid beetle (*Lara avara*) and larvae of a cranefly genus (*Lipsothrix* spp.; Dudley and Anderson 1982). An estimate of the quantitative contribution of wood to stream food webs has still not been attempted.

Bank Stability and Windthrow

Vegetation growing along the riparian area helps stabilize the stream channel in several ways. Plant roots bind to mineral substrate, making the streambank better able to resist the erosive forces of moving water (e.g., Eaton et al. 2004; Sakals and Sidle 2004). If riparian vegetation is of sufficient size (e.g., large trees), it can also trap wood that is transported during floods, and thereby contribute to bank stability, the formation of gravel bars, and the initiation of debris jams (Swanson et al. 1998). Windthrow can either stabilize or destabilize channels, depending on how it interacts with fluvial sediment transport processes. Windthrown streamside trees can increase sediment inputs to the channel via the root wad (Grizzel and Wolff 1998).

ORGANIC MATTER DYNAMICS IN STREAM-RIPARIAN SYSTEMS

Autochthonous Inputs

Primary production (photosynthesis) is the source of most biologically fixed energy available to food webs. We distinguish between *in situ* production (autochthonous) and production derived outside the local system (allochthonous). In riparian areas, many kinds of plants contribute to productivity. Likewise, within streams, primary producers such as algae can contribute to the energetic basis of stream food webs. In general, plant productivity is limited by nutrients (e.g., nitrogen, phosphorus, and potassium) or light, or some combination of these two factors (Kiffney et al. 2003, 2004). In streams with relatively open canopies (i.e., high light environments), primary production can be the dominant contributor to instream production (Minshall 1978). Some types of primary producers in streams are described below (see "The Biota of Streams and Their Riparian Areas" below).

Allochthonous Inputs to Streams

Various types of organic matter from the riparian and upslope areas can enter a stream (i.e., they are allochthonous; Figure 13.1). These materials occur as particulate (e.g., leaf litter, terrestrial invertebrates) or dissolved forms of matter (e.g., via groundwater discharge). In most streams, organic matter in the form of leaf litter and wood provides the main form of energy for stream food webs (Richardson et al. 2005a). The rate, timing, particle size, and quality of organic inputs vary with stream size, time of year, and forest type. Small streams have the highest inputs of leaf litter per unit surface area; as stream size increases, advection of particulate matter from upstream becomes the dominant source of fluvial organic matter within a stream reach.

Dissolved organic matter (DOM), or dissolved organic carbon (DOC), reaches the stream via groundwater discharge. DOC is colloidal and not truly dissolved, and is operationally defined as organic matter that can pass through 0.63-µm filter paper (Richardson et al. 2005a). Quantitatively, DOC may be the single largest flux of organic matter through streams (Kiffney et al. 2000); however, it is not easily stored because it gets flushed through the channel. It is used as an energy source primarily by bacteria, but it may also flocculate (weakly aggregate into larger particles) and can then be captured and consumed by organisms such as blackfly larvae (Ciborowski et al. 1997). Dissolved organic carbon often makes water tea-coloured, enhancing interception of UVB radiation that would otherwise damage stream organisms (Kelly et al. 2003). The specific qualities of DOC vary widely, and its value as a resource depends partly on its source (McArthur and Richardson 2002).

Particulate organic matter includes mainly leaf litter, seeds, small branches, and bark, all of which can contribute to the energy base of streams (Richardson 1992). It is generally classified as coarse

particulate organic matter (CPOM; > 1 mm^2) or fine particulate organic matter (FPOM; < 1 mm^2 and larger than dissolved). The distinction by particle size relates to the two primary groups of decomposers: fungi decompose CPOM and bacteria decompose FPOM. The size fractions also match the modes of foraging by consumers: CPOM is eaten by animals (mostly invertebrates) known as "shredders" and FPOM is eaten by "collectors."

