Understanding Processes and Downstream Linkages of Headwater Systems

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Headwater systems, the areas from which water originates within a channel network, are characterized by interactions among hydrologic, geomorphic, and biological processes that vary from hillslopes to stream channels and from terrestrial to aquatic environments (Hack and Goodlett 1960). Although hydrologic, geomorphic, and biological processes in headwater systems have been studied for the last 50 years and much knowledge related to these systems is available (Hack and Goodlett 1960, Hewlett and Hibbert 1967, Likens et al. 1977), the roles of headwater streams within the watershed and the linkages from headwater to downstream systems are poorly understood. Headwater systems are critical areas for nutrient dynamics and habitat for macroinvertebrates, fish, and amphibians within watersheds (Meyer and Wallace 2001). Because of their geographical isolation, headwater systems also support genetically isolated species; thus, they support an important component of biodiversity in watersheds. For instance, new and endangered species are often found in headwater streams because such streams are relatively unexplored (Dieterich and Anderson 2000). Therefore, understanding the spatial and temporal variations of hydrologic, geomorphic, and biological processes in headwater systems is the key to comprehending the diversity and heterogeneity of riparian and riverine ecosystems.

Headwater systems are also important for understanding and protecting downstream ecosystems, because they are intimately linked. However, because headwater streams are small and numerous, the roles of headwater systems are typically underestimated and inadequately managed compared with larger downstream systems. Furthermore, management practices for protecting and restoring headwaters are different from those for larger systems, because headwater systems have greater drainage density and different land use types and intensities. Consequently, for the roles and downstream linkages of headwater systems to be understood, inherent differences between processes in headwater systems and larger watersheds need to be recognized in both conceptual and field studies. Therefore, our objectives for this article are to review characteristics of and differences in processes between headwaters and larger watershed systems; we also demonstrate spatial and temporal variations of hydrologic, geomorphic, and biological processes in headwater systems and the linkages of headwaters to downstream systems.

> HEADWATERS DIFFER FROM DOWNSTREAM REACHES BY THEIR CLOSE COUPLING TO HILLSLOPE PROCESSES, MORE TEMPORAL AND SPATIAL VARIATION, AND THEIR NEED FOR DIFFERENT MEANS OF PROTECTION FROM LAND USE

Our primary focus is on steep headwater systems in forested areas (> 4-degree gradient channels). Geomorphic time and space scales in this study are up to 1000 years and 100 square kilometers (km^2), respectively. Thus, we do not consider the effects of glaciation, tectonics, volcanism, and Holocene climate change, although we acknowledge that the landforms

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(e.g., glaciated U-shaped valleys) set the template for process rates in headwater systems.

The flow of sediment and woody debris from episodic landslides has a direct effect on headwater channels in mountainous regions (Dietrich and Dunne 1978, Benda and Cundy 1990, Whiting and Bradley 1993). The zones of initiation and deposition of these mass movements often both occur within headwater systems (Sidle et al. 1985), and the processes of mass movement affect the accumulation and distribution of woody debris throughout the channel network. Channel reach types (e.g., cascades, steps, and pools) in headwater channels vary because of sediment supply, larger substrate, exposed bedrock, and woody debris (Montgomery and Buffington 1998, Halwas and Church 2002). Furthermore, hydrologic processes in hillslopes and zero-order basins (unchannelized hallows) control stream-flow generation (Tsukamoto et al. 1982, Sidle et al. 2000) and stream chemistry (Likens et al. 1977). The expansion and shrinkage of wetted areas and stream channels in response to changing precipitation conditions significantly modify subsurface flow paths (Hewlett and Hibbert 1967). Such changes affect landslide probability in hillslopes (Sidle et al. 1985), as well as organic matter and nutrient fluxes from terrestrial to aquatic environments (Dieterich and Anderson 1998).

Biological processes in headwater systems also respond to the complex interactions of geomorphic and hydrologic processes at various temporal and spatial scales (Hynes 1975, Meyer and Wallace 2001). Leaf litter and woody debris from riparian zones and hillslopes (allochthonous input, that is, originating from outside the stream channels) are important sources of food and habitat for biota in small streams (Richardson 1992, Wallace et al. 1999). Relatively large substrate and woody debris in headwater channels modify channel hydraulics and provide sediment storage sites (Zimmerman and Church 2001); this in turn alters habitat types and accumulation of organic matter (Webster et al. 1999). Stream- and storm-flow generation processes modify organic matter dynamics (Kiffney et al. 2000), as well as biological community structure and life cycles of aquatic fauna in headwater channels (Dieterich and Anderson 2000).

Because the spatial extent of headwater systems makes up a major portion (70% to 80%) of the total catchment area (Sidle et al. 2000, Meyer and Wallace 2001), headwater systems are important sources of sediment, water, nutrients, and organic matter for downstream systems. Sediment produced in headwater systems moves through channel networks and alters channel morphology (Hogan et al. 1995, Benda and Dunne 1997a, 1997b). Floods induce scour and deposit sediment along channels, thus damaging riparian vegetation (Swanson et al. 1998). Sediment transported from headwater tributaries creates various channel environments (Gregory et al. 1991, Nakamura et al. 2000) and modifies patterns of channel morphology, riparian structure, and hyporheic exchange (exchange of water between saturated sediment surrounding the open channel and the channel itself; Wondzell and Swanson 1999), as well as macroinvertebrate communities in downstream reaches (Rice et al. 2001). Large amounts of allochthonous organic matter are transported from headwater tributaries (Cummins et al. 1983, Webster et al. 1999, Kiffney et al. 2000). Movement of detrital material and invertebrates from headwater reaches supports the downstream food web; this in turn alters productivity, population density, and community structure of stream biota in downstream reaches (Wipfli and Gregovich 2002).

Conceptual structures of stream ecosystems

Many conceptual studies have demonstrated the functional relationships of scales and processes in geomorphology, hydrology, and biology that contribute to our understanding of stream ecosystems. Recognition of stream systems as a continuum was a major advance in developing a functional and dynamic perspective from upstream to downstream systems (Hynes 1975, Vannote et al. 1980). Understanding and organization of temporal and spatial scales and their causality have affected paradigms in modern science and land use management. In geomorphology, Schumm and Lichty's comprehensive paper (1965) first demonstrated the dependent and independent processes of landform evolution at various temporal and spatial scales. Church and Mark (1980) discussed proportional characteristics of landforms and their behaviors at different scales.

