

# The Multiple Linkages of Forests to Streams

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## INTRODUCTION

Headwater stream ecosystems in forested watersheds are intimately related to their vegetative setting. The riparian zone, the source area of soil-forest products which enter the stream, contributes to channel stability and generates biologically active organic substrates. Large woody debris often constitutes stable geomorphic features which retain mineral sediment and finer organic material (Swanson and Lienkaemper, 1978; Swanson, Triska, this volume). Inputs of organic solutions and particulates (and inorganic nutrients) provide energy for the stream community over an annual cycle (Fisher and Likens, 1973). The stream also represents a potential source area for the riparian zone of the forest ecosystem at times of greater than bankfull discharge (Merritt and Lawson, 1979).

Thus, because of the interactive nature of forest-stream ecosystems, stream community structure and function should be studied within a watershed context (Cummins, 1974; Hynes, 1975).

## BACKGROUND

Prior to the 1960's the primary emphasis in stream ecosystem investigations was on invertebrates as food organisms for game fish in specific stream reaches. In these studies a wide variety of methods was employed to sample plants and animals associated with the channel sediments (see review by Cummins, 1962), but the key role played by the watershed in supplying organic substrates utilized by stream organisms was largely neglected.

The heterotrophic nature of forested, headwater stream ecosystems and their allochthonous-based energy source was formally recognized in the early 1960's (Hynes,

1963; Ross, 1963). A major development of the 1970's has been the measurement of watershed material-balance budgets. Such studies have shown that streams are not merely conduits that export forest ecosystem products from within the boundaries of surface watersheds and subsurface source areas, but rather that they store and biologically process organic inputs (Fisher and Likens, 1973; Sedell et al., 1974). Budgets for reaches, rather than for entire watersheds, require that appropriate segments be chosen for study with all inputs adequately taken into account (Fisher, 1977). In all budget studies it is important to measure storage carefully and to relate release from (or accrual to) storage to the annual inputs. Also, the losses to and introduction from storage must be related to the seasonal and long-term flow regime (Swanson, this volume).

## PERSPECTIVES

The 1970's also have involved the development of conceptual models of headwater stream ecosystem structure and function (Cummins, 1974; Minshall, 1978). Refinement of existing models and elaboration of new ones will undoubtedly continue to be a major feature of stream-watershed research in the 1980's. Examples would be evaluating and testing the "River Continuum" and "Nutrient Spiraling" hypotheses. The former depicts stream-river drainage nets as continua of biological organization that reflect geomorphic control (Cummins, 1975; Vannote et al., 1980) from low order headwater streams to higher order receiving rivers (Strahler, 1957; Leopold et al., 1964). "Nutrient Spiraling" (Webster, 1975) refers to the partially open nutrient cycles characteristic of running waters. Portions of the inputs to a given reach are stored and processed and some fraction released

downstream. The incomplete efficiency of storage and processing provides energy and inorganic nutrients for downstream communities. The more efficient reaches (i.e., higher retention and processing) are considered to have the "tightest" spirals.

#### The River Continuum

A major distinction between lotic ecosystems can be made on the basis of the relative importance of in-stream primary production versus inputs of terrestrial origin as the major source of organic matter for community processes (Vannote et al., 1980). In forested ecosystems, small, shaded, cool headwater streams (approximately orders 1-3) may derive more than 90 percent of their organic carbon from the terrestrial surroundings (Fisher and Likens, 1973; Sedell et al., 1974). The riparian zone vegetation functions both in light attenuation and as the source of allochthonous inputs, including long-term structural (wood debris) and annual energy supplies.

The ratio of daily gross primary production (P) to total daily community respiration (R) (Odum, 1956) reflects the relative dominance of autotrophy versus heterotrophy. However, as Minshall (1978) has shown, even when primary production exceeds upstream and riparian inputs of organic matter, the in-stream derived organic substance is used primarily in a moribund state in detrital food chains. Where riparian vegetation has been removed, as in clearcut timber harvest, or is naturally sparse (high altitudes and latitudes and xeric regions), autotrophy dominates ( $P/R > 1$ ). In wide shallow, generally warmer, well-lighted mid-sized rivers (orders 4-6), primary production is also the dominant source of organics.