The largest proportion of the organic matter load enters the stream in autumn and is used up by the following spring, which may result in periods of food limitation (Richardson 1991). In British Columbia, organic matter enters stream channels year-round. In particular, red alder, a common riparian tree in coastal British Columbia, can drop large numbers of leaves starting as early as June in most years, with peak leaf drop occurring in October and November.

Cross-ecosystem Subsidies

Stream ecosystems receive large inputs of organic matter from the riparian zone, especially leaf litter from riparian vegetation, but also by inputs of seeds, fruits, and terrestrial invertebrates that often drop from the riparian zone to the stream surface. These inputs represent a "cross-ecosystem resource subsidy," whereby organic matter production in one ecosystem is consumed by (and subsidizes) another (Polis et al. [editors] 2004; Marczak et al. 2007b; Richardson et al. 2009). The significance of these subsidies is increasingly recognized. Another example of a resource subsidy is the input of terrestrial invertebrates falling from the riparian canopy into streams. For example, some salmonids, such as coho and cutthroat trout, may gain more than 50% of their food energy from terrestrial invertebrates (Wipfli 1997). Other species, such as water striders, also depend on inputs of terrestrial invertebrates; consequently, aquatic organisms may have to compete for fast access to these inputs (Marczak et al. 2007a).

Cross-ecosystem subsidies can also transfer energy from the stream to the riparian zone. For example, adult aquatic insects are used as food sources by some riparian species, such as birds, bats, and dragonflies. Subsidies also operate along the stream network; for example, invertebrates are transported downstream from fishless headwater streams to larger, fish-bearing reaches. In addition, terrestrial vertebrates such as bears and mink depend on fish as a significant food source, although these latter sources of food may not strictly be subsidies (see Richardson et al. 2009 for further details).

Small streams can have relatively high rates of productivity and some of that production is moved downstream to larger streams where consumers, such as salmonid fish, may be able to capitalize on these resources (Wipfli and Gregovich 2002). Subsidies of resources and materials from headwaters to downstream ecosystems can be substantial (Wipfli et al. 2007). The magnitudes of these fluxes make it apparent that small streams are important contributors to fish production downstream. Within large rivers, the processing of materials to finer particles can provide an enormous flux of particles to downstream reaches (Malmqvist et al. 2001).

THE BIOTA OF STREAMS AND THEIR RIPARIAN AREAS

Terrestrial Species

Streams and riparian areas provide critical habitat for many terrestrial animals, plants, and other organisms during some stage of their life cycles. These organisms are referred to as "riparian obligates" and include stream-breeding amphibians and some species of waterbirds and mammals. "Riparian associates" are species that are more abundant in riparian than in upland areas, but do not depend solely on riparian areas to complete their life cycle (Richardson et al. 2005b; Mallik and Richardson 2009).

Amphibians are typically riparian obligates (some Plethodontidae salamanders in British Columbia are not) because they depend on water for their larval stages or other life history stages. In British Columbia, three species of amphibians are obligate stream-breeders: (1) the coastal tailed frog (*Ascaphus truei*), (2) the Rocky Mountain tailed frog (*A. montanus*), and (3) the coastal giant salamander (*Dicamptodon tenebrosus*). These species lay eggs in cobble-bottomed streams and the larvae are restricted to streams until metamorphosis (which may take as long as 4 years). In these three species, larval growth is affected by stream productivity and temperature (Kiffney and Richardson 2001; Mallory and Richardson 2005; Matsuda and Richardson 2005). Populations of these stream-associated amphib-

ians are negatively affected when fine sediments are introduced into the aquatic environment—growth rates are reduced, interstitial habitats are in-filled, and their capacity to hold on to the rocky substrate is potentially impaired (Welsh and Ollivier 1998). Toads and other amphibians are also sensitive to changes in freshwater habitats, such as increases in sedimentation, changes in algal resources, and increases in water temperatures (e.g., Wood and Richardson 2009).