The functional relationships among geomorphic processes in space and time are recognized as controls on the continuity of material transport in stream ecosystems. The equilibrium concept of geomorphology (Leopold et al. 1964), which demonstrated the relationship between sediment supply and transport, led to the development of the geomorphic perspective of fluvial processes in a continuum from upstream to downstream reaches. For instance, Hey (1979) suggested that a process–response model with functional linkages from upstream to downstream systems is needed to explain and predict channel responses to a set of input conditions. Sediment budgets and routing were used to describe the spatial and temporal linkages of sediment movement along channels (Dietrich and Dunne 1978). Additionally, Wolman and Millar (1960) and Dunne (1991) demonstrated temporal and spatial linkages between hydrologic and geomorphic processes with respect to rainfall–landslide thresholds and channel network development. Benda and Dunne (1997a, 1997b) examined the occurrence of mass movement in hillslopes and related sediment routing processes through a channel network from a stochastic viewpoint; they concluded that continuity and discontinuity of sediment transport occur within watersheds because of changes in valley width and channel gradient.

Continuity and discontinuity of biological processes from upper to lower reaches have been discussed in the context of heterogeneity of habitat, population, and community dynamics. The river continuum concept (Vannote et al. 1980) depicts upstream linkages and downstream adjustment of stream ecosystems, based on changes in channel morphology through streams and rivers (Leopold et al. 1964). Based on the river continuum concept, Ward and Stanford (1983, 1995) developed a serial discontinuity concept, whereby a dam or channel morphology (e.g., confined headwaters, meandering and braided reaches) disconnects the upstream to downstream continuum. In a separate attempt to characterize stream ecosystems, others have shown how surface and subsurface flow interactions along channel corridors are important to nutrient cycling and biotic communities (Newbold et al. 1982, Stanford and Ward 1993). A hierarchical classification of stream ecosystems was proposed to examine continuity and discontinuity of impacts on stream biota at different scales within watersheds (Frissell et al. 1986). Patch dynamics, formed by microtopographic attributes, may indicate the fragmentation of habitat and community structure in stream ecosystems (Pringle et al. 1988). Disturbances (e.g., landslides, debris flows, floods, and droughts) may control the patch distribution of organisms in and around stream systems (Townsend 1989, Gregory et al. 1991). Montgomery (1999) demonstrated that geomorphic processes set the templates of biological processes of disturbance, the river continuum, and patch dynamics in his process domain concept.

Although the importance of channel network structure for material dynamics has gradually been recognized (Johnson et al. 1995, Benda and Dunne 1997b, Meyer and Wallace 2001, Rice et al. 2001), when most of the earlier conceptual and field studies were conducted, watershed processes were assumed to be linear, and thus network structures such as tributary pattern, density, and junction effects were disregarded. The river continuum concept (Vannote et al. 1980) evokes not a network (branching shape), but a linear concept from upper to lower stream reaches. Similarly, the nutrient spiraling concept (Newbold et al. 1982) presents a more complex, but still linear, abstraction of solute dynamics in stream ecosystems within channels and hyporheic zones (Fisher 1997). However, Minshall and colleagues (1985) and Johnson and colleagues (1995) observed that landform attributes, such as tributary junctions in channel networks, affect the river continuum concept. Kirkby (1993) and Robinson and colleagues (1995) demonstrated the importance of channel networks in drainage basins for understanding and forecasting flow regimes, sediment transport processes, and landform evolution. Fisher (1997) noted that a paradigm shift from linear to network (branched shape) systems is necessary to understand the processes and linkages of physical and biological dynamics in stream ecosystems. Benda and colleagues (1997b) and Rice and colleagues (2001) emphasized the importance of channel network structure to understand the longitudinal variations in sediment movement and aquatic environments.

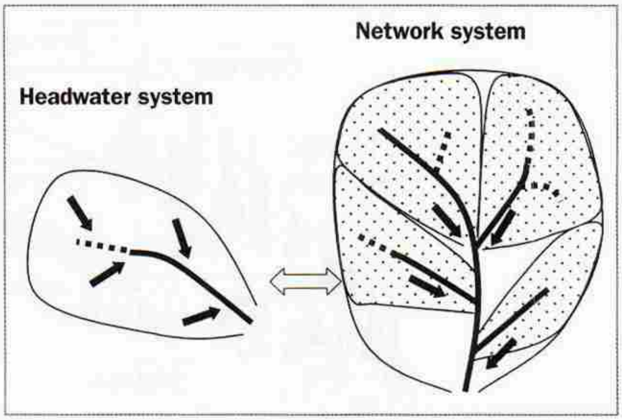

Figure 1. Structural differences between headwater and network systems. Arrows show the movement of sediment, water, nutrients, and organic material. Solid and broken lines show perennial and intermittent streams, respectively.

Headwater and network systems. The watershed network can be partitioned into two systems, headwater and network systems, on the basis of process characteristics. Structural differences and the continuous versus discontinuous nature of processes are critical for distinguishing between headwaters and larger watershed systems. Hydrologic, geomorphic, and biological processes in headwater systems cascade from hillslopes to streams (figure 1), and because hillslopes and streams are tightly coupled, material transport within headwater systems thus can be predicted as processes from hillslopes to stream channels. In contrast, material routing in larger watersheds is controlled by the channel network structure, because numerous headwaters are nested within it. Therefore, network structure must be considered in predicting material transport in larger watershed systems (figure 1; Fisher 1997). Nevertheless, processes from headwaters to downstream systems are often discontinuous because of changes in valley width, tributary junction angle, substrate size, and channel gradient (Benda and Cundy 1990, Ward and Stanford 1995, Bravard and Gilvear 1996, Rice et al. 2001).

Headwater systems contain four topographic units with distinctive biological and hydrological processes (Hack and Goodlett 1960): (1) hillslopes; (2) zero-order basins; (3) ephemeral or temporal channels emerging from zero-order basins, termed "transitional" channels; and (4) first- and second-order stream channels depending on linkages from hillslopes to channels (figure 2). Hillslopes have either divergent or straight contour lines, typically with no channelized flow. A zero-order basin is defined as an unchannelized hollow with convergent contour lines (Tsukamoto et al. 1982). Colluvial material, that is, debris transported by gravity from adjacent hillslopes, typically fills such hollows. Although saturated overland flow may be observed in zero-order basins and at the foot of hillslopes during storms, biological activity in such hillslopes and zero-order basins is terrestrial (Hack and Goodlett 1960).

