

Material Spiraling in Stream Corridors: A Telescoping Ecosystem Model

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ABSTRACT

Stream ecosystems consist of several subsystems that are spatially distributed concentrically, analogous to the elements of a simple telescope. Subsystems include the central surface stream, vertically and laterally arrayed saturated sediments (hyporheic and parafluvial zones), and the most distal element, the riparian zone. These zones are hydrologically connected; thus water and its dissolved and suspended load move through all of these subsystems as it flows downstream. In any given subsystem, chemical transformations result in a change in the quantity of materials in transport. *Processing length* is the length of subsystem required to “process” an amount of substrate equal to advective input. Long processing lengths reflect low rates of material cycling. Processing length provides the length dimension of each cylindrical element of the telescope and is specific to subsystem (for example, the surface stream), substrate (for instance, nitrate), and process (denitrification, for example). Disturbance causes processing length to increase. Processing length decreases during succession following disturbance. The whole stream-corridor ecosystem consists of several nested cylindrical elements that extend and retract, much as would a telescope, in

response to disturbance regime. This telescoping ecosystem model (TEM) can improve understanding of material retention in running water systems; that is, their “nutrient filtration” capacity. We hypothesize that disturbance by flooding alters this capacity in proportion to both intensity of disturbance and to the relative effect of disturbance on each subsystem. We would expect more distal subsystems (for example, the riparian zone) to show the highest resistance to floods. In contrast, we predict that postflood recovery of functions such as material processing (that is, resilience) will be highest in central elements and decrease laterally. Resistance and resilience of subsystems are thus both inversely correlated and spatially separated. We further hypothesize that cross-linkages between adjacent subsystems will enhance resilience of the system as a whole. Whole-ecosystem retention, transformation, and transport are thus viewed as a function of subsystem extent, lateral and vertical linkage, and disturbance regime.

Key words: stream; riparian; disturbance; nutrients; hyporheic; hydrology; telescoping ecosystem.

INTRODUCTION

In his classic *A Sand County Almanac and Sketches Here and There*, Aldo Leopold's (1949) poetic description of the odyssey of atom X is a harbinger of the

landscape-level nutrient-cycling studies of the last decade. The odyssey is tortuous, involving plants and animals of many species in a multitude of landscape patches; the journey, haltingly, but inexorably, seaward:

“Living plants retard the wash by impounding atoms; dead plants by locking them into decayed tissues. . . . mice and men, soils and songs, might merely be ways to retard the march of atoms to the sea.” (Leopold 1949, p 106)

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The landscape is a patchwork of many patch sizes and shapes. Materials follow a large number of routes from uplands to oceans. The path is stochastic and often downhill because the predominant transporting vehicle is water. Because these hydrologic linkages are driven by weather, the path is episodic and jerky. Within patches, characteristic rates of uptake, transformation, and release occur; thus, as the vehicle (water) travels, its load (elements) is adjusted in response to patch-specific material dynamics.

Catchments consist of upland ecosystems, where substantial material transformation and transport occurs, and lowland aquatic ecosystems (streams, rivers, and associated riparian zones), which receive water and materials from uplands and further transform and transport them. In this article, we emphasize the aquatic subsystem and its role in transport and transformation in the context of disturbance, largely by floods. Links between upland and aquatic subsystems will be considered briefly later.

Streams connect upland terrestrial systems with downflow lakes or seas, all of which display residence times for transportable substances that far exceed those typical of streams. Precipitation and seawater differ greatly in terms of their dissolved and suspended loads, and much of this difference has been attributed to terrestrial processes such as erosion, mineralization, and biotic uptake and release of materials (Gibbs 1970). But streams, rivers, and associated wetlands also contribute to this change in the quality, quantity, and temporal regime of transported materials through storage, breakdown, transformation, and augmentation of materials in transit. The net effect of these processes is a basic ecological property of running-water ecosystems. In this report, we consider what factors influence the capacity of running-water ecosystems to retain materials. We believe this question to be at the heart of stream ecology and to address a property that defines the essence of running-water ecosystems.

Our goal is to describe and develop a conceptual model, which we refer to as the *telescoping ecosystem model* (TEM). The model is intended to contribute to theory of pattern–process interaction that has developed primarily in the field of landscape ecology. Such theory recognizes the importance of spatial heterogeneity, often in a spatially explicit sense (Turner and Gardner 1991). The TEM deals with patterns and mechanisms of material movement in stream-corridor landscapes in the context of disturbance. The telescope metaphor describes a stream corridor as consisting of nested, concentric cylin-

ders, centered on the surface stream and extending into the riparian zone. The length of each of these elements is *processing length*, which is defined as the linear distance required to transform biogeochemically certain materials in transport. Processing length increases or decreases in response to disturbance; thus, the stream ecosystem as a whole extends and retracts as would a simple telescope. Whole-system nutrient retention thus depends on degree of connectedness among spatial elements (of the telescope) and the sensitivity of these elements to disturbance. We develop this model verbally and mathematically and discuss its relevance to terrestrial–aquatic linkages and to the concept of nutrient filtration by wetlands, riparian zones, and other landscape patches.

RELEVANT STREAM ECOSYSTEM CONCEPTS

Early watershed studies either ignored in-stream contributions to watershed function (Likens and others 1967) or combined streams and catchments in a common watershed–stream ecosystem perspective (Likens and others 1977). In the last quarter-century, the role of streams as transformers of inorganic and organic materials has been increasingly acknowledged (Cummins 1974; Newbold and others 1981; Meyer and others 1988; Mulholland 1992). Processing of materials in stream channels and retention or export of residuals has been recognized as a basic property of streams and rivers (Triska and others 1989; Fisher 1997). Streams are now receiving recognition as important landscape elements that process materials derived from terrestrial catchments and greatly affect the nature of inputs to downstream lakes, reservoirs, estuaries, floodplains, and groundwater (Billen and others 1991).

Until recently, most stream models have drawn boundaries at the surface water's edge and have considered stream ecosystems as well-mixed reactors without spatial detail. Minshall (1967) and Fisher and Likens (1973) demonstrated high rates of organic matter processing in streams considered to be homogeneous in structure. Stream nutrient dynamics were elegantly described with two-component spiraling models (Webster and Patten 1979; Newbold and others 1981) applied to streams as if they were uniform, homogeneous, and without tributaries. Early ideas of self-purification viewed streams and rivers in terms of longitudinal change in attributes imposed at points [point input of pollutants (McColl 1974)].

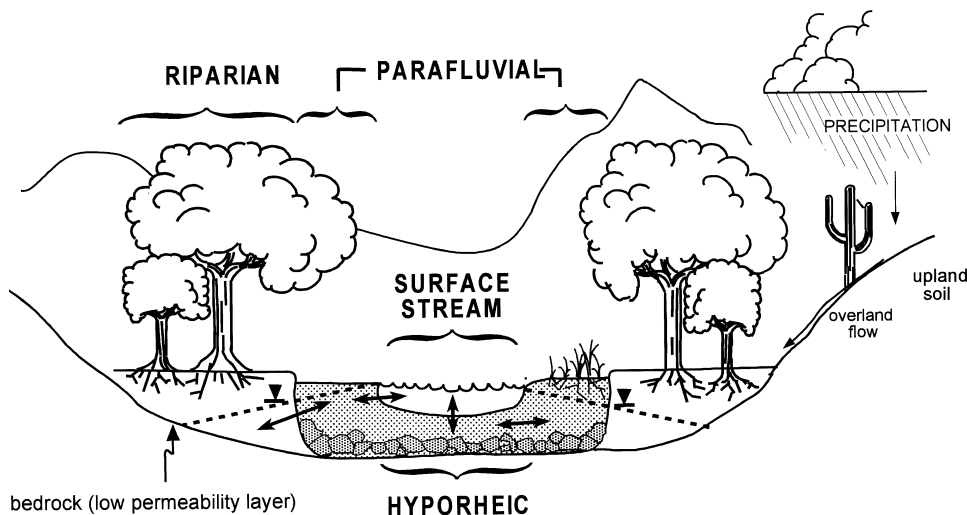


Figure 1. Diagram of the stream-corridor ecosystem in cross section, showing the surface stream, hyporheic zone, parafluvial zone, and riparian zone subsystems. The water table is shown by dashed line, and double-headed arrows denote hydrologic interactions among subsystems (cross-links).