Other vertebrate riparian obligates use riparian zones for foraging and (or) nesting. Riparian obligates typically rely on streams as a source of food. For example, dippers, harlequin ducks, spotted sandpipers, and water shrews feed largely on stream invertebrates, whereas river otters, kingfishers, and mergansers prey heavily on fish. The beaver is another riparian-obligate species that depends on deep-water habitats, usually created by dams, for refuge from predators and as a place to store winter food supplies. In turn, beavers modify stream channels in ways that provide important habitat elements for other species (e.g., Stevens et al. 2007). A large percentage of British Columbia's vertebrates are considered riparian obligates, and over half of all terrestrial vertebrate species in the province are considered at least riparian associates.

Many species of invertebrates, bryophytes, vascular plants, and fungi are also associated with riparian zones; however, our lack of basic knowledge about many species within these groups makes it difficult to determine the nature of their dependence on riparian areas. In one set of studies conducted in Sweden, bryophytes and snails were shown to be strongly associated with the riparian areas of small streams, and were seriously affected by forest harvesting even when 10-m reserves were provided (Hylander et al. 2004). Some spiders may be specially adapted to capture the emergent adults of aquatic insects (e.g., Marczak and Richardson 2007). Other organisms, such as dragonfly adults, also take advantage of this food source.

Vascular Plants, Mosses, Algae, and Microbes

A diverse assemblage of organisms including all the kingdoms of life, many of which are microscopic, inhabit streams. A number of vascular plants, also referred to as macrophytes, are found in moving water, although usually slow-moving water. These include pondweeds of the genus *Potamogeton*, as well as sedges, rushes, and cattails found along marginal areas. In general, rooted plants are relatively uncommon in British Columbia's streams. Mosses can be prevalent on stable rock surfaces in streams.

The complex mixture of small organisms generally referred to as biofilms are attached to most surfaces in streams. The organisms within this mixture include algae, bacteria, and fungi, as well as small organisms (protists and small animals) that feed on the biofilms. Biofilms develop very rapidly, have very high productivity, and may be a predominant source of food for consumers in some streams (Allan and Castillo 2007). The term "periphyton" is sometimes used, although this refers strictly to the algae component, and algae are usually associated with other organisms of the biofilms, so biofilm is the correct term for most applications.

Algae are single-celled, primary producers; that is, they are photosynthetic and grow on any surface (rocks, wood, plants, invertebrates) where they get energy from light and nutrients (e.g., nitrogen and phosphorus) from water. Algae are a taxonomically diverse grouping and represent many different phyla (divisions) within the plant and protist kingdoms. These groups include diatoms, green algae, red algae, and golden algae (Figure 13.3). Blue-green algae (Cyanobacteria) are a phylum of photosynthetic, nitrogen-fixing bacteria that are not constrained by the amount of fixed nitrogen in water. Most algae are small cells attached in some way to mineral and organic surfaces, where they form a thin, slippery mat tens of micrometres thick. Some species of algae form long filaments of cells, often protected by a mucilaginous sheath, which makes it difficult for small animals to eat them and allows the species to grow in the short term without control other than limitations of nutrients and space. Cyanobacteria can also avoid consumption by producing toxins as well as physical defences. One species of diatom (*Didymosphenia geminata*) forms thick mats that cause various problems in streams around the world, including within British Columbia. For more information on stream algae see Stevenson et al. (1996).

Bacteria are ubiquitous in streams, and generally obtain energy from DOC and nutrients from the passing water (or DOC excreted by algae within the biofilms). Bacteria are found on any surface, and some are thought to extract energy from both FPOM and DOC. Particles of FPOM that are fecal aggregates from stream invertebrates provide a large surface area for bacterial growth. Most bacteria are not generally harmful to humans, but certain types are toxic, and agencies monitor specifically for groups

