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Coniferous Forest Streams

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INTRODUCTION

Forest streams have long been used to integrate physical and chemical processes on a watershed; however, measurements of processes such as water flux, erosional yield, and nutrient loss consider only the transport function of streams. Streams, in addition to their transport function, also serve as temporary pools for particulate and dissolved materials lost from the surrounding forest. Watershed topography concentrates these particulate and dissolved materials into an area composing less than 1 percent of the watershed and permits establishment of a distinctive biological community. The stream program in the coniferous forest biome program has attempted to examine holistically the processing efficiency and capability for energy flow and nutrient cycling by this separate biological system and its relation to canopy density, retention capacity, and carbon and nutrient quality of particulate inputs within a stream reach. The relation of biological structure and function with physical and chemical structure of streams was examined, as well as their variations through time and space. This chapter is a synthesis of research dealing with stream structure and function, organic matter budgets, spatial and temporal aspects of the coniferous forest stream, and forest land-use impacts. Most data presented here were collected at five sites in or adjacent to the H. J. Andrews Environmental Forest, Oregon: watershed (WS) 10 stream, Devil's Club Creek, Mack Creek, Lookout Creek, and the McKenzie River (see Figure 1.4 for stream locations and Table 1.5 for physical characteristics).

The stream on WS 10 is first order (Strahler 1964; see Table 1.4), drains 10.24 ha, and rises from 430 m at the outlet stream gauging station at 670 m at its highest elevation. The overall slope of the stream channel is 45 percent. Side slopes, however, range up to 90 percent. Stream discharge varies from around 0.23 liter/s in summer to about 140 liters/s during winter freshets. The uppermost reaches are intermittent during summer. Mean annual precipitation on the watershed is 240 cm. Mean width of the stream channel ranges from 0.25 m in the upper reaches to 1.0 to 1.5 m at the base of the watershed. The streambed is a "stairstep" series of small pools connected by free-fall zones or riffles running on bedrock. Pools are usually formed behind accumulations of wood debris. The substrate consists of loose rocks and gravel from tuff and breccia bedrock.

Devil's Club Creek is also a first-order stream channel with large accumulations of coarse organic debris derived from the surrounding old-growth (>400 years) forest. Debris consists of large logs of Douglas-fir and western hemlock and leaf litter (primarily huckleberry, devil's club, maple leaves, and Douglas-fir needles). Autochthonous production is nearly zero in this heavily shaded tributary of Mack Creek.

Mack Creek is one of three major drainages of the Andrews Forest (see Figure 1.6). Morphology of this third-order stream is a stairstep of pools, free-fall zones, and turbulent water around boulders. Woody debris is an important morphological feature but is found in lower concentrations than in Devil's Club Creek. The forest canopy is open slightly because of tree mortality, blowdown, and a wider stream channel. This allows some light to reach the stream. Benthic primary production occurs but is not the major organic input. Leaf fall from maple and Douglas-fir, some windfall, and upstream input from tributaries are the principal inputs. Mack Creek is a major tributary of Lookout Creek.

Lookout Creek, receives runoff from the entire Andrews Forest (see Figure 1.4). Morphology of this fifth-order stream is extensive shallow riffles interspersed with pools. Substrate is either large cobble or bedrock. Smaller amounts of wood debris are present here than in Mack Creek. The canopy is open and there is an extensive periphyton (attached algal) community.

The McKenzie River is a major sixth-order stream draining the western Cascade Mountains (see Table 1.5). Morphologically it is 85 percent riffle with a few calm water areas. Substrate is cobble and large boulders. Woody debris is not important to this river either morphologically or biologically. Inputs are primarily from upstream transport and benthic primary production. A small amount of allochthonous input occurs from alder and Douglas-fir along the river banks. Autochthonous input occurs from a zone of moss (*Fontinalis* sp.) that extends out 5 m from both banks and from a moderate to dense periphyton community that colonizes the entire substrate.

STREAM STRUCTURE AND FUNCTION

If an aerial photograph of an old-growth watershed containing a third-order stream were examined, determination of drainage patterns would have to be made from topographic features since the actual watercourses would be obscured by forest canopy. This dense vegetation ties the stream both morphologically and biologically to the adjacent landscape.

Morphologically, first- and second-order streams in the Cascades are characterized as high gradient with some areas of exposed bedrock. Inputs of old-growth boles and large limbs lie where they fall, trap sediments, and create habitats for various aquatic organisms. As the stream becomes larger (third- and fourth-order), high storm flows build enough hydrologic force to clump debris into larger accumulations. These debris dams constitute important morphological features that retain finer organic debris. In addition to its physical role, wood also functions biologically as a refractory carbon source, processed abiotically by water movement and biologically by microbes and invertebrates (Figure 10.1).