In reality, streams are heterogeneous ecosystems and consist of many interacting patches. Spatial heterogeneity in stream-corridor ecosystems has been conceptualized hierarchically to enhance understanding at community and ecosystem levels (Frissell and others 1986; Gregory and others 1991; Grimm and Fisher 1992). Constraints and mechanisms of nutrient cycling have been shown to vary as a function of hierarchical level and scale (Grimm 1994; Fisher and others 1997). Spatial heterogeneity has certainly been recognized in terms of habitat for algae, invertebrates, and fish and its influence on community dynamics (Pringle and others 1988).

Spatial heterogeneity can also influence processing rates. For example, patches of inorganic and organic materials have been shown to support different rates of inorganic nutrient uptake in streams (Munn and Meyer 1990; D'Angelo and Webster 1991) and to thus influence uptake length on a patch-specific basis (Martí and Sabater 1996).

Recent studies of streams have expanded ecosystem boundaries beyond the surface-water channel and have included saturated subsurface as well as riparian and floodplain components as spatially distributed subsystems (Pinay and Decamps 1988; Triska and others 1989; Holmes and others 1994; Jones and others 1995a). These laterally and vertically connected subsystems are physically, chemically, and biologically quite different from the surface stream. Processing rates also vary widely on this template, and the extent to which the larger stream-corridor ecosystem retains, transforms, and transports materials is inexorably linked with this spatial heterogeneity.

In the 1990s, lotic and watershed biogeochemists have begun to meet on the middle ground of the riparian ecotone. Whereas stream ecologists now

recognize that the stream is more than surface water, terrestrial ecologists have begun to appreciate the extent of biogeochemical processing that occurs in wetter patches (Peterjohn and Correll 1984; Groffman and others 1992; Nelson and others 1995). Common to both groups of researchers is the insight that nutrient cycling occurs in heterogeneous environments, and biogeochemical transformations are consequently variable in space. A central question, therefore, is whether spatial configuration influences material retention.

Before we can answer this question, the spatial configuration of any ecosystem must be described. Our conceptualization of an arid land stream-corridor ecosystem borrows from landscape ecology. The ecosystem is characterized by a spatially explicit arrangement of landscape patches (subsystems), which we will refer to as its *configuration*. The term configuration is not scale specific and, in general, refers to the kind, size, shape, distribution, orientation, abundance, and connectivity among different landscape components. In this report, however, we restrict our discussion to configuration at the *reach scale* (Grimm and Fisher 1992). A more general discussion of configuration effects at multiple scales is presented by Fisher (1997) and Fisher and others (1997). Subsystems of a reach are the surface stream, the hyporheic zone beneath it, the lateral parafluvial zone (gravel bars with underlying saturated sediments within the annually flooded channel), and the more distal riparian zone, also with underlying saturated sediments (Figure 1). In desert streams, in particular, these subsystems are easily distinguished both on the ground and in aerial photographs. Although physical boundaries at the junction of subsystems are clear, we recognize that these boundaries are fluid and not always distinct.

Important features of this configuration are the lateral and vertical hydrologic connections (cross-links) among subsystems: the hyporheic zone interacts with the stream vertically; the parafluvial zone interacts with the stream and hyporheic zone laterally; and the riparian zone interacts laterally with the parafluvial zone (Figure 1).

THE TELESCOPING ECOSYSTEM MODEL

Overview

The nutrient spiraling concept (Webster and Patten 1979; Newbold and others 1981) provides a useful model for envisioning material retention in streams; however, it considers neither spatial heterogeneity nor configuration of subsystems. The TEM incorporates multiple subsystems and the interactions among them, in a disturbance context. In simplest terms, we could consider the movement of water between the surface stream and lateral gravel bars of the parafluvial zone. Water moves into (and out of) gravel bars at some measurable rate. At some distance below a given point, an amount of water equivalent to stream discharge at that point will have entered gravel bars. This length of stream is the *hydraulic uptake length*, that is, the length of stream required to remove an amount of water equal to discharge [see also Mulholland and others (1994)]. Note that no net change in the amount of water flowing down the channel occurred; that is, there was no net retention of water in that *release length* is the same as uptake length (Table 1). *Flowpath length* refers merely to the distance traveled by a given parcel of water in one subsystem (for instance, a gravel bar) before it enters another subsystem (for example, the surface stream).

Because solutes are transported with water, this concept should be applicable to solutes as well, provided we account for uptake, release, and transformation. Whereas we have referred to the dependent variable in the hydrologic example as uptake length, for transported materials we introduce the term *processing length*. This term is preferred over uptake length because material transformations are varied, and not all of them result in removal of materials from advective transport. As an example, consider changes in nitrate concentration in surface stream and parafluvial flowpaths of Sycamore Creek (Figure 2). We can calculate uptake and nitrification processing lengths (Figure 2) by using background changes with knowledge that algal uptake (surface stream) and nitrification (parafluvial) are the predominant contributors to concentration change

along these flowpaths (Grimm 1987; Holmes and others 1994).

The myriad processes that contribute to an ecosystem or subsystem's retention (defined as input minus output for some time period; Table 1) of a material each can be characterized by a processing length. Collectively, uptake, mineralization, and other transformations sum to system *retention*. Retention also may be expressed as a length (*retention length*); however, because retention can be negative (output > input), we think of a negative retention length as the length of stream (or subsystem) required for input flux to double (Table 1). Subsystems with negative retention are sources of the material; those with positive retention are sinks. Whole-system material retention is a consequence of the configuration of subsystems and the retention characteristics of each subsystem, which in turn is a result of individual processing lengths for the material.

In addition to incorporating configuration and heterogeneity in the model, we also must consider the influence of disturbance. Nowhere is this more true than in stream ecosystems of arid regions, which are infrequently but severely disturbed by flash floods. Because intervals between such "resetting" events are long, successional sequences are extended (Fisher 1983, 1990). The TEM therefore includes an explicit consideration of effects of time since disturbance (successional status) on processing and retention lengths. The latter are based on logical extensions of models of nutrient retention during succession [for example, see Vitousek and Reiners (1975), Bormann and Likens (1979), Gorham and others (1979), and Grimm and Fisher (1986)], and are discussed in detail later.