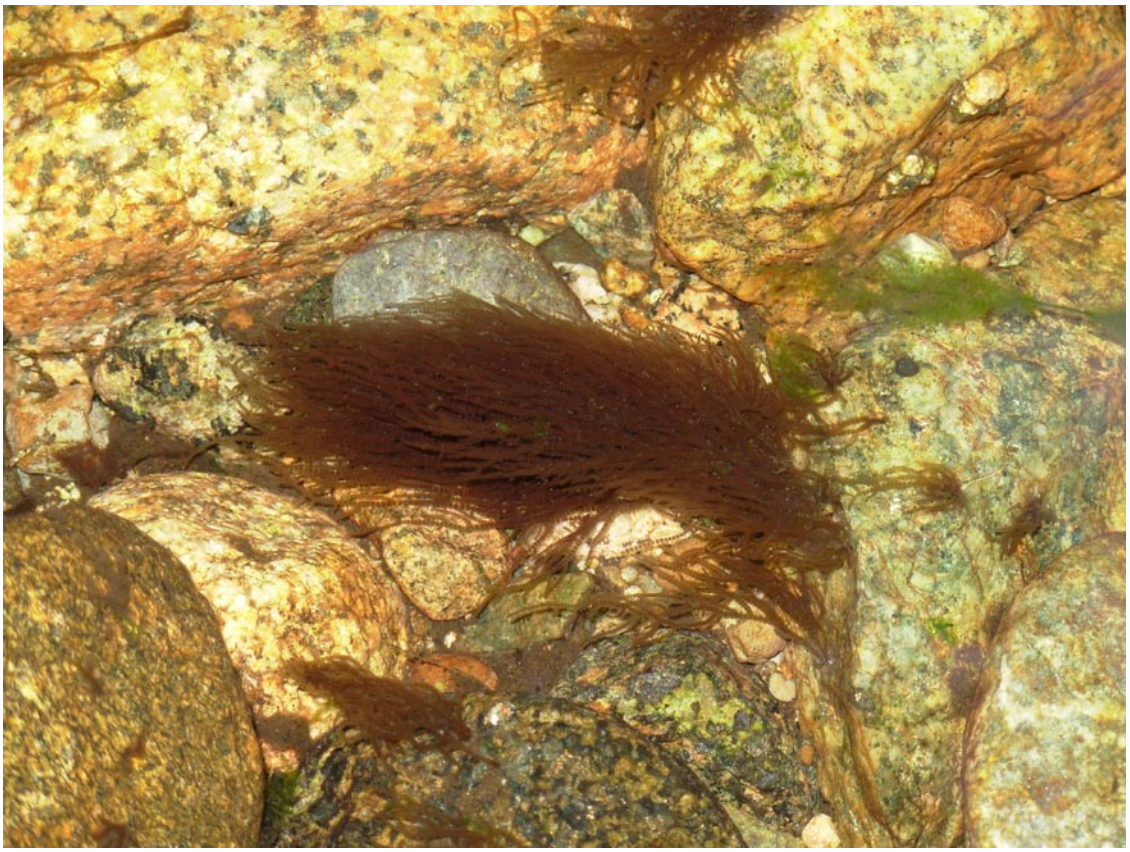


FIGURE 13.3 *Examples of two types of macroscopic stream algae, one a red algae (Rhodophyta) and the other a green algae (Chlorophyta) (top right of photo). The large clump of red algae in the middle is about 10 cm long. Most algae are microscopic. (Photo: J. Richardson)*

considered dangerous, such as *E. coli* and coliform-shaped bacteria.

Fungi in streams, referred to as "aquatic hyphomycetes," include hundreds of described species, but their taxonomic status and relation to terrestrial fungi is unclear. Fungi use CPOM (wood, leaves) as a carbon source and obtain nutrients from the water. Fungal spores colonize CPOM, establishing a mycelium (similar to a root system) that requires particles greater than about 1 mm in diameter. Because these fungi require a large particle of organic matter, they are found only in biofilms growing on organic surfaces. Fungi are considered to dominate the process of decomposition of leaves, wood, and animal carcasses in streams, and serve as an intermediate trophic level making cellulose (and other complex carbohydrates) available to consumer animals.