Channels with defined banks may emanate from zero-order basins (Tsukamoto et al. 1982); if channels exist at the outlet of these basins, they represent the headmost definable channels with temporary or ephemeral flow. Temporary channels have more or less continuous flow at least 4 to 5

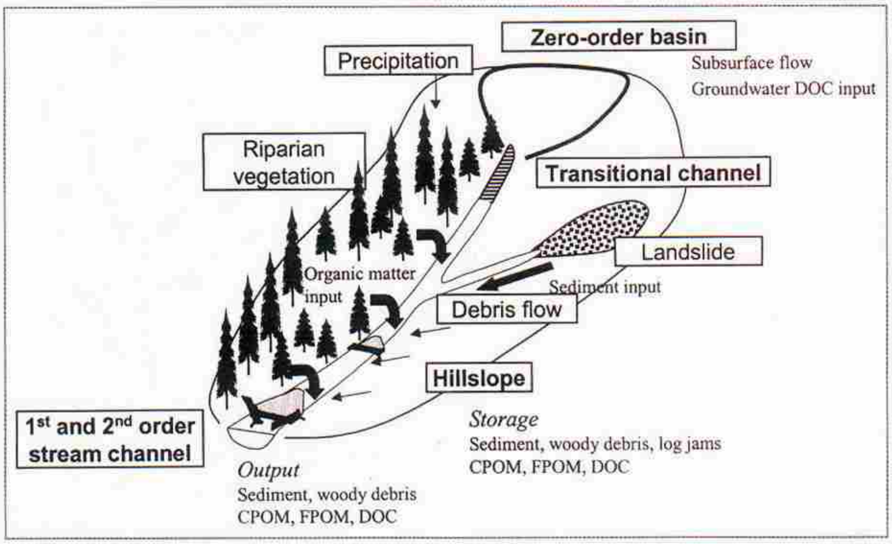

Figure 2. Processes and structures in headwater systems. Four topographic units compose headwater systems (bold type): hillslopes, zero-order basins, transitional channels (temporary or ephemeral channels emerging from zero-order basins), and first- and second-order stream channels. DOC, dissolved organic carbon; CPOM, coarse particulate organic matter; FPOM, fine particulate organic matter.

months in an average year, whereas ephemeral channels flow only for several days during wet periods (Dieterich and Anderson 2000). Thus, temporary and ephemeral channels emanating from zero-order basins typically cannot support the complete life cycles of the juvenile stages of aquatic macroinvertebrates, except for those species with a long diapause stage or other strategies for tolerating absence of surface flow (Anderson 1997, Meyer and Wallace 2001). Despite the inability to support macroinvertebrates, such channels are integral parts of channel networks and have distinct roles (e.g., temporary storage of organic matter; Dieterich and Anderson 1998, 2000, Halwas and Church 2002); thus, we call such streams transitional first-order channels, or simply transitional channels (figure 2). Transitional channels may gradually or abruptly begin from zero-order basins, depending on concentration (critical length) of saturated overland flow, infiltration–excess overland flow, and seepage erosion (by means of return flow). Such channels may also contain discontinuous segments prior to entering first-order channels (Montgomery and Dietrich 1989).

First-order streams are the uppermost, unbranched channels with either perennial flow or sustained intermittent flow (more than 4 to 5 months during an average year). First-order channels may directly emanate from the outlet of zero-order basins, depending on flow generation mechanisms (e.g., springs and seeps). Second-order (one branch) or even higher order (multiple branch) streams may be considered headwater streams, depending on degree of coupling between hillslopes and channels (e.g., transport distance of debris flow), which is discussed later in this article. Both first- and second-order channels may have intermittent reaches (dry parts), depending on groundwater level and volume of alluvium (sediment deposited by flowing water).

Size of headwater systems. In the river continuum concept (Vannote et al. 1980), headwater streams were defined as first- to second-order channels, based on Strahler's (1957) channel classification. However, there are potential problems with such classifications: (1) stream orders depend on scales of maps; (2) stream orders are modified by basin-scale topography (e.g., steep mountains versus plains); and (3) stream orders are not suitable for explaining hydrologic, geomorphic, and biological processes, as well as the importance of headwater streams. Meyer and Wallace (2001) noted that most detailed topographic maps did not include most headwater channels that might be found in field inventories. Thus, "headwaters" defined by Strahler's system and the river continuum concept pose ambiguities related to identification and interpretation of the sizes of headwater systems.

Processes from hillslopes to streams are important for defining the downstream limits of headwater systems. For instance, the transition from mass movement–dominated to fluvial process–dominated reaches occurs in headwater streams of Oregon for drainage areas up to 1.0 km^2 (figure 3a; Benda and Dunne 1987). The major causes for the deposition of debris flows are decreasing channel gradient, abrupt tributary junction, and flow divergence (Benda and Cundy 1990). Swanson and colleagues (1998) also noted that drainage areas from 0.01 to 1 km^2 (1 to 100 ha) are appropriate for distinguishing headwater streams based on physical and biological processes. Using digital elevation models (DEMs), Montgomery and Foufoula-Georgiou (1993) demonstrated that a shift from colluvial to alluvial geomorphic processes occurred from 0.1 to 1.0 km^2. However, digital elevation models have limitations related to identifying headwater swales. With developments in laser altimetry, DEMs with contour intervals less than or equal to 2 meters can be developed; such precision will facilitate identification of geomorphic hollows and other features.

Variation of discharge in drainages less than 1 km^2 was greater than for drainages larger than 1 km^2, based on the representative elementary area concept (figure 3B; Woods et al. 1995). Researchers (Wood et al. 1988, Woods et al. 1995) have noted that hydrologic processes within a 1 km^2 area are governed by hillslope processes related to soil depth, topography, rainfall intensity, and vegetation. Such site factors create greater variation of unit area discharge. In contrast, hydrological response in basins greater than 1 km^2 is more affected by routing processes and the structure and extent of the floodplain.