In addition to increases in primary production related to higher light regimes, another significant feature of the adjustment of biological communities to changes in geomorphology, channel configuration, and vegetational setting downriver (along the "continuum") concerns the size distribution of the particulate organic matter (POM,  $> 0.5 \mu\text{m}$  particle size) resources. Headwater streams characteristically have greater inputs of coarse material (CPOM,  $> 1 \text{ mm}$  particle size) and, therefore, greater concentrations of the microbial and macrobial biota for which coarse material is the primary nutritional resource (Cummins, 1974). With increasing stream size and reduced importance of direct riparian inputs, a larger proportion of the POM is fine particulate organic matter (FPOM,  $< 1 \text{ mm}$  particle size) transported from the headwater drainage net. The

greater abundance of FPOM is reflected by a change in community structure; for example, larger populations of collectors (filter feeding invertebrates) (Wallace and Merritt, 1980).

#### Nutrient Recycling

Present research on nutrient relationships--particulate and dissolved (DOM,  $< 0.5 \mu\text{m}$ ) organic matter and inorganic ions--viewed as partially closed cycles, points up the need for measurements of both physical storage and biological processing. The use of radioactive tracers (Ball et al., 1963; Ball and Hooper, 1963) or stable isotope ratios--e.g.,  $^{13}\text{C}/^{12}\text{C}$ --(Rau, 1978) can provide data for determining pathways and residence times of nutrients in stream ecosystems.

Storage pools or compartments can be defined as locations where organic matter accumulates and is processed (utilized) at rates slower than the average or exposed (oxygenated) sites in the channel. There are three general areas: the deep sediments (low oxygen), the inner core of woody debris jams (low oxygen), and the upper bank or floodplain (low moisture). When organic material buried in the sediments and within debris jams is excavated, or that on the upper bank is captured, and re-enters the aerobic stream channel processing regime, it is utilized at a faster rate (Cummins and Klug, 1979; Merritt and Lawson, 1979). Thus, the annual--and longer--hydrographic pattern is critical in determining the proportion and timing of processing and export of annual terrestrial inputs.

Along with channel and upper bank storage or retention, biological processing is the major control of quantities of material introduced and their rates of recycling. The prediction from the "River Continuum" hypothesis (Vannote et al., 1980) is that spiraling would be tighter, especially for coarse particulate organic matter (CPOM,  $> 1 \text{ mm}$  particulate size), in headwater streams due to more efficient retention and processing.

#### ORGANIC RESOURCES AND FUNCTIONAL GROUPS

The quantities and qualities of organic resources exert a major influence on stream community structure (Cummins, 1974; Hynes, 1975; Minshall, 1978) which is expressed in the functional roles of macroinvertebrate species. Different functional groups have adapted morphologically, behaviorally, and

Table 1. Categorization of organic resources in lotic ecosystems (modified from Cummins and Klug, 1979)

| Resource category                                     | Approximate particle size range            | Major sources                                      | Ratio of carbon to nitrogen (C/N)       | Macroinvertebrate functional feeding group using resource |
|-------------------------------------------------------|--------------------------------------------|----------------------------------------------------|-----------------------------------------|-----------------------------------------------------------|
| Periphyton (microproducers)                           | < 500 > 10 $\mu$ m                         | In-stream photosynthesis                           | 5-10:1                                  | Scrapers                                                  |
| Macrophytes (macroproducers)                          | > 1 cm (some macroalgae)<br>< 1 cm > mm    | In-stream photosynthesis                           | 13-70:1                                 | Shredders, scrapers                                       |
| Woody detritus                                        | > 10 cm (coarse)<br>< 10 cm > 10 mm (fine) | Riparian zone (upstream tributaries during floods) | 200-1,300:1                             | Shredders (gaugers)                                       |
| Nonwoody detritus (particulate organic matter or POM) | > 0.5 $\mu$ m                              | Riparian zone, upstream                            | 70-80:1;<br>(microbial portion 10-11:1) |                                                           |
| Coarse (CPOM)                                         | > 1 mm                                     | Riparian zone                                      | 20-80:1                                 | Shredders                                                 |
| Fine (FPOM)                                           | < 1 mm > 0.5 $\mu$ m                       | Upstream, riparian zone                            | 7-40:1 <sup>1</sup>                     | Collectors                                                |
| Dissolved organic matter (DOM)                        | < 0.5 $\mu$ m                              | Subsurface source areas, upstream, riparian zone   | < 17 (labile portion lower)             | None                                                      |
| Animal tissue                                         | > 100 $\mu$ m<br>(microforms > 10 $\mu$ m) | In-stream                                          | < 17                                    | Predators                                                 |