Stream Invertebrates

Freshwater invertebrates are described in numerous ways, either taxonomically or by functional attributes. Invertebrates are often called "benthos" (or described using the adjective "benthic"), which refers to their association with the bottom of a water body such as the streambed. Invertebrates occupy all major ecological roles one could expect in streams. They are consumers of basal resources (algae, biofilms, organic matter), and secondary consumers. They are the link from basal resources to higher trophic levels, including fish. One common way of describing freshwater invertebrates is by functional feeding group, or FFG (Cummins 1973; Merritt et al. 2008), a categorization based on what the species feeds on and how it gets its food. The primary FFGs, known as the "predators," include groups that engulf food as well as those that pierce and suck their prey. Another group, known as the "shredders," includes detritivorous invertebrates that feed on coarse particulate organic matter. Species that gather fine particulate organic matter are referred to as "collectors"; these organisms may use a filter of some

sort ("filterers"; e.g., a modified body part or a net made of silk or mucous) or gather food using mouth brushes or other modifications ("gatherers"). Organisms that eat biofilms or algae from rock or wood surfaces are known as "scrapers" or "grazers." A special kind of grazer is a group of organisms known as "xylophages" that scrape wood surfaces. The last of the invertebrate feeding groups are parasitic, and include species from the Nematoda (wire worms) and the Nematomorpha (horsehair worms).

Few accurate estimates exist of the numbers of invertebrate species in British Columbia. Cannings (2002) estimated that 87 species of dragonflies and damselflies (order Odonata) occur in the province. Of these dragonflies, 20 are either red- or blue-listed species. Molluscs, including freshwater mussels, snails, limpets, are another taxonomic group of invertebrates that includes many at-risk species in British Columbia, with 21 species either red- or blue-listed. Other orders of freshwater invertebrates in British Columbia are much less known, but species number easily in the thousands.

One particular use of freshwater invertebrates is as indicators of water quality and environmental condition. The community structure (composition and relative abundances) of invertebrates reflects the physical, chemical, and biological condition of a site by integrating all local and catchment-scale influences. Two primary sets of indicator tools have been developed: the "Reference Condition Approach" and "Benthic Index of Biotic Integrity." These approaches compare the community structure of a set of reference sites (assumed to be without environmental impacts) to a test site in order to determine whether the community structure diverges from what is predicted (e.g., Bailey et al. 2004; and see Chapter 17, "Watershed Measurement Methods and Data Limitations").

Fish

Many species of fish, particularly salmonids, are associated with streams. British Columbia has 75–80 species of freshwater fish (McPhail 2007). Most of these species are resident (i.e., non-anadromous), spending their entire life cycle in freshwater, although not necessarily always in streams. Some species move to different freshwater habitats depending on their life stage and the time of year (e.g., white sucker, Chinook salmon, bull trout, grayling).

Adults of anadromous species, such as salmonids and smelts (e.g., oolichan), return from the marine realm to freshwaters in large numbers. This return is an important part of stream ecology, form, and function (e.g., Hassan et al. 2008; Chapter 14, "Salmonids and the Hydrologic and Geomorphic Features of Their Spawning Streams in British Columbia"). Salmon provide direct and indirect inputs to aquatic environments by providing nutrients and an easily consumed resource complete with protein and fatty acids in the form of the carcass or salmon eggs (e.g., Zhang et al. 2003); however, toxins that bioaccumulate in the bodies of fish when they are in the marine environment can also be carried into terrestrial food webs (Christensen et al. 2005). For additional information on fish of British Columbia, see Groot and Margolis (editors, 1991), Richardson et al. (2000), and McPhail (2007).

ECOLOGICAL FUNCTIONS OF STREAMS IN WATERSHEDS

Longitudinal and Lateral Linkages

Streams are the receiving environment for materials transported by processes within catchments (watersheds) and are intimately linked to the surrounding basin. As described earlier in this chapter, these linkages take many forms. For example, groundwater entering streams carries with it signatures of the organic material in the forest floor and chemistry of the soils and bed materials it flows through. The concentration of DOC carried by groundwater varies through time (Kiffney et al. 2000) but little is known about the qualitative differences in organic components (McArthur and Richardson 2002). Leaf litter and other organic materials enter streams directly from the riparian forest canopy, although these materials are also carried in laterally from adjacent areas (referred to as "lateral transport"). Lateral delivery mechanisms include wind, advection from ephemeral channels, or even saturation overland flow.