The findings of such studies indicate that the largest drainage area of headwater systems is likely 1 km^2 (figure 3a,

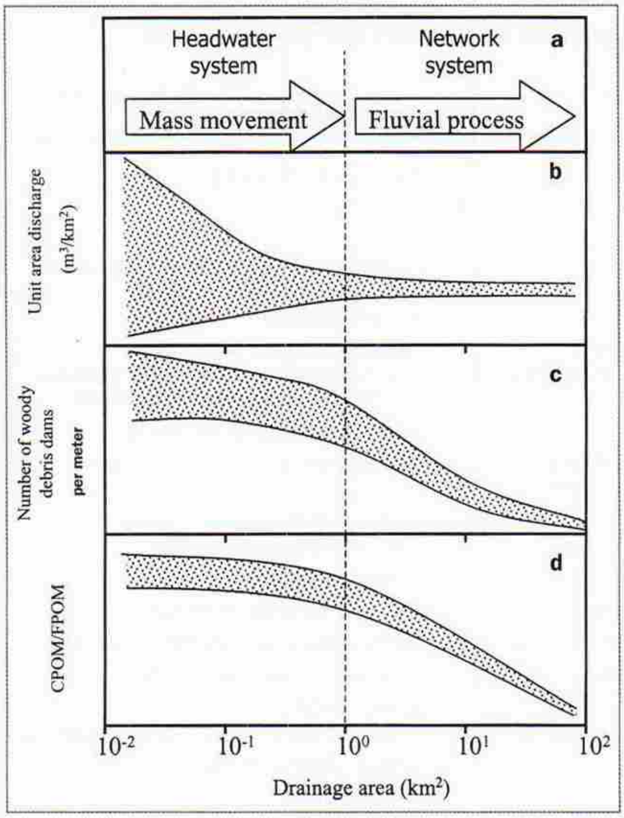

Figure 3. Downstream changes of hydrologic, geomorphic, and biological processes. Shaded area indicates ranges of each parameter. (a) Transition from debris flow–dominated to alluvium-dominated processes occurs at drainage areas ranging from 0.1 to 1.0 km^2 (Benda and Dunne 1987). (b) Variation of unit area discharge is greater within basins less than 1.0 km^2 (Woods et al. 1995). (c) Number of woody debris dams in headwater streams without mass movement is greater, compared with larger watershed systems, because relatively small woody debris can form dams. (d) Ratio in coarse particulate organic matter (CPOM $\geq$ 1 mm) and fine particulate organic matter (0.5 µm $\leq$ FPOM < 1 mm) may rapidly decease in drainage areas greater than 1.0 km^2, because CPOM is retained more in headwater streams and greater amounts of FPOM are transported from headwaters.

3B). Although we suggest a relative upper size limit (1 km^2) for headwater systems, depending on the region, process-based criteria are more important for the definition of headwater systems than simply catchment area (Whiting and Bradley 1993, Montgomery 1999). In the following sections, we review hydrologic, geomorphic, and biological processes in headwaters ($\leq$ 1 km^2 in drainage area) and network systems (> 1 km^2 in drainage area).

Hydrogeomorphic and biological processes

Different magnitudes and frequencies of hydrologic processes occur in headwaters and large watershed systems (Woods et al. 1995). Geomorphic processes in headwaters are largely stochastic, whereas more chronic processes related to routing of sediment, water, and wood are common in channel network systems (Benda and Dunne 1997a, 1997b). Such different hydrogeomorphic processes between headwater and network systems also modify biological community structure and distribution as well as recovery processes of stream biota from disturbances (Rice et al. 2001).

Hydrogeomorphic processes

Headwater systems. Water inputs of headwater systems are unique, compared with larger watershed systems. Because headwaters occupy the highest positions in catchments, precipitation and snow accumulation in headwaters are generally greater than in lower elevation zones (table 1). Rainfall inputs vary greatly among headwater systems; thus, isolated precipitation is typically observed more in headwater systems than in the overall watershed. The relative temporal fluctuation of peak flows in headwaters is greater than in larger watersheds (table 1, figure 3b; Robinson et al. 1995, Woods et al. 1995). Water inputs strongly affect hillslope and channel conditions because of the close coupling of hydrologic and geomorphic processes within confined and steep valleys of headwater systems (figure 2; Sidle et al. 2000). Stream temperature and water chemistry in headwater channels are closely related to soil pore structure and bedrock fractures in hillslopes and zero-order basins. Subsurface discharge from hillslopes contributes base flow and storm flow to headwater channels, initiates certain erosion processes, and is important for the development of headwater topography (Dunne 1991).

Storm flow responds rapidly to intense rainfall in headwaters because of their relatively small storage capacity and shorter flow paths. Storm flow generation in headwater channels is also affected by the responses of hillslopes and zero-order basins to changing antecedent moisture conditions (figure 4; Hewlett and Hibbert 1967, Sidle et al. 2000). Storm flow is primarily generated by direct runoff from saturated riparian areas and channel interception during lower antecedent moisture conditions. Throughflow from the soil matrix at the foot of hillslopes and riparian areas gradually increases with increasing wetness of the basins. During wet conditions, zero-order basins with relatively shallow soils start contributing surface runoff, and preferential flow from hillslopes augments storm flow. Zero-order basins and preferential flow paths are major contributors to storm flow during very wet conditions (Sidle et al. 2000). Transitional channels emerging from zero-order basins typically flow during such storms, when the storms are preceded by very wet conditions (figure 4). During rain and rain-on-snow events, nearly saturated conditions in hydrologically responsive areas (e.g., zero-order basins) may induce slope failure (Sidle et al. 1985). During the dry seasons, however, intermittent (dry) reaches may be found in headwater channels, depending on groundwater level and depth of alluvium.

Table 1. Characteristics of hydrologic, geomorphic, and biological processes in headwater and network systems, particularly in forested mountains in the Pacific Northwest.