<sup>1</sup>A significant portion of the nitrogen may be biologically very resistant.

physiologically to utilize various components of the spectrum of available resources (Cummins, 1974, 1975; Merritt and Cummins, 1978; Cummins and Klug, 1979).

### Organic Resources

The basic categories of organic resources in running waters (Table 1) differ significantly in nutritional content as defined by microbial and animal growth. In addition to animal tissue used by predators, there are three general classes of organic resources: (1) those with chlorophyll (living micro- and macroproducers), (2) detritus, ranging in size from large wood to particles less than 1  $\mu\text{m}$  and all with associated microorganisms, and (3) dissolved organics (which can be taken up by microbes). If the ratio of carbon to nitrogen (C/N) is used as an index of resource nutritive value, ratios of 17 or less are generally considered in the high quality range (Russell-Hunter, 1970). However, low ratios may be misleading, as in the case of some FPOM (Table 1), because the nitrogen may be in a recalcitrant form (Ward and Cummins, 1979).

Fungi are relatively more important on CPOM where mycelia can develop, and bacteria are predominant on FPOM (Cummins and Klug, 1979). Because the microbial biomass associated with detritus is nutritionally superior (e.g., low C/N) to the organic particle substrate which is high in cellulose and lignin, it exerts the major control on the rate of detritus processing. This is mediated both through direct microbial metabolism of the detrital substrate and regulation of invertebrate feeding (Petersen and Cummins, 1974). Substrates, such as different species of leaf litter, vary in the rate at which microbial colonization and metabolism and, therefore, invertebrate feeding proceed. Thus, differences in quality of inputs are realized as differences in stream community metabolism.

The distribution of detrital size fractions in stream ecosystems is a function of the vegetative and soil characteristics of the riparian zone, hydrologic events, and biotic processing. Dissolved organic matter (DOM) generally accounts for 50 percent or more of the total annual organic flux in forested headwater streams (Fisher and Likens, 1973; Sedell et al., 1974). A significant proportion of the DOM generated is quite labile, being physically adsorbed and flocculated, and biologically incorporated by microorganisms at rates approximately equal to its production. This is exemplified by similar measured daily changes in DOM as compared

to those observed annually (Cummins et al., 1972; Manny and Wetzel, 1973). The rapid incorporation of the labile fraction of DOM onto particles and into microbes constitutes the important retention characteristic of streams because of the reduced probability of export of particles as opposed to solutions. Of the remaining annual organic flux, about one-half is fine particulate organic matter (FPOM); the greatest percent of CPOM is found in headwater streams, reflecting the close association with the riparian zone.

Annual POM input, exclusive of large woody debris, to headwater forested streams ranges from 300 to 800 g AFDW  $\text{m}^{-2}$  (Anderson and Sedell, 1979). Although annual inputs may be low, headwater streams characteristically have large standing stocks of large wood (approximately  $> 2 \text{ cm}$ ): from 1 to 2  $\text{kg m}^{-2}$  in Michigan streams to 10 to 15  $\text{kg m}^{-2}$  in western Oregon streams (Anderson et al., 1978; Swanson and Lienkaemper, 1978). The coarse woody debris undoubtedly plays a major role in retaining nonwoody POM inputs, resulting in mean annual standing stocks of approximately 200 to 500 g AFDW  $\text{m}^{-2}$ .