To illustrate components of the TEM, we consider the example of changes in inorganic nitrogen (N) concentration along surface stream, parafluvial, and hyporheic flowpaths (Figure 3). Because of algal uptake, inorganic N decreases in stream water, whereas it increases along subsurface flowpaths because of mineralization of surface-derived organic matter and subsequent nitrification. Each of these spatial patterns becomes more pronounced in successional time, steepening the gradient as biomass and hence areal processing rates increase (and thereby shorten processing lengths). Other processes come into play at the ends of gradients. In the surface stream, N limitation fosters growth of cyanobacterial N fixers, which may result in a downstream increase in the inorganic N concentration. As the processing length for N fixation shortens, the overall retention length will increase. In subsurface environ-

Table 1. Definition of Terms and Units Used in the Text: Units Are Expressed Using the International System (that is, M, Units of Mass; L, Units of Length; and T, Units of Time)

Parameter	Units	Definition
Material	M	An element, ion, compound, or complex mixture in a dissolved or particulate state. To avoid confusion, the material under consideration must be clearly specified (for example, total fixed nitrogen, dissolved phosphorus, or nitrate).
Advective material flux	$M L^{-1} T^{-1}$	Movement of materials through a subsystem via the movement of a medium such as water. In our case, advective flux occurs as dissolved and particulate load. Other input vectors exist (for example, litter fall or nitrogen fixation), but are not considered in our model.
Processing	$M L^{-2} T^{-1}$	Any chemical or physical transformation that results in a change in the form or state of a material.
Processing length	L	Average subsystem distance required to process an amount of material equal to the advective influx. This distance is material and process specific (for example, nitrification length).
Uptake	$M L^{-2} T^{-1}$	Processing that results in removal of a material from advective transport. It can be biologically, chemically or physically mediated (for example, assimilation, precipitation, or adsorption).
Uptake length	L	Average subsystem distance required to remove an amount of material equal to the advective influx.
Release	$M L^{-2} T^{-1}$	Processing that results in return of a material to advective medium. It can be biologically, chemically or physically mediated (for example, ammonium excretion, dissolution, or particle suspension).
Release length	L	Average subsystem distance required to release an amount of material equal to the advective influx. Synonymous with turnover length.
Spiraling length	L	Average distance required for a given material to complete a cycle (that is, for the stream to remove and then release an amount of material equal to advective influx).
Retention	$M L^{-2} T^{-1}$	Net amount of material removed from advective transport. It is the collective input-output result of all processes (uptake and release). Retained material may be either temporarily stored or exported by nonadvective means.
Retention length	L	Average subsystem distance required to result in a net removal of material equal to advective influx. Values can be either positive (uptake > release) or negative (uptake < release). If negative, length is the distance required for advective influx to double. Negative lengths indicate that the subsystem is acting as a source rather than a sink for the material of interest.
Retention efficiency	%	Net amount of material removed from advective transport (retention), relative to advective influx of material at a reference point. Retention efficiency is usually calculated for an arbitrarily selected length of stream and is very sensitive to the length chosen.

ments, exhaustion of oxygen may favor denitrification, resulting in loss of nitrate at the end of the parafluvial or hyporheic flowpath. Although in both subsystems processing lengths continue to shorten over successional time, the net result (retention) is a shift in the overall retention characteristics of each

subsystem: the surface stream is initially a sink for inorganic N but later becomes a source; whereas the parafluvial zone may be an inorganic N source in early succession and a sink in late succession (Figure 4). These idealized successional changes find support in some, but not all, empirical studies; for

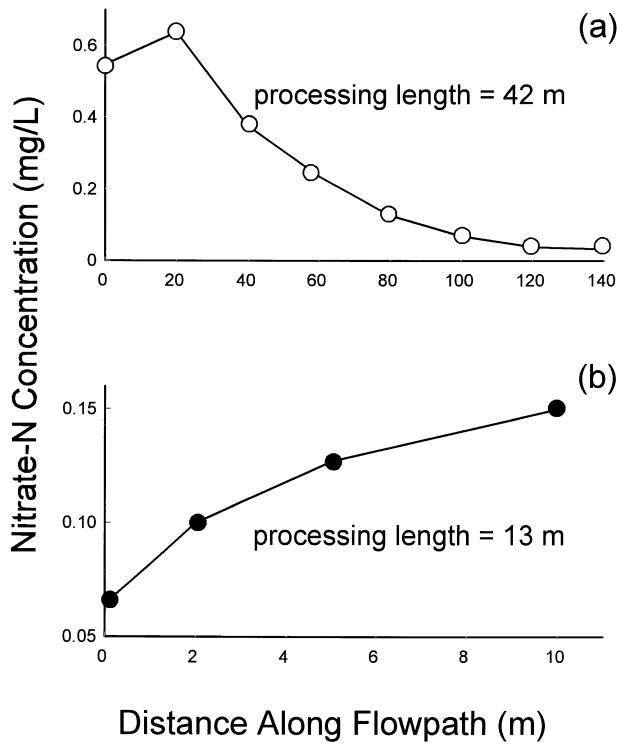


Figure 2. Changes in nitrate–nitrogen concentration along surface stream (a) and parafluvial (b) flowpaths. The numbers on each plot are processing lengths for nitrate uptake and net nitrification, respectively. Data are from flowpaths in Sycamore Creek (a, unpublished data, 1995; b, Holmes and others 1994).

example, denitrification in parafluvial gravel bars appears unrelated to oxygen (Holmes and others 1996). Nevertheless, according to the TEM, processing lengths become shorter over successional time. To the extent that processing lengths in each subsystem are contracted or extended, the whole stream–riparian ecosystem is analogous to a nested set of telescoping cylinders; hence the name of the model.

This general description of the TEM has two essential elements: (a) the currencies of material processing can be expressed for each subsystem in units of channel length, analogous to the spiraling length; and (b) lengths vary temporally within each subsystem, primarily in response to disturbance. The telescope may expand and retract in response to exogenous events other than flood—fire in the riparian zone, drying, pulsed addition of toxic substances—or to nondisturbance, endogenous events, such as seasonality or grazer population fluctuations. Although the TEM is a disturbance-related concept, the static view is also useful in that it stresses the view of stream–riparian ecosystems as

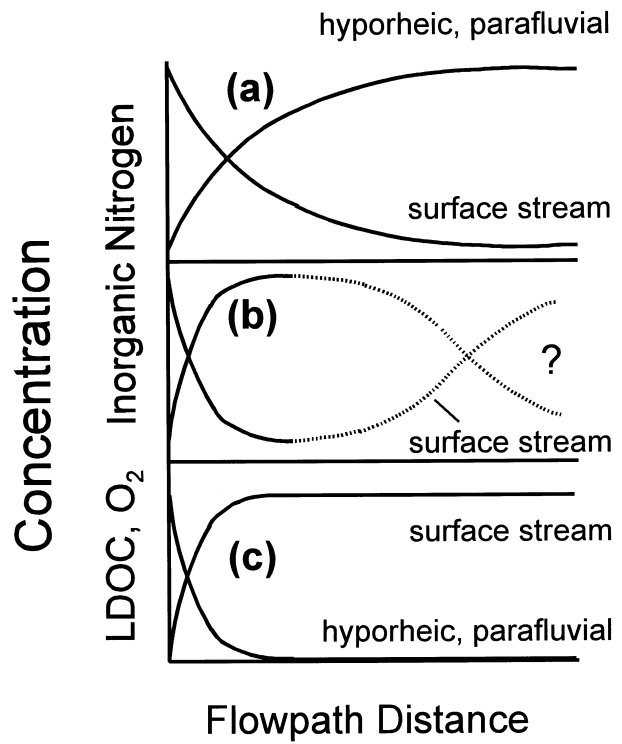


Figure 3. Hypothesized changes in concentration of materials along surface stream and subsurface (hyporheic and parafluvial; see Figure 1) flowpaths in the active channel. Inorganic nitrogen in middle (a) and late (b) succession, respectively. (c) Changes in labile dissolved organic carbon (LDOC) and dissolved oxygen in late succession.

consisting of multiple, laterally arrayed, and linked subsystems.