Process	Characteristic	Headwater system	Network system
Hydrology	Precipitation	Greater precipitation Greater snow accumulation	Lower snow accumulation
	Heat dynamics	Canopy closure Dependent on groundwater flow	Canopy open
	Flow generation	Subsurface and groundwater flow in zero-order basins and hillslopes	Saturated overland and return flows in flood plain, riparian zones Tributary outflows
	Flow regime	Smaller absolute discharge volume Greater variation of unit-area peak discharge	Larger absolute discharge volume Smaller variation of unit-area peak discharge Synchronized or desynchronized outflows
	Hyporheic zone	Smaller volume	Greater lateral and vertical volume
	Stream chemistry	Soil pores, bedrock fractures, lithology Flow path in hillslopes and zero-order basin	Tributary outflows, hyporheic exchange
Geomorphology	Morphology	Higher mean altitde Steeper gradient and confined valley	Lower mean altitude Lower gradient and wider valley
	Dominant sediment movement	Episodic mass movement	Chronic bedload movement
	Channel reach type	Colluvial, cascade, step pool, bedrock	Step pool, pool riffle, ripple dune
	Roughness element	Woody debris, boulder, bed form (e.g., step)	Woody debris, logjams, bed form (e.g., bar)
Biology	Energy input	Allochthonous and lateral (from hillslope) input	Autochthonous and tributary outflows
	Organic matter	CPOM > FPOM DOC from groundwater flows and leaching	CPOM < FPOM DOC from tributaries and in-stream processing
	Nutrient source	Groundwater, riparian vegetation	Tributary outflows, floodplain
	Dominant functional group	Shredder	Gatherer, filterer
	Disturbance	Landslides and debris flows Drought	Flood pulses and bedload movement

DOC, dissolved organic carbon; CPOM, coarse particulate organic matter; FPOM, fine particulate organic matter.

Landslides and debris flows are dominant geomorphic processes in headwater systems (table 1). Such mass movements transport sediment and woody debris from hillslopes to channels and modify stream and riparian conditions. Sediment and woody debris are routed as channelized debris flows and deposited in the downstream reaches of headwater systems (Benda and Cundy 1990). Exposed bedrock and less woody debris typify scour and runout zones (Gomi et al. 2001). In contrast, massive piles of woody debris and sediment are found in deposition zones of debris flows (Hogan et al. 1995). Logjams at the terminal end of debris flows often modify both longitudinal and planimetric profiles of channels (e.g., braiding, forming side channels). Such geomorphic processes also alter riparian forest structure; for instance, alder (*Alnus* spp.) typically invades scour and deposition disturbance zones created by mass movement in the Pacific Northwest of the United States and Canada. Adjustment of channel morphology after landslides and debris flows largely depends on sediment and woody debris inputs. The regeneration of riparian stands in scour and deposition zones of debris flows begins to restore the recruitment of woody debris 20 to 50 years after mass movement in headwater streams (Gomi et al. 2001).

Channel morphology in headwater systems can be characterized by channel obstructions such as large woody debris and boulders (table 1; Zimmerman and Church 2001). Channel depth in headwaters tends to be shallower relative to the average diameters of such channel bed obstructions. Because substrate materials are not well sorted, interlocking boulders and cobbles modify the stability of channels, forming channel steps and creating sites for sediment storage (Zimmerman and Church 2001). Woody debris pieces also store sediment and modify channel roughness, and owing to the narrow channel width, relatively small woody debris pieces and jams have similar functions in headwater channels (Gomi et al. 2001). Therefore, headwater streams may have more woody debris dams than larger watershed systems because smaller woody debris can form these dams (figure 3c). The accumulation and distribution of woody debris alter the distribution of channel reach types such as cascades, step pools, and bedrock (Montgomery and Buffington 1998, Halwas and Church 2002).

Network systems. Observations of single headwater systems cannot be simply extrapolated to network systems where upstream contributions dominate base flow and storm flow generation. Because of the longer routing processes of water and greater storage capacity, peak flows in downstream reaches are often attenuated, lost partly to deep percolation and desynchronized flows that buffer peaks between headwaters and downstream locations. Floodplain and riparian zones also contribute to storm flow generation in larger watershed systems. Synchronized outflows from headwaters enhance peak flow in downstream reaches, whereas desynchronized outflows from headwaters attenuate flood peaks (table 1, figure 5; Robinson et al. 1995, Ziemer and Lisle 1998). Timing of outflows may be altered by hillslope and channel storage capacity (e.g., soil and substrate depth), amount of deep percolation from headwater systems, routing length, woody debris and other roughness elements in channels, and riparian vegetation characteristics.

More regular sediment transport, such as bedload movement, dominates sediment transport in downstream reaches (table 1). Sediment delivery from headwater to downstream is often interrupted because sediment is temporarily stored in or along the streambed, banks, terraces, and debris fans (Hey 1979, Benda and Dunne 1997a, Nakamura et al. 2000). Sediment transport from tributaries alters patterns in the downstream fining of substrate size (Rice et al. 2001). Sediment movement may appear as sediment waves through channel networks from headwater to downstream systems (figure 6; Benda and Dunne 1997b). Sediment deposits and accumulations induce local aggradation with the fining processes of sediment in the downstream direction. Such processes also modify channel reach types, sinuosity, and formation of side channels. Channels may shift laterally as banks erode and bars form in the unconfined floodplains of downstream reaches. Synchronized and desynchronized landslides and debris flows in headwater systems alter the impacts of sediment movement on geomorphic and biological conditions in downstream reaches (figure 6). Synchronized landslides and debris flow deposits aggregate extensively within confined reaches of downstream channels during relatively short periods. In contrast, desynchronized mass movements gradually aggregate in larger reaches of channels. Sediment transit time from headwaters to the main channel depends on the presence of unconstrained reaches, tributary junction angles, channel gradient, timing of various mass movements, and amount of runoff (Benda and Cundy 1990, Bravard and Gilvear 1996, Nakamura et al. 2000).

However, sediment transport to downstream reaches is not as simple as shown in figure 6. Woody debris often forms jam structures in the transition zone between headwaters and downstream reaches because of deposits from landslides and debris flows, fluvial transport, and recruitment from riparian areas (e.g., by wind throw and natural mortality). Logjams often store sediment for 40 to 50 years until the structures collapse or channel courses change (Hogan et al. 1995). Changing valley configurations, channel gradient, and material types also modify sediment transport from headwater to downstream systems (Whiting and Bradley 1993, Nakamura et al. 2000). Spatial distribution of mass movement occurrence influences sporadic sediment transport throughout network systems (Benda and Dunne 1997b).