An important distinction between the headwater and downstream portions of a stream network is the degree of coupling between the stream and the hillslopes. In headwater streams, this coupling is strong, so that disturbances occurring on the slopes (e.g., an increase in soil erosion) can directly influence

stream processes. In downstream reaches where the stream may flow within a low-gradient floodplain, the coupling is weaker, and stream processes are more sensitive to disturbances in the riparian zone, or to disturbances in the headwaters that propagate downstream. For these reasons, it is appropriate to adopt different management strategies in different portions of the stream network.

Materials delivered to streams from upslope source areas or the riparian zone can be transported downstream (Chapter 10, "Channel Geomorphology: Fluvial Forms, Processes, and Forest Management Effects"). Small streams, especially most headwaters, are relatively incompetent to carry large materials, and therefore tend to accumulate large clasts and wood that remain in place for long periods of time (i.e., colluvial material). This material only moves downstream to larger channels during infrequent, large debris flows (Chapter 8, "Hillslope Processes"). In environments where debris flows do not occur (e.g., low-gradient headwaters in the Interior Plateau), rates of downstream transport of mineral sediment and wood are constrained by the rates at which this material weathers or decays in situ to size classes that the stream is competent to move.

Channelized debris flows occur as brief, punctuated episodes, but as a consequence of moving large amounts of rock and wood stream channels are reshaped along with the habitat they provide (e.g., Swanson et al. 1998). The resulting changes in morphology can be long lasting. Some elements of the stream system recover relatively quickly (e.g., Lamberti et al. 1991) but others may take decades to stabilize.

Over longer time scales, stream erosion shapes the morphology of the riparian zone (e.g., by bank erosion and channel migration) and also interacts with hillslope processes (e.g., by undercutting footslopes). In these ways, stream erosion can modify the nature of coupling between the stream, its riparian zone, and the catchment as a whole.

The organization of the stream network and its lateral interactions varies with physiographic setting. For example, mountainous catchments typically have high gradients in the headwaters, with a dominant trend to lower gradients and decreased coupling in the downstream direction. In contrast, streams draining the interior plateaus may have relatively low-gradient reaches in their headwaters, often including wetlands, ponds, and small lakes, located upstream of reaches with high gradient and strong coupling where the streams are actively cutting through the plateau bedrock toward the level of a larger stream occupying a major valley (e.g., streams draining the Bonaparte and Nehalliston Plateaus located west of the North Thompson River).

Conceptual Models of Stream Ecosystem Organization

Three primary conceptual models highlight the spatial and temporal scaling of ecological processes within streams: (1) the River Continuum Concept (Vannote et al. 1980), (2) the Riverine Productivity Model (Thorp and Delong 1994), and (3) the Flood Pulse Model (Junk 1999). The River Continuum Concept (RCC) describes the linear variations in stream ecology from a stream's source to its mouth based on changes in characteristics such as stream size, gradient, biological energy sources, and temperature regime. As described above, the intensity of the linkages between a stream and its surroundings scales with stream size, particularly in relation to width; however, channel gradient and maximum flows also vary with stream size, producing longitudinal variations in stream power and tractive force. Although the RCC captures several important scale linkages governing stream ecology, it does not account for the branching network structure of a channel network and the important ecological role of tributaries (Gomi et al. 2002; Grant 2007). In addition, the RCC provides a static description of stream ecology, and does not explicitly recognize that streams evolve through time and interact with their landscape (Ward 1989). Some of the physical features observed in a stream can reflect the antecedent conditions caused by past channel-modifying flows or sediment inputs rather than the current flow regime and sediment supply.