Hypotheses of the Telescoping Ecosystem Model

Our statement of the conceptual structure of the TEM leads directly to hypotheses about how the stream–riparian ecosystem as a telescoping system responds to disturbance. Figure 5 shows the ecosystem at four different “snapshots” in time. When a long time has elapsed since the previous disturbance, the components of the telescope (stream, hyporheic, parafluvial, and riparian zones) are maximally contracted—that is, processing lengths are short. Disturbance causes elongation of the components to varying degrees, and they retract during postdisturbance recovery at different rates. The extent to which each component is elongated by disturbance is a measure of resistance, whereas the rate of retraction reflects resilience [definitions of resistance and resilience follow those of Webster and others (1975)]. This leads to the first two hypotheses of the TEM, regarding ecosystem stabil-

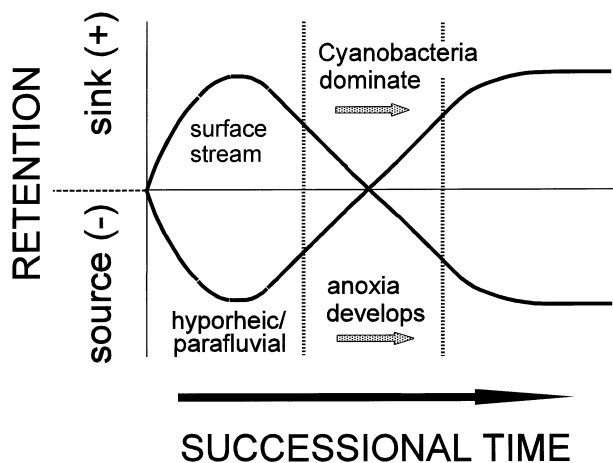


Figure 4. Hypothesized successional changes in inorganic nitrogen retention within surface stream and subsurface (hyporheic and parafluvial; see Figure 1) subsystems. Positive and negative retention indicate whether a subsystem acts as a source or sink for the nutrient, respectively. Retention changes over successional time in response to development of anoxia or colonization by cyanobacteria.

ity: (H1) resistance (inverse of the degree of extension of processing length) increases with distance from the center of the telescope, and (H2) resilience (rate of contraction of processing length following disturbance) decreases with distance from the center of the telescope. Note that disturbances themselves vary in magnitude; thus, some may cause no extension at all in the outer elements of the telescope ("minor disturbance," Figure 5).

Resistance and resilience (inverse of maximum extension and rate of retraction) might seem like obvious consequences of differences in organism life history in the different subsystems, but we stress that these hypotheses focus on functional attributes of each subsystem: processing lengths. Thus, this model is specific in its applicability to nutrient-processing characteristics. While these characteristics in part determine disturbance-induced changes in processing length for each component subsystem, interactions among subsystems also play a role. The third hypothesis of the TEM deals with these interactions, which we term *cross-links*: (H3) cross-links enhance resilience of the stream-riparian ecosystem (Figure 6).

What are cross-links? The primary connection between adjacent subsystems is via hydrologic routes, yet cross-links are not restricted to movement of water. Organism movements and organic matter transfers (that is, leaf fall and lateral export of algae), for example, can be viewed as cross-links. Cross-links studied to date include the transport of

nutrient-rich hyporheic water to the surface stream at upwelling zones, which has been shown to enhance postflood algal growth (Valett and others 1994), and downwelling of surface water high in labile dissolved organic carbon, supporting rapid recovery of subsurface microbial respiration after floods (Jones and others 1995a). The effect of these cross-links is likely to be most pronounced when they connect subsystems that are net sources with those that are net sinks.

Elements of the Mathematical Model

Our mathematical model is based on the nutrient spiraling concept (Newbold and others 1981; Elwood and others 1983); however, to describe ecosystem retention, we have expanded these ideas to the stream-corridor ecosystem by including different subsystems (stream channel, parafluvial zone, hyporheic zone, and riparian zone) and the linkages among them (Figure 1). Stream-corridor material retention (that is, net amount of material removed from advective transport; Table 1) depends on hydrologic retention, on the net result of all biological and chemical transformations occurring within each subsystem for a given element, and on the relative areal proportions of the different subsystems. Hydrologic retention can be defined as the increase in hydraulic residence time in the stream-corridor ecosystem attributable to transient storage. The increase in residence time may be due to physical complexity of each subsystem and cross-links between subsystems that result in slower water velocities than those predicted by advective transport in the surface stream subsystem (Morrice and others 1997). In this model, we first describe spatial variation in material flux in each subsystem (that is, downstream pattern) as influenced by material transformations occurring within it. We then describe material retention. Finally, we incorporate effects of cross-links (in this case, water and solute inputs from and outputs to adjacent subsystems), because these linkages may modify biogeochemical transformations and thereby enhance resilience of the stream-corridor ecosystem.

If we consider a single subsystem in isolation, longitudinal variation of material flux can be described as:

$$F_x = F_0 \cdot e^{-K_L x} \quad (1)$$

This equation states that material flux per unit stream width (F , $M L^{-1} T^{-1}$) at one point (x) is dependent upon the flux at an upstream point (0) and the downstream material change coefficient (K_L , L^{-1}). K_L represents the proportion of material flux taken up (or transformed) per unit stream

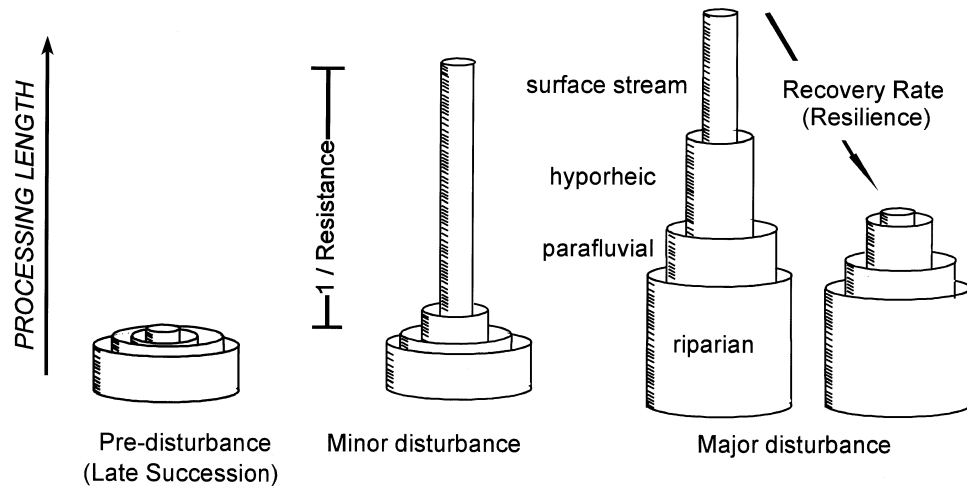


Figure 5. Pictorial representation of the telescoping ecosystem model, where the lengths of the telescoping cylinders (processing lengths) are inversely related to rates of biogeochemical transformations. In late succession (that is, a long time since disturbance), all components of the telescoping stream-riparian corridor ecosystem are maximally retracted (left). A minor disturbance may affect only the most central (least resistant) elements of the telescoping ecosystem (center). Following a major disturbance, components extend and subsequently retract (during succession) to varying degrees (right).