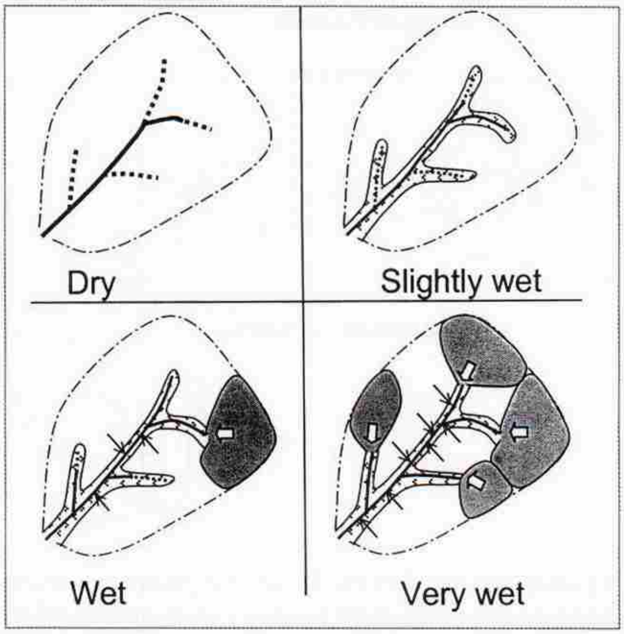

Figure 4. Conceptual view of dynamic, hydrologically active areas in headwaters. For dry conditions, riparian zones and direct precipitation on channels are the only active sites of flow generation. Throughflow from the soil matrix at the foot of hillslopes and riparian areas gradually activates with increasing wetness. Zero-order basins (shaded areas) with relatively shallow soils begin to contribute surface runoff (broad white arrows) during wet conditions, while preferential flow (thin black arrows) from hillslopes contributes less to stream flow. Water begins to flow in transitional channels emerging from zero-order basins. Zero-order basins and preferential flow actively contribute to storm flow during very wet conditions. Figure adapted from Sidle and colleagues (2000).

Biological processes

Terrestrial and aquatic processes in headwater systems. Because forested headwater streams are typically narrow with closed riparian canopies, biological processes (terrestrial and aquatic) in hillslopes and streams are closely linked (figure 2). Retention and routing of organic materials from allochthonous inputs (that is, riparian and lateral input of leaf litter and woody debris) are important factors affecting biological processes in headwater systems (table 1). Allochthonous energy sources are larger than autochthonous energy sources (e.g., primary production in streams; Bilby and Bisson 1992). Because of relatively small discharges and numerous roughness elements (e.g., boulders and woody debris), coarse particulate organic matter (CPOM ≥ 1 millimeter) tends to be stored behind in-stream obstructions, retained for longer periods in headwater channels, and transformed to smaller particles (Kiffney et al. 2000); such organic matter accumulations thus are important sources of food and habitat for macroinvertebrates (Richardson 1992). The dominant functional group of macroinvertebrates in headwater channels

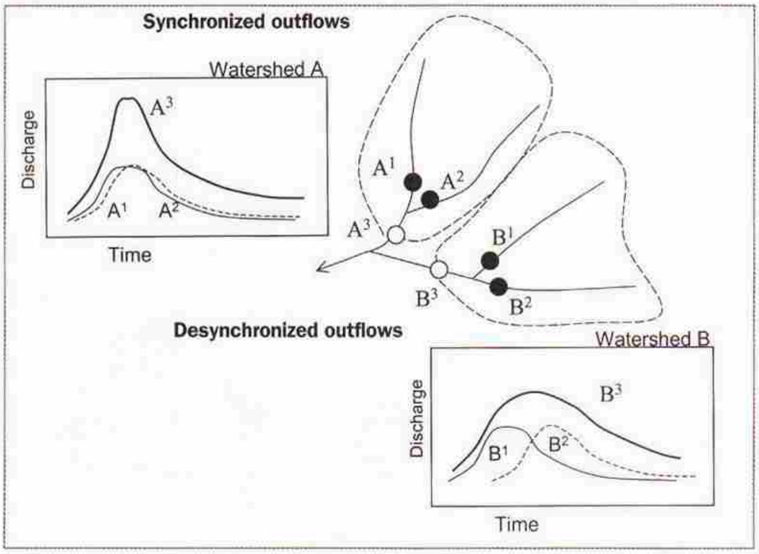

Figure 5. Synchronization of hydrologic processes in network systems. Volumes of outflows in tributaries of watersheds A and B are similar; however, peak discharges are different at A^3 and B^3 because of the different arrival time of peak flow. Figure adapted from Ziemer and Lisle (1998).

is shredders; they break larger particles into smaller sizes (table 1; Cummins et al. 1989). Fungi and bacteria also help to break CPOM into fine particulate organic matter ($0.5\ \mu m \leq$ FPOM < 1 mm) and dissolved organic carbon (DOC), which can benefit secondary consumers (Heard and Richardson 1995).

Terrestrially derived invertebrates that are associated with riparian vegetation are important for aquatic biota in headwater streams (Wipfli 1997). Riparian canopy closure also modifies heat and solar radiation available to stream channels (table 1). Groundwater and subsurface flows from hillslopes and zero-order basins contribute nutrients (e.g., DOC and nitrate) and influence water temperature (table 1). Availability of nutrients and light as well as water temperature modify algal growth; this in turn alters rates of nutrient leaching and litter decomposition. Headwater hyporheic zones are smaller, and their nutrient exchange is less, than in downstream reaches (Stanford and Ward 1993). Lateral habitat diversity in riparian zones may be low because of the confined valleys of headwater streams, whereas longitudinal variation of habitat may be high because of changes in discharge, channel gradient, and sediment supply. Transitional streams emerging from zero-order basins are also important habitat and sources of organic matter (Meyer and Wallace 2001).

Species composition and life history of vertebrates are also unique in headwaters. In the Pacific Northwest, there are relatively limited numbers and fewer species of fishes (e.g., cutthroat trout [*Oncorhynchus clarki*] and bull trout [*Salvelinus confluentus*]), because of the topographic harshness (steep channel gradients and shallow water). Owing to geographical isolation, populations of such trout may have unique genetic characteristics in headwater systems. Adult coho salmon (*Oncorhynchus kisutch*) spawn and some juvenile coho reside in refugia within lower headwater reaches during high flows (Bryant 1984). Some amphibians (e.g., tailed frogs [*Ascaphus truei*]) are also found primarily in headwater channels and associated riparian zones.