### Macroinvertebrate Functional Feeding Groups

Recognition of stream microinvertebrate functional groups (Fig. 1) has shown considerable promise as a tool for assessing the ecological state of a running water community (Cummins, 1974; Merritt and Cummins, 1978). The relative abundances of the groups reflect environmental conditions, particularly the quantity and quality (i.e., nutritional value) of particulate organic matter inputs and periphyton growth. Arduous and incomplete efforts at taxonomic description can be reduced or circumvented by concentrating on morphological-behavioral adaptations for food acquisition. In addition, because most species are omnivores, this method avoids the lack of resolution associated with concentration on macroinvertebrate diets. Thus, the ratios of various functional groups reflect the nature of the organic food resources available (Cummins and Klug, 1979; Wiggins and Mackay, 1979).

There are five basic macroinvertebrate functional feeding groups. Figure 1 links each group with a nutritional resource that it is morphologically and behaviorally adapted to harvest and physiologically adapted to assimilate. The highest quality nutritional resources are animal tissue, nonfilamentous periphytic algae, and the microbial biomass component of detritus (Table 1) (Anderson and Cummins, 1979).

The CPOM: fungal-bacterial:shredder association (Fig. 1), is exemplified by large invertebrates such as larvae of the crane fly *Tipula*, which feed on conditioned leaf litter. Conditioning involves rapid leaching of soluble organics followed by colonization and growth of aquatic fungi and bacteria. After microbial populations have softened the substrate, shredders begin actively feeding on CPOM (Cummins, 1974; Cummins and Klug, 1979). Shredders selectively feed on the CPOM with the maximum microbial biomass, and account for at least 30 percent of the total processing (conversion of CPOM to  $\text{CO}_2$ , FPOM, and consumer biomass) (Petersen and Cummins, 1974). The shredder functional group represents the closest invertebrate linkage with the riparian zone, with growth and survival dependent upon the quantity and quality of the terrestrial inputs.

The FPOM:bacterial:collector association (Fig. 1) includes macroinvertebrates that feed by filtering particles from the passing water, for example, with filtering fans (blackflies) or silt nets (net-spinning caddisflies), and those that gather

particles from the stream bottom sediments (many species of midges). Although collectors require the presence of microbial biomass on ingested FPOM for adequate nutrition, they show less adaptation for selective feeding (i.e., selection for highest food quality) than shredders (Cummins and Klug, 1979). The relationship of collectors to the riparian zone is less direct because a significant portion of the FPOM is generated within the stream ecosystem (Fig. 1). Therefore, the ratio of shredders to collectors in a stream community reflects the balance between CPOM and FPOM and the relative dominance of the riparian zone.

Macroinvertebrates of the periphyton: scraper association have adaptations for removing attached algae (primarily nonfilamentous forms) from surfaces (Fig. 1). Because they frequently feed in exposed sites, scrapers are also adapted morpho-behaviorally for maintaining position in the current; for example, the heavy mineral cases of scraper caddisflies or the dorso-ventral flattening of heptageniid mayflies that allows them to avoid the main force of the flow. Abundance and growth of scrapers