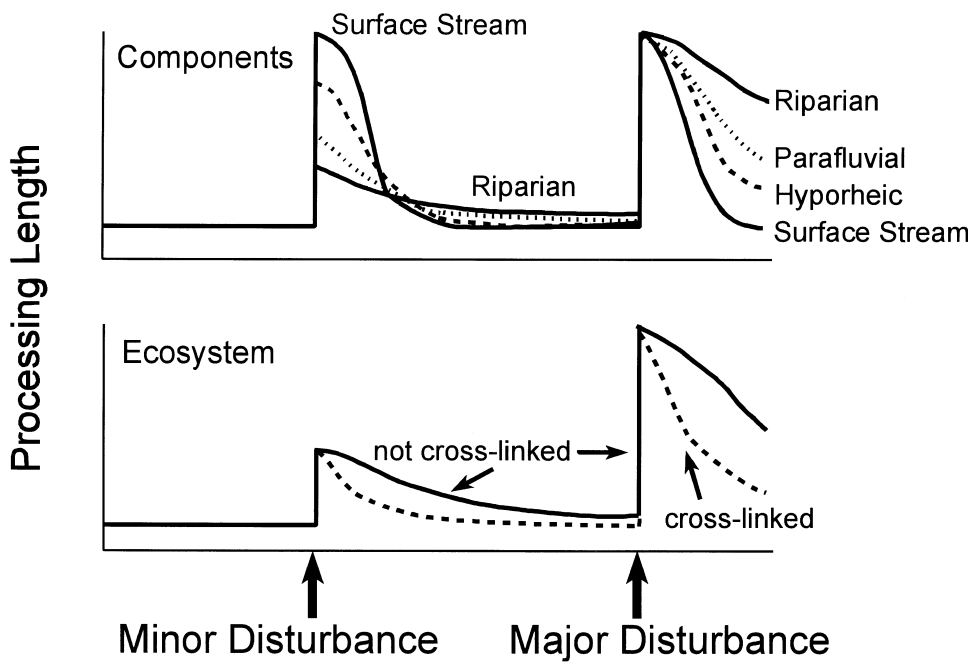


Figure 6. Hypotheses of the telescoping ecosystem model. Top: Changes in processing lengths of each component subsystem across a disturbance. Bottom: Effects of cross-links on resilience (rate of retraction of telescope components; that is, shortening of processing lengths).

length. Equation 1 was originally intended to describe longitudinal variation of solute flux in the surface stream subsystem due to uptake (Newbold 1992). Unlike the nutrient-spiraling model that deals with one system (the surface stream), our model includes several subsystems that are distributed parallel to the surface stream in which several material transformations take place. Therefore, we will use Eq. 1 in a more general sense to describe longitudinal variation of any material in different subsystems due to any given process. Material flux

per unit stream width in a subsystem i is defined as

$$F_i = C_i \cdot v_i \cdot d_i \quad (2)$$

where C is solute concentration (M/L^3), v is water velocity (that is, advection, L/T) and d is water depth (L). To compare different subsystems, water velocity in each subsystem can be expressed as a fraction of velocity in the surface stream subsystem (that is, maximum velocity). In subsystems where water flows through sediment interstices (that is, subsurface flow), water depth should be calculated by

accounting for depth of the saturated zone and sediment porosity.

Processing rate per unit stream area ($M L^{-2} T^{-1}$) is applicable to any transformation that results in a change in form or state of any material (Table 1). Processing rate can be expressed as a function of the processing rate coefficient (K_p, T^{-1}) and the standing stock of material per unit area (M/L^2). K_i is material specific, process specific, and subsystem specific. This coefficient is equivalent to the nutrient uptake rate coefficient [K_c (Stream Solute Workshop 1990)] when describing solute uptake in the surface stream subsystem. In contrast to K_c , K_i can be positive (that is, removal of material from water) or negative (that is, release of material to the advective medium) depending on the material and process of interest. For example, to describe nitrification, K_i will be negative for nitrate but positive for ammonium. For simplification, Eq. 1 considers that the material processing rate is constant over space in each subsystem. However, if we consider that subsystems are themselves spatially heterogeneous, then K_i could be expressed as a function of distance along a flowpath or horizontal position. K_i also can vary over time in response to changing physical, chemical, and biological conditions.

In the nutrient-spiraling model [for example, see Newbold (1992)], the downstream material change coefficient, K_L , is used to calculate nutrient uptake length ($S_W = -1/K_L$). Uptake length, the average distance traveled by a nutrient atom before it is removed from advective transport, can be directly measured in streams by using short-term additions of nutrients (low concentrations) or stable isotopic tracers (Stream Solute Workshop 1990). In the TEM, the absolute value of the inverse of K_L is material processing length, which is analogous to uptake length (Table 1). Like the processing rate coefficient, processing length is material, process, and subsystem specific. K_L is directly related to the processing rate coefficient (K_p, T^{-1}) and inversely related to water velocity in the subsystem ($v, L/T$).

Material retention also can be expressed in units of stream length. Here, we consider the net longitudinal variation of an element (for example, N, P, or C) in a subsystem or in the whole stream-corridor ecosystem as the result of all uptake processes (that is, removal of material from advective flow; Table 1) minus all release processes (that is, return of material to the advective medium; Table 1). The downstream material change coefficient (K_L) describing material (element) retention is expressed as:

$$K_L \text{ (retention)} = \sum K_L \text{ (uptake)} - \sum K_L \text{ (release)}. \quad (3)$$

The inverse of K_L is the material retention length, defined as the length of a subsystem required for removal (positive retention) or release (negative retention) of an amount of material equivalent to advective influx (Table 1). Retention length is an indicator of the relative importance of material removal and transport (that is, material retention efficiency; Table 1).

Hydrologic linkages between adjacent subsystems (that is, cross-links) can be seen as material inputs to or outputs from a specific subsystem in addition to advective inputs. Changes in material supply can affect processing rates and, ultimately, material retention. Therefore, to incorporate effects of cross-links on the model's description of longitudinal material variation (that is, retention length), F_0 should be modified to include these additional fluxes. Variation in material flux through a subsystem (F_{xi}) is described by modifying Eq. 1 to incorporate cross-links:

$$F_{xi} = \left[F_{0i} + \sum_{j=1}^{j=n} (\beta_j \cdot F_{0j}) \right] \cdot e^{-K_L x} \quad (4)$$

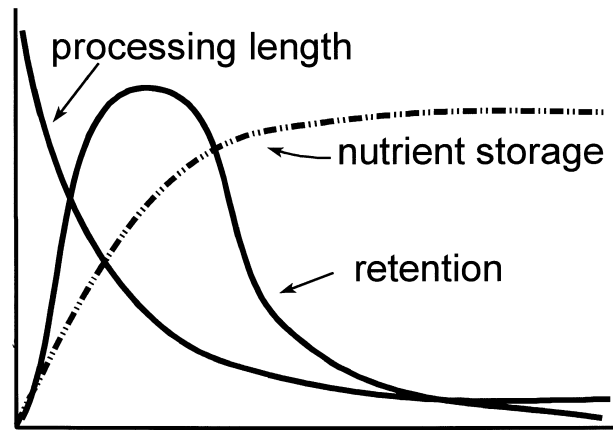
When hydrologic linkages are incorporated, solute flux entering each subsystem i is the result of advective flux within the subsystem (F_{0i}) plus the flux to or from n adjacent, linked subsystems (j). The terms included in Eq. 4 indicate that a fraction of material flux ($\beta \times F$) enters or leaves a particular subsystem i due to cross-links. The hydrologic exchange coefficient (β) is expressed as a percentage of total flux in a subsystem and indicates both direction (sign) and magnitude (value) of hydrologic linkages between two adjacent subsystems. The sign of β is determined mainly by hydraulic head differences between two adjacent subsystems, whereas its magnitude [values range from -1 (output) to $+1$ (input), with 0 indicating no linkage] is a function of hydraulic conductivity and head in each subsystem and the cross-sectional area of interaction, weighted by the total flux of the subsystem of origin. Linkage direction and strength also may change longitudinally. For example, surface-hyporheic interactions occur at discrete points along the stream (upwelling and downwelling zones). Finally, the magnitude of β also may change over time as discharge changes, for example, due to changes in sediment transmissivity. Equation 4 suggests that changes in β and in K_L over successional time will affect the downstream pattern of material flux, elongating or shortening processing lengths. These changes will alter material retention within each

subsystem as well as in the stream-corridor ecosystem as a whole.