Responses to and recovery from disturbances in headwater systems. The dynamic nature of geomorphic and hydrologic processes affects the biotic community through disturbances. The frequency, intensity, and duration of disturbances are important factors altering responses and recovery time of riparian vegetation, channel morphology, and biological communities (Townsend 1989, Gregory et al. 1991, Swanson et al. 1998). Mass movement is the major disturbance in headwater channels, though forest fires, floods, and droughts also occur with varying frequencies (table 1). The movement of sediment and woody debris during landslides and debris flows drastically alters in-channel habitat (e.g., pool depth and interval) and macroinvertebrate communities (table 1; Lamberti et al. 1991). Because of limited refugia and larger moving particles in relatively confined headwater channels, macroinvertebrates and fish may be killed or washed away during peak flows or find refuge locally and in downstream reaches (Sedell et al. 1990).

Recovery processes in riparian and stream ecosystems differ according to level of disturbance. For instance, exposed bedrock is found in scour and runout zones of landslides and debris flows, and sediment and woody debris accumulations are distributed in deposition zones; this physical template characterizes the resistance and resilience of biotic communities and recovery processes from the disturbances. Either narrow bands of even-aged vegetation (typically alder in the Pacific Northwest) or mixed conifer and deciduous riparian corridors may be established along headwater channels depending on the level of disturbance (e.g., level of soil damage). Such differences in riparian vegetation modify long-term recovery processes of the biological communities in headwater ecosystems because of changes in the recruitment of leaf litter, woody debris, and sediment (Bilby and Bisson 1992, Gomi et al. 2001). Recovery of headwater biotic communities from disturbances may also depend on the continuity of headwater systems. Aerial dispersal from undisturbed downstream to upstream reaches is important for recovery. If undisturbed subreaches exist in otherwise disturbed upper reaches, invertebrates and organic matter that drift to disturbed reaches may induce quicker recovery of biotic communities (Lamberti et al. 1991).

Seasonal drought significantly affects the life cycles and community structure of invertebrates in headwater systems (table 1; Dieterich and Anderson 2000, Muchow and Richardson 2000). Temporary streams with flow duration greater than 4 to 5 months have similar faunal assemblages, whereas life cycles of macroinvertebrates are altered in intermittent streams with less than 3 months of flow. During the dry periods, aquatic insects move to hyporheic zones, remnant wetted pools, and permanently flowing channels (e.g., downstream reaches and other streams). Aquatic invertebrates also emerge as adults and other desiccation-resistant forms, largely through diapause. During much drier years, first- and second-order channels may be entirely dry and exert greater effects on macroinvertebrates.

Downstream assemblages in network systems. Materials from headwater tributaries modify downstream biological assemblages and processes in channel networks (table 1). Spatial and temporal variation of riparian and channel structures, related to mass movement as well as flow characteristics in headwater tributaries, creates different patterns of biological assemblages in channel network systems. Changes in channel morphology from confined headwater systems to braided and meandering channels in downstream systems may affect interaction between riparian and stream ecosystems, as well as habitat types (Ward and Stanford 1995). Sediment transport from tributaries affects the distribution of substrate sizes and thus modifies macroinvertebrate communities (Rice et al. 2001). Supplies of nutrients and organic matter to larger streams depend largely on inflows from tributaries. Most of the CPOM generated in headwater streams (70% to 90%) is transported downstream (Webster et al. 1999, Kiffney et al. 2000, Wipfli and Gregovich 2002). FPOM concentrations typically increase along headwater channels because of biological and physical processing (breakdown). Therefore, the CPOM/FPOM ratio may decrease rapidly with increasing drainage area: CPOM decline is due to lower inputs relative to channel size, and FPOM increases are due to breakdown processes (table 1, figure 3D; Webster et al. 1999). Types of vegetation (deciduous and coniferous) related to mass movement and timber harvesting histories in headwater systems may modify the amount and seasonal variation of CPOM and FPOM export to downstream reaches (Kiffney et al. 2000). For instance, leaves from deciduous trees and shrubs typically decompose 2 to 3 months after entering streams, whereas conifer needles take 200 days to 2 years to be processed by bacteria and macroinvertebrates (Gregory et al. 1991). Drifting organic materials and macroinvertebrates from fishless headwater tributaries support both growth rates and density of stream vertebrates in downstream systems (Wipfli and Gregovich 2002). Therefore, the food webs and community structures of network watershed systems may be modified through the drifting of materials (invertebrates and detritus) from headwater tributaries.

Because disturbances have different characteristics and magnitudes, their impacts on biological communities in headwaters and downstream reaches differ. The acute impact of a single debris flow may destroy biotic communities and habitat in headwater systems. In downstream systems, however, collective effects of sediment transport pulses and flood surges from headwater systems affect riparian vegetation and the biotic community (table 1; Nakamura et al. 2000). Basin-wide drought may increase the number of intermittent reaches and decrease linkages between headwaters and main channels. However, more refugia such as side channels and undisturbed tributaries are accessible in downstream reaches than in confined headwaters (Reice et al. 1990). The effects of disturbances in headwater systems on the channel network strongly relate to material routing processes from headwaters to downstream reaches.

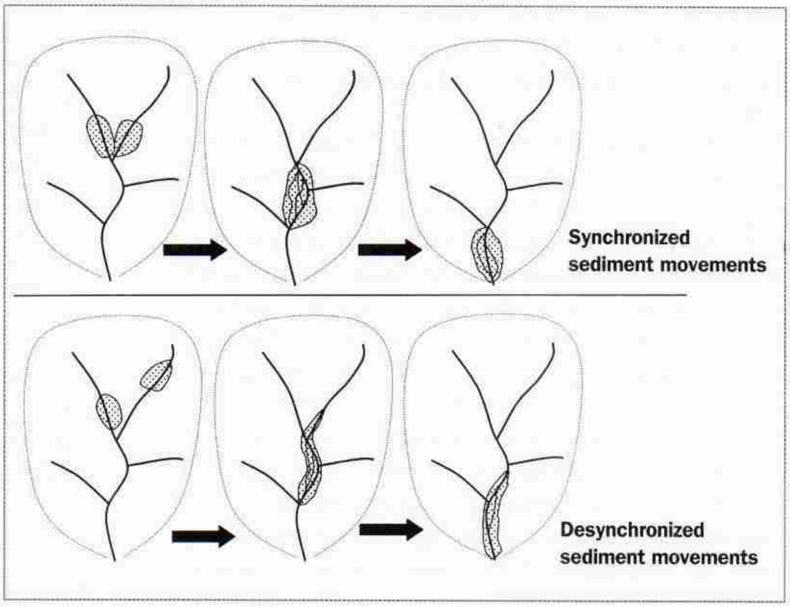

Figure 6. Synchronization of sediment movement in network systems. Shaded area shows sedimentation caused by landslides and debris flows. Accumulated sediments from headwater systems may alter the formation of braided and side channels. Figure adapted from Montgomery and Buffington (1998).