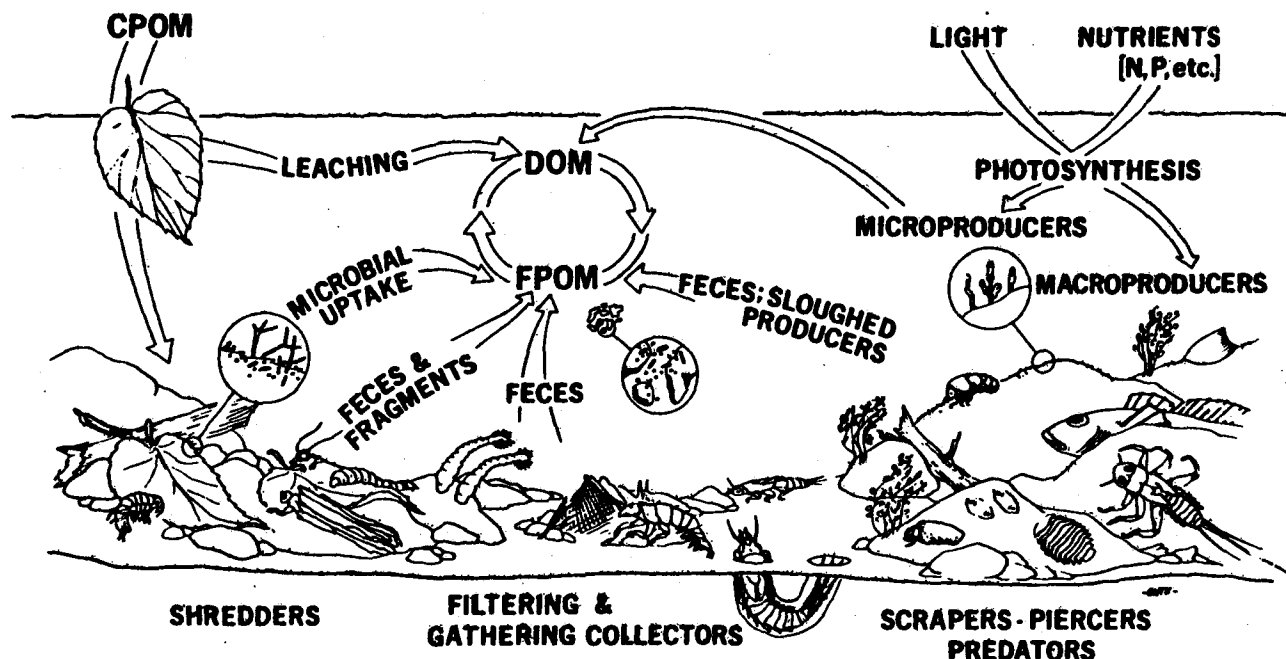


Figure 1. Diagrammatic representation of major resource inputs and partitioning among invertebrate functional groups in forested, headwater stream ecosystems. The major inputs shown, CPOM, light, and nutrients (FPOM and DOM also enter from the riparian zone, not shown), are partitioned among five general processing subsystems associated with macroinvertebrate functional feeding groups. These are the CPOM:fungal-bacterial:shredder; FPOM:bacterial:collector; algal:scraper; macrophyte:piercer; and predator:prey associations. Production of DOM from CPOM and pathways of FPOM generation are also shown. (Shredders--amphipod, detrital stonefly, caddisfly, and crane fly; filtering collectors--blackflies and net spinning caddisfly; gathering collectors--burrowing mayfly; scrapers--tortoise-shell case caddisfly, limpet, heptageniid mayfly, waterpenny beetle larva; piercers--micro-caddisflies; predators--predaceous stonefly, sulpin.)

is correlated with in-stream algal primary production, for example, P/R ratio (Anderson and Cummins, 1979). Ratios of shredders or collectors to scrapers are indicative of the importance of CPOM or FPOM relative to periphyton as nutritional resources.

The piercer:macrophyte association (Fig. 1) in streams is represented almost exclusively by microcaddisflies, which utilize filamentous macroalgae by sucking the fluids from individual cells. As primary producer communities in streams shift from diatoms to macrophytes, the ratio of piercers to scrapers increases. The piercers are a unique group in that the major utilization of macrophytes in streams is in detrital food chains (Minshall, 1978).

Predator:prey associations (Fig. 1) in stream communities appear to be relatively constant and ubiquitous. Animal tissue represents the highest quality food resource (Anderson and Cummins, 1979), but the relatively low density of prey relative to other nutritional resources means that predators are required to expend more energy in acquiring food.

#### MANAGEMENT CONSIDERATIONS

The multiple and intimate relationships between the riparian zone and the stream ecosystem in forested watersheds make this a critical interface for management. The riparian zone should be maintained as a suitable source area for long-term physical channel structure (e.g., wood debris) and annual organic resources. Tools are available for evaluating the stream community response to changes in the riparian source area, such as: the C/N of nutritional resources, community metabolism (P/R, and macroinvertebrate functional group ratios).

Because the quality and quantity of inputs to forested headwater stream ecosystems from the riparian zone exerts a major control on community structure and function, a number of management strategies are possible. For example, selective harvest or enhancement of tree, shrub, or herbaceous species in the riparian zone would be possible. Species such as alder generate rapidly processed litter which produces nitrogen-rich leachate that is quickly converted to FPOM, while conifer needles (e.g., Douglas-fir) are utilized at much slower rates over longer time periods.

In general, management of riparian zones is management of headwater streams, and management of headwater streams is critical for managing the larger receiving streams and rivers.

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