Implications for Nutrient Retention and Efficiency

Long-standing interest in how nutrients are retained by ecosystems undergoing succession was catalyzed by E. P. Odum's (1969) hypothesis that "mature" ecosystems are more retentive ($I \gg O$) than successional ecosystems. In a challenge to that view, Vitousek and Reiners (1975) argued that when net biomass increment (approximately net ecosystem production, NEP) is positive (as during succession) ecosystems should be maximally retentive, but in mature ecosystems with near zero NEP nutrient inputs should equal outputs. In open ecosystems like streams, positive NEP and positive retention of *inorganic* nutrients may be maintained even at steady-state biomass if export of particulate organic material (that is, algal drift) balances net nutrient uptake (Grimm and Fisher 1986). The consequences of Vitousek and Reiners' model for retention length of a given element (all forms) are retraction followed by extension over the course of succession, even though processing length for uptake of *inorganic* nutrients in the surface stream could continue to shorten (Figure 7). The ecosystem capacity for retention increases asymptotically, but because processes resulting in nutrient release increase in importance as net biomass increment declines, retention similarly declines (and retention length increases or even becomes negative).

What happens when the linked subsystems of the telescoping ecosystem model are considered together? Because many stream corridors are subject to disturbance, riparian, parafluvial, and surface stream components (for example, gallery forests, shrub stands on gravel bars, and algal assemblages) frequently may be successional [for example, see Campbell and Green (1968) and Gregory and others (1991)], although rates of succession differ according to life cycles of major organisms (Fisher and Grimm 1991). Subsurface components in all of these subsystems (the hyporheic zone, parafluvial flowpaths, and riparian groundwater), on the other hand, are always characterized by negative NEP and may frequently exhibit negative retention lengths ($I \ll O$). In addition, hydrologic retention is greater in subsurface zones (Bencala 1993; Morrice and others 1997). For the active channel, which is annually flooded and includes hyporheic, parafluvial, and surface stream subsystems, positive NEP and positive retention in the surface stream may ultimately be nearly balanced by negative NEP and negative retention in subsurface flowpaths (Grimm



Successional Time

Figure 7. Changes in processing length, retention (correlated with net biomass increment or net ecosystem production), and total nutrient storage over successional time. The curves describe the predicted pattern for any subsystem or for the stream-corridor ecosystem as a whole, and are based on models developed for forests.

and Fisher 1984; Holmes and others 1994; Fisher and others 1997). Thus, these hydrologically linked subsystems may alternately be sources and sinks for nutrients, with no net retention overall but with distinct spatial variation in nutrient availability in any given subsystem (for example, the surface stream). The challenge for the TEM is to predict how retention length changes for the entire stream-corridor ecosystem over the course of succession, incorporating differences in hydrology, successional rate, and resistance to disturbances of different magnitudes. As an initial stance, we contend that models developed in forests (Vitousek and Reiners 1975; Bormann and Likens 1979) should be applicable to stream-corridor ecosystems (Figure 7).

Changes in retention discussed so far are predicted based on changes in NEP, but other processes can confound those predictions [for example, see Gorham and others (1979)]. In stream-corridor ecosystems, gaseous inputs and outputs such as nitrogen fixation (Grimm and Petrone 1997), denitrification (Peterjohn and Correll 1984; Duff and Triska 1990; Hill 1991; Triska and others 1993; Pinay and others 1994; Holmes and others 1996), and methane evasion (Meyer and Pulliam 1992; Jones and others 1995c) are likely to change during succession. Threshold responses may be evident for successional change in denitrification or nitrogen fixation rates (that is, sudden shifts in redox potential, reduction of inorganic nitrogen concentration to a level that is unavailable for uptake). The

implications of such changes for total retention depend on absolute rates of processes (that is, transformation-specific processing lengths), where they occur (subsystem-specific processing lengths), the configuration of the ecosystem (size, shape, and arrangement of subsystems), and linkage among subsystems.

Nutrient retention relative to advective influx is an indicator of nutrient *retention efficiency* of the stream-corridor ecosystem (Table 1) and is the conceptual basis for the management use of wetlands as nutrient filters. By considering cross-links between subsystems, advective input to each subsystem will depend not only on the downstream flux within the subsystem but also on lateral and vertical fluxes from adjacent subsystems. Processing rates in each subsystem can also depend on nutrient supply from other subsystems (Jones and others 1995a, 1995b); the extent of this dependence and the degree of connection between subsystems will clearly influence the overall retention efficiency of the reach. A hypothesis of the TEM is that interaction among subsystems (cross-linkages) increases resilience of stream-corridor ecosystem function (in terms of nutrient processing or retention) to disturbances. Magnitude and, in some cases, direction of hydrologic linkages can vary over time as a result of changes in stream discharge. Accordingly, effects of interactions between subsystems on ecosystem nutrient retention will also vary over time. Some studies have shown that surface–subsurface interaction is weak when discharge is high (D'Angelo and others 1993; Valett and others 1996; Martí and others, 1997). On the other hand, in Sycamore Creek, we have observed that linkages between surface stream and riparian zone are strong during floods, and a significant fraction of floodwater is diverted into the slow-moving subsurface waters of the riparian zone (unpublished data). Variation in retention efficiency over time thus is closely related to hydrologic variation. The TEM provides a context for synthesizing the effects of hydrologic connections, biomass accrual, and other nutrient transformations as they change in response to the existing disturbance regime.

Implications for Different Materials

Most of our research in the desert Southwest on stream-corridor nutrient dynamics has focused on nitrogen because it often limits primary productivity, it is biogeochemically active, and nitrate pollution is common regionally and worldwide. Other elements also are biogeochemically active in stream sediments, and their transformations contribute to whole-system retention. The TEM may be applied

to any material that is transported hydrologically between subsystems. Expectations for the behavior of any given element (in its various forms) depend on whether it is conservative or reactive and, if the latter, whether it exhibits biological or abiotic reactivity (or both). Material retention also varies depending on the type of cycle; atmospheric cycles such as those of N and S are characterized by transformations that can result in net gain or loss of elements from the ecosystem, whereas transformations of elements with sedimentary cycles (P and metals) will result in changes in form but no net change in the total amount of element in the system. Finally, interactions among element cycles and, in particular, the stoichiometry of processes within subsystems may result in otherwise unexpected outcomes of subsystem interaction (Likens and others 1981; Schindler 1981; Elser and others 1996).

Conservative materials, such as chloride and many other major ions, are not reactive and are of no further interest here. Elements and compounds that react abiotically, for example, via adsorption/desorption reactions, will exhibit processing lengths that reflect the nature of sediment or soils and the chemical environment of each subsystem. Ammonium may be strongly adsorbed in riparian soils while being relatively mobile (and biologically reactive) in the surface stream (Avanzino and others 1994). Biologically reactive elements may be classified as either potentially limiting (N, P, C, and K) or nonlimiting. For limiting elements, cross-links have the potential to enhance productivity and facilitate resilience, as shown for upwelling (hyporheic discharge) sites rich in N (Valett and others 1994).