Linkages of headwater and network systems

The nature and degree of linkages between headwater and downstream systems are important aspects of the roles of headwater streams and routing processes of organic and inorganic matter. The degree of linkage varies spatially and temporally owing to topographic aspects and mass movement occurrences; such characteristics relate to long-term geomorphic (e.g., glaciation and tectonic) activities and the physical characteristics of rock, or lithology. Debris fans and floodplains are geomorphic attributes that support the linkages from headwaters to main channels. Sediment movement may be modified by channel gradient, tributary junction angle, and reach constraints (Benda and Cundy 1990, Nakamura et al. 2000). Beaver ponds, wetlands, and intermittent channel reaches also alter the connectivity between headwater and downstream systems; intermittent channel reaches also disrupt this connectivity. In addition, temporal variation related to mass movement, wind throw, wildfire, and land use change, as well as their respective recovery processes, affect the degree of connection between headwater and downstream systems. Biologically, connectivity is important for species migration, habitat, and refugia (Sedell et al. 1990) and for the flux of organic matter and nutrients (Cummins et al. 1983).

Tributary junctions between headwater and larger channels are very important as network nodes for regulating material flows in watersheds, and they have unique hydrologic, geomorphic, and biological attributes. Heterogeneity of water, sediment, and woody debris movement is higher at tributary junctions. Abrupt changes in channel gradient and valley width may cause sediment deposition, including terraces and debris fans. Riparian structure at such tributary junctions is complex, because riparian vegetation is frequently destroyed by floods, sediment deposition, and scour. Plant seeds transported by headwater streams may initiate riparian regeneration. Channel geometry at tributary junctions varies, depending on sediment and flow regimes from headwater systems and their degree of synchronization. Scour pools and gravel bars typically form along tributary flow margins, depending on junction angles (Bristow et al. 1993). Such sediment and woody debris deposits modify channel forms, for example, braiding and side channels. Hydrologic and geomorphic variability at tributary confluences also influences habitat types (pool size and distribution as well as substrate type) and biological processes in the area of the junction. Habitat, and therefore species composition, may be very diverse at confluences, because sediment and woody debris accumulations form pools, steps, and side channels (Rice et al. 2001). Drifting materials from headwater tributaries also mix at junctions. Hyporheic processes may be enhanced at junctions because of the accumulation and exchange of materials, but this subject has not been studied. Both nutrient and gas exchange in the hyporheic zone may be significant when sediment and woody debris accumulate and braided channels form at confluences.

Conclusions

Headwater systems are important sources of sediments, water, nutrients, and organic matter for downstream reaches. Despite the significant roles of headwater systems within the channel network, the ecological values of headwater systems are underestimated, and their processes have been extensively modified by land use (Meyer and Wallace 2001). Process characteristics differ between headwaters and larger watershed systems, which needs to be considered in establishing management guidelines. Hydrologic, geomorphic, and biological processes in and along hillslopes, zero-order basins, transitional channels, and first- and second-order channels characterize headwater systems in the following ways:

- Processes are tightly linked between hillslopes and channels and from terrestrial to aquatic environments.
- The expansion of hydrologically active areas (e.g., riparian zones, zero-order basins, bogs) during periods of increasing wetness increases the probability of mass movements and alters flow paths between terrestrial and aquatic environments.
- Landslides and debris flows that dominate geomorphic processes alter distributions and accumulations of sediment and woody debris.
- Recovery of invertebrate communities after such disturbances depends on drift, migration, and recolonization of biota from undisturbed upper and lower reaches.
- Succession and conversion from deciduous to coniferous riparian stands (and vice versa) modify availability of nutrients and light, recruitment of wood and organic materials, habitat types, and structure of biotic communities.

The numerous headwater tributaries that flow into downstream reaches affect hydrologic, geomorphic, and biological processes and attributes in downstream reaches of channel networks in the following ways:

- Synchronized or desynchronized inflows of water, sediments, nutrients, and organic matter from headwater tributaries create a variety of channel conditions and biological assemblages in downstream reaches.
- Temporal variations of disturbance regimes and riparian succession in headwater tributaries alter physical and biological conditions of channels, as well as input of materials (sediment, invertebrates, and detritus), which in turn modifies food webs and their productivity in downstream reaches.
- Connectivity of headwater systems to downstream reaches affects both the cumulative and dispersed nature of material transport processes within watershed systems.
- Tributary junctions are unique in their physical and biological processes and are important as network nodes.
- Spatial and temporal variations of processes in headwater systems are critical factors affecting the dynamics of stream ecosystems, as well as the heterogeneity of riparian and riverine landscapes in channel networks.

Because the characteristics of headwaters vary as a result of biogeoclimatic factors (e.g., riparian structure, precipitation, discharge, drainage density) and management and disturbance regimes, both similarities and differences of processes among headwater systems are important for evaluating the role of headwaters within the watershed network. Two general types of studies are needed to understand headwater processes and downstream linkages. Process-related studies within headwater systems are essential. Despite the progress in elucidating hydrogeomorphic (Sidle et al. 2000) and biological (Richardson 1992, Wallace et al. 1999) processes from hillslopes to stream channels, a better understanding of the functional linkages among wood, sediment, nutrients, and water in headwater systems is needed to address the relevant ecosystem process. It is also necessary to evaluate the influence of headwater processes on downstream systems (Benda and Dunne 1997b, Rice et al. 2001, Wipfli and Gregovich 2002). The connectivity of headwaters to downstream reaches must be evaluated in future studies to understand cumulative effects of changes in headwaters.

Ecology and management of downstream riparian zones have been extensively studied and applied in the context of stream restoration during the past 10 years (Naiman et al. 2000). However, the role of headwater systems has recently attracted more attention with respect to conservation, restoration, and management of downstream reaches. Consequently, management of headwater streams and riparian zones is important, and there are benefits to considering the linkages of headwater and downstream systems. The collection of appropriate information will require collaboration of interdisciplinary teams of hydrologists, geomorphologists, and biologists.

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