The stream network concept is particularly important in relation to population dynamics and species diversity, especially in headward streams that can vary in their disturbance histories across a landscape. Streams high in the network may experience relatively higher rates of local extinction because of the limited population sizes they can support, as well as relatively lower rates of recolonization because of the distance from nearest sources (Fagan 2002). These extinction-recolonization dynamics may be one reason for the occurrence of relatively fewer species, especially large-bodied species, as one goes up a drainage network. The network perspective provides important insights for the conceptualization and management of watersheds that are only just starting

to permeate management agencies (Richardson and Thompson 2009).

The Riverine Productivity Model (RPM) emphasizes the lack of a continuous, longitudinal gradient in streams, and points to the nesting of hydrogeomorphic patches in streams (Thorp and Delong 1994). This view integrates variation in channels as an array of geomorphic elements at many spatial and temporal scales, more in line with a geomorphic perspective. It also highlights the local influence of hydrogeomorphology on species occurrences and biological processes. The RPM, as with the Flood Pulse Concept, better integrate lateral connectivity with floodplains than does the RCC (Junk 1999). The Flood Pulse Concept emphasizes the links across the stream-floodplain margin that result in movements of nutrients, sediments, wood, and species across the boundaries, and it varies temporally, especially during floods (Junk 1999; Richardson et al. 2009). This latter concept suggests that stream processes cannot be understood without consideration of the connections with the surrounding floodplain, riparian areas.

Spatial and Temporal Dynamics: Disturbance Regimes, Nutrient Spiralling, and Serial Discontinuity

Periodic disturbances can rearrange structures and functions of aquatic ecosystems, and allow the organizing processes to re-exert themselves. Disturbance is defined in many ways. One simple approach considers disturbances as events where some process exceeds the long-term mean plus two standard deviations (see Resh et al. 1988). In streams, disturbances include floods, low flows, channelized debris flows, fire, and other events that dramatically alter the streamscape. For example, extreme flows can mobilize large structural elements of streams and rearrange large wood and boulders, disrupting the physical habitat and food supplies within the channel and beyond.

Streamflow in channels moves materials, including organic particles and dissolved nutrients as well as large particles of mineral substrate. Particles or nutrients can be taken up by biological and physical processes in the bed, and then subsequently released back to the flow, resulting in cycling of particles between the bed and the flow in conjunction with downstream displacement. This pattern of coupled vertical cycling and downstream transport is known as "nutrient (or particle) spiralling" (Newbold et al. 2005). One important implication of nutrient spiralling is that it slows the downstream transport of nutrients, thus promoting primary production and biogeochemical processing within a given stream reach.

Humans can disrupt the natural patterns of stream dynamics by, for instance, installing dams to regulate flow and store water. These modified patterns rarely duplicate those naturally found at streams flowing from lakes (Richardson and Mackay 1991). This interruption of the longitudinal connections along the fluvial network is referred to as "serial discontinuity." This discontinuity can result in the interception of sediment and organic materials transported from upstream, alteration of flow and temperature regimes, changes in water chemistry, and suspended particulates.

SUMMARY

Streams and their riparian zones are complex systems that respond to transfers of water, sediment, nutrients, organic matter, and heat both laterally and longitudinally, all of which vary on time scales ranging from diurnal, synoptic (storm systems), and seasonal, to decadal and much longer. The current structure and function of a stream-riparian system reflects not only the influences of recent events but also those of past events and disturbances higher up in the stream network, which may be slowly propagating downstream. Because of the range of time scales associated with different types of disturbances and the rates at which different components of stream-riparian systems respond, it is inappropriate in many, if not most, cases to assume that stream structure and function are in a steady-state configuration (e.g., that the volume of instream wood is in equilibrium with long-term rates of input from the riparian forest). This dynamic nature of response to disturbances contributes to the spatial variability of stream conditions over a landscape, in addition to variations resulting from fundamental physiographic differences among catchments. This fact suggests that it may be difficult to use field measurements to

define reference conditions for use as management targets.

Significant advances have been made in our understanding of stream and riparian ecology over the last two decades, particularly in relation to organic-matter dynamics and the dynamics and function of instream wood. Nevertheless, significant gaps still exist that limit our ability to develop robust management guidelines.

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