Processing lengths of elements with sedimentary cycles, such as phosphorus and metals, are constrained by input from the watershed. In deserts, such inputs are episodic, while, in other biomes, the supply of P to stream-corridor ecosystems may be more continuous, but in either case input should vary with geologic age of the watershed (Vitousek and Farrington 1997). Processing lengths of P should correspond to the predominant metabolic pathways of subsystems; that is, for an autotrophic surface stream in the desert, P uptake length would contribute to positive retention, whereas the heterotrophic subsurface subsystems might be expected to release P, showing negative retention. Expectations for elements with atmospheric cycles are complicated by transformations that are independent of uptake and release associated with metabolism; denitrification, for example, results in retention of nitrate in heterotrophic subsystems.

In any subsystem, the stoichiometry of uptake varies with primary producer type (trees vs algae vs nitrifiers), because of differences in these organisms' needs relative to element availability. A stoichiometric approach to nutrient uptake and release can be traced to the seminal paper by Redfield (1958). Release of nutrients during decomposition is a function of relative stoichiometry of decomposing material and available external nutrient sources. An understanding of stoichiometry at the whole (sub)-system level must consider alternative sources of nutrients, the balance of processes for each element and, finally, how each element affects dynamics of the others. For example, if a process such as denitrification is limited by the supply of labile carbon (Holmes and others 1996), then processing length of C will constrain that of N in flowpaths where denitrification occurs.

Another example of the influence of stoichiometry from Sycamore Creek is a contrast between the asymptotic pattern of increase in nitrate along subsurface flowpaths, which is attributed to coupled mineralization–nitrification, and the nearly linear increase in soluble reactive phosphorus (SRP) along those same flowpaths. Nitrification rates are highest at the surface stream–parafluvial/hyporheic interface (Holmes and others 1994; Jones and others 1995b). Compression of biogeochemical activity to the interface may result from exhaustion of carbon supplied from the surface stream, but whatever the cause, there are rapid increases in nitrate concentration in the first few meters (or even centimeters) of the flowpath and relatively slow changes thereafter. By contrast, SRP increases at a constant rate, thus N:P initially increases and then declines (Figure 8) (Holmes 1995). For the composite data presented here, N:P never increased sufficiently to result in potential P limitation; however, at times or places in Sycamore Creek or certainly in other streams, localized shifts in the identity of the limiting nutrient (for example, from N to P) are conceivable given this kind of subsurface–surface interaction.

Model Extensions

Spatial configuration. The conceptual structure of the TEM is robust but simple; yet a number of refinements are desirable before the model can be widely adapted to disparate systems. Most notably, the conceptual model describes a uniform reach of stream. In reality, subsystem configuration will likely vary longitudinally. Ultimately a spatially explicit version of this model is desirable—all the more so if the ordered sequence of patches through which water and materials flow is an important determinant of output.

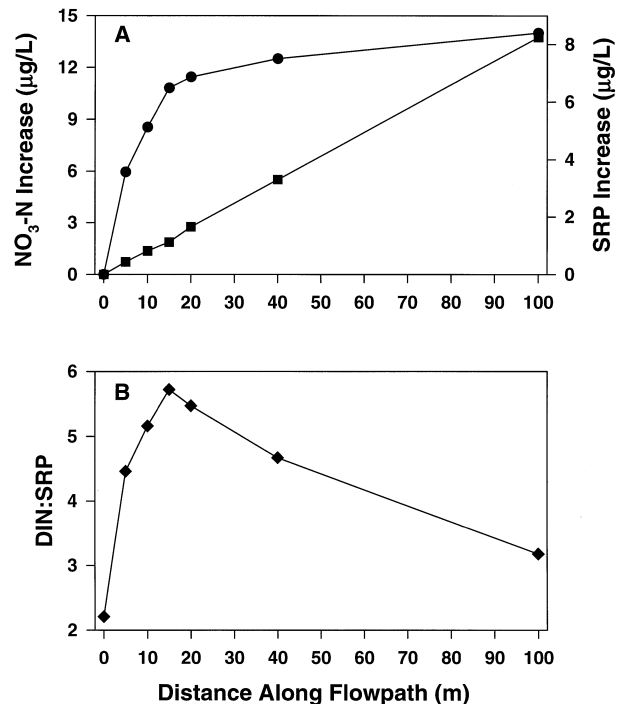


Figure 8. Changes in nitrate, soluble reactive phosphorus (SRP), and molar N:P (nitrate/SRP) along a “composite” parafluvial flowpath in Sycamore Creek, Arizona. Nitrate and SRP concentration changes along a composite flowpath were estimated from mean changes along 24 flowpaths sampled between 1 June and 17 September 1994 (Holmes 1995). Nutrient concentrations at 40 m were estimated from a subset of these flowpaths ($n = 6$), and nitrate and SRP concentrations at 100 m are extrapolations.

Other disturbances. We have so far considered only disturbance by flood. Other disturbances influence the riparian corridor, for example, drought, fire, overgrazing, pathogen outbreak, species invasions, siltation, and point inputs of various materials. Multiple disturbances are common. The modes of action of different disturbance agents will vary in proportion to the extent to which subsystems are differentially “reset.” Drought is common, especially in arid regions, and its effects can be severe (Stanley and others 1997). Shrinking of the surface stream and diminished surface flows accentuate the influence of lateral components due to limited dilution and lower surface stream area. Mean velocity of material transport thus decreases. Eventually the stream becomes spatially intermittent, surface flow ceases, and essentially all flow occurs through peripheral subsystems. The central element of the telescope disappears. This central element is an important conduit to the atmosphere [for example, see Kling and others (1991)], and its loss coupled with increased residence time of organic materials

subjects the system to anoxia. Anoxia may shift biogeochemical transformations toward reductive pathways, which may alter spiraling relationships (for example, by generating soluble reduced compounds such as ferrous iron and manganous manganese). Processing lengths of some substances may thus increase as flow decreases; others may decrease. It should be noted that as flow declines, streams become spatially intermittent; thus, reaches that sustain surface flow exhibit different (and usually longer) processing lengths than do interposed reaches without surface flow.

Larger scales. Configurational changes in stream channels will also alter processing lengths, interactions among elements, and operation of the telescoping response to disturbance. Components of processing length are in linear units; however, these can be reckoned in terms of either channel length or valley floor length. This difference can be significant when streams meander. From a watershed view, sinuosity enhances retention and shortens processing length relative to a straighter channel. Because of greater edge length, sinuosity should enhance lateral linkages; however, this may be offset somewhat by decreased hydraulic heads as channel slope declines in response to channel lengthening.

Our model (as well as most of the conceptual constructs of stream and river ecology) is basically linear (Fisher 1997). In reality, streams are branched ecosystems, and this fact becomes important when watersheds are the systems of interest. An understanding of the response of the larger-scale river drainage to disturbance requires that the linear telescope model be scaled up, according to assembly rules dictated by local geomorphology, to yield a branched structure that incorporates all channels in all orders represented in the drainage; that is, the model must be assembled in a spatially explicit way. Although we do not know how different branching patterns, bifurcation ratios, channel densities, and tributary junction angles influence material retention and processing at the drainage scale, these structural elements vary greatly from region to region. We believe that a breakthrough in stream and river ecology lurks in an explicit consideration of branching pattern as a driving independent variable, affecting not only river ecosystem functioning but various habitat-based understandings of rivers as well [see Fisher (1997)].

Upland linkage. Our model explains how materials are processed once they enter the stream-riparian corridor. Many upland variables interact to determine the amount and chemistry of water entering the stream corridor: for example, precipitation regime, vegetation type and successional status,

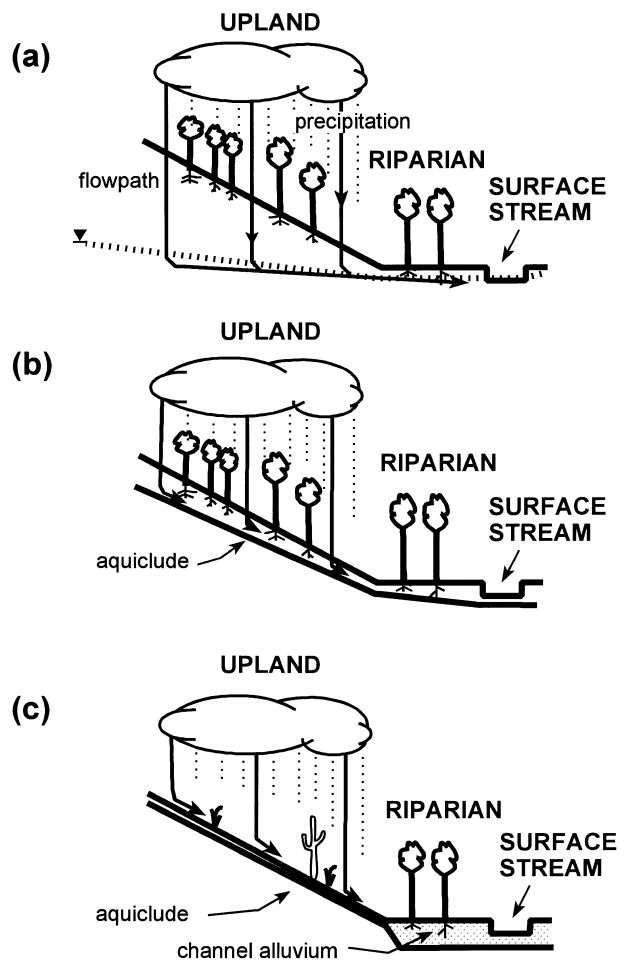


Figure 9. Linkage of upland ecosystems with stream-corridor ecosystems in (a) forested landscapes with deep, well-drained soils, where water percolates well beyond the rooting zone; (b) forested landscapes with shallow soils, where underflow intercepts the rooting zone; and (c) arid and semiarid landscapes, where soils of low permeability force overland flow.

soil development, parent materials, slope, and hydrologic routing (Hill 1996). In catchments with deeply weathered, permeable soils, precipitation percolates vertically to shallow groundwater and then laterally to stream channels. The rooting zone is passed once, and plant uptake or release of nutrients can influence water chemistry entering streams (Figure 9a). Where aquicludes are near the surface, water may percolate laterally through the rooting zones of several plant associations ad seriatim (Figure 9b). Giblin, Shaver, and colleagues (Giblin and others 1991; Shaver and others 1991) showed that shallow permafrost forced subsurface water through the rooting zones of several distinct plant associations along a toposequence. Resulting chemistry of water entering the stream was dependent on the vegeta-

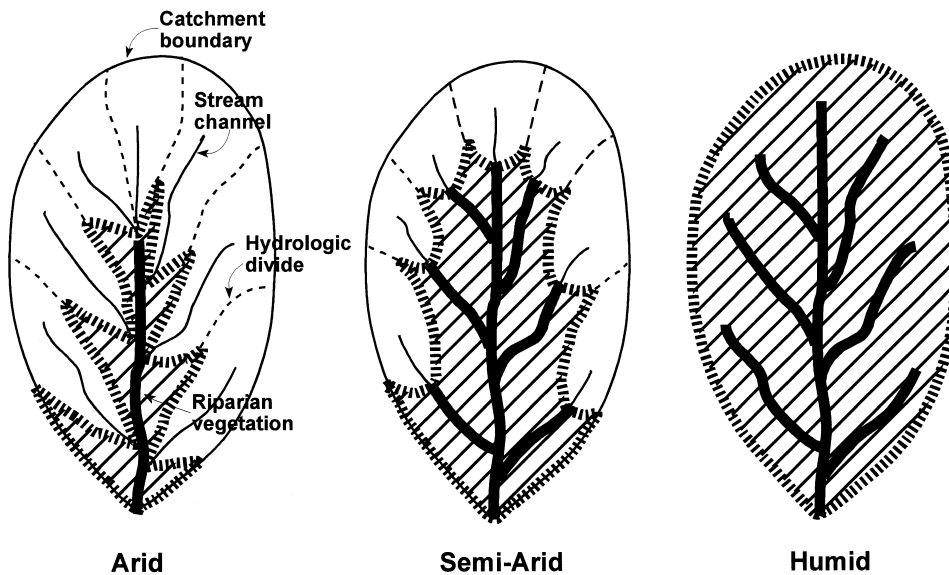


Figure 10. Extent of interception of laterally flowing runoff by riparian zones in arid, semiarid, and humid watersheds. In arid regions, riparian vegetation is restricted to larger channels whereas, in semiarid regions, gallery forest may occupy only the lower reaches of tributary streams. In humid areas, riparian vegetation is found along the lengths of all tributaries in a forested catchment. Runoff from the shaded area of catchments must move through the riparian zone before entering the stream channel. Runoff from the unshaded areas enters the stream channels directly.

tion patches transected and probably their explicit ordering. In arid environments with rocky desert pavement-type soils and extensive shallow caliche layers, precipitation runs off rapidly as sheet flow across the soil surface during storms. Between storm events, the upland is hydrologically disconnected from stream channels (Figure 9c). Stream flow is maintained between storms by release of abstracted water in channel alluvium. It is when these alluvial sediments are saturated that modest storm events generate flash floods. After long periods of drought, channel abstraction greatly dampens flood intensity.

In arid lands such as the Sonoran Desert where this model was developed, much of the water entering larger stream channels does so via a dense network of rills and lower-order washes without first transecting the rooting zone of riparian vegetation. The watershed area contributing flow through the outer edge of the riparian strip is small (Figure 10). In semiarid landscapes, the riparian zone extends farther up small tributaries and, in humid areas, all tributaries of natural catchments may be lined with riparian trees beneath which water flows before entering stream channels (Figure 10). While this hydrologic description is an oversimplification, the salient points are these: (a) Upland flow paths represent a conceptual continuum with those of the stream-corridor ecosystem. Material processing at the catchment scale must include these upland processes as well. (b) Material transformation continues in the stream corridor. (c) In arid-land streams, most processing by riparian vegetation occurs *after* water enters the channel and then moves back into

the riparian zone. Time and hydrologic routing militate against riparian processing of materials *before* water enters channels.

Functional optimization. Until more data are available, we have no basis from which to speculate about the relative overall retention efficiencies of differently structured river-corridor ecosystems, nor about the relative contributions of one subsystem versus another. We have avoided the implication that optimal retention of one material or another is vested in a “natural” or “pristine” configurational state. If there are central tendencies in river ecosystem retention efficiency, their revelation awaits further research. Sadly, management options for river systems often do not include return to pristine condition; however, any management program that involves restoration, rehabilitation, or preservation should include a concern for ecosystem-functioning consequences at the landscape level. The TEM provides a nascent framework around which to organize that effort.

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