A second biologically available input from the terrestrial landscape is forest litter. Input and processing of leaf litter has attracted considerable attention by stream researchers over the past ten years. In fact, leaf litter often constitutes the energy base of small forest streams on an annual basis. Within a day after it enters the stream, leaf litter has been divided into two components: a dissolved fraction that enters the dissolved organic material (DOM) pool and a residue processed slowly by the microbial community (Figure 10.1). Once conditioned by microbial colonization this residue forms a readily available food source for invertebrates called "shredders" (Cummins 1973). While some of the conditioned litter is used by invertebrates for tissue synthesis and maintenance, most is egested and enters the fine particulate organic matter (FPOM) pool. The FPOM pool consists of organic particulates less than 1 mm but greater than 0.45 μm in size. Fine organic particles, whether derived from physical, chemical, or biological processes, serve as a food source for collector invertebrates.

Thus, in heavily shaded first-order streams where primary production is minimal, two major organic substrates, wood and leaf litter, constitute the

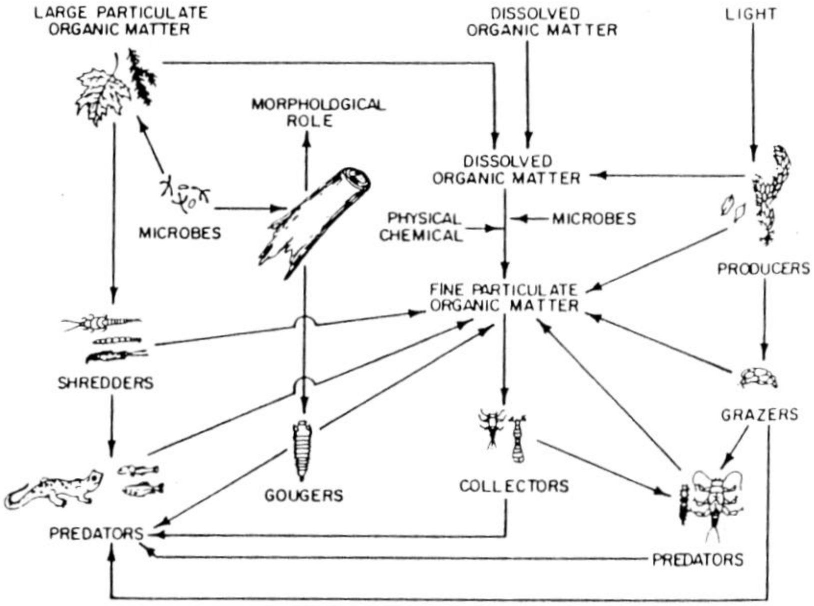


FIGURE 10.1 *A generalized view of biotic structure and function in a coniferous forest stream (after Cummins 1973).*

iergy base. These respective substrates differ greatly in terms of amount and ne required for processing (Table 10.1). Although it may vary by season, less an 5 percent of particulate organic matter in the benthic standing crop is in the rm of leaves and needles; greater than 60 percent is in the form of small, oody substrates (cones, branches, twigs, bark). This does not include large oles, which dominate small streams. Leaf inputs occur primarily during au-imn. Wood inputs, on the other hand, occur erratically, particularly blow-own during major windstorms. Since leaf litter has a higher nitrogen (N) and wer fiber content than wood, it is utilized more rapidly by the microbial and ivertebrate community but has little morphological impact on the stream. Of ie two detrital inputs, the smaller pool of leaf litter is characterized by a rapid irnover dominated by microbial processes and shredding, and the extremely irge wood pool by a long turnover time dominated by microbial processes and ouging. The product of both pools (FPOM) is further processed by collector rganisms. As a refractory pool, wood effectively buffers the system physi-ally and to a lesser extent metabolically. On the other hand, FPOM buffers the ystem metabolically but not physically, since it is readily exported. In fact, POM constitutes the major fraction of particulate organic matter exported to ownstream reaches.

In addition to large inputs of terrestrial litter, primary production occurs vhere sunlight penetrates the canopy and reaches the stream bottom. In small treams with extreme canopy cover, primary production is undertaken almost xclusively by mosses. Where the canopy is open, however, an attached algal ommunity, primarily diatoms, colonizes bottom mineral substrates. This eriphyton is consumed by grazer invertebrates. Feces from both shredders and razers enter the FPOM pool and become available to the collector community. inally, all three invertebrate functional groups may in turn be consumed by redators, primarily insects, salamanders, and cutthroat trout.

leterotrophic Function

Biological functioning in streams (that is, energy flow and nutrient cy-ling) through the heterotrophic pathway is a complex series of events depen-lent on interactions between various biological components. One good exam-le of such an interaction is microbial colonization (conditioning) of leaf litter rior to shredder consumption. Leaf litter is processed by the microbial com-nunity at a continuum of rates dependent on biochemical composition. Figure 0.2 illustrates such a continuum of decay rates from various species of leaf itter from Mack Creek, H. J. Andrews Forest, and from Augusta Creek, Aichigan. In each stream various leaf species exhibit differential rates for leaf rocessing. This processing is a function of the time required for leaf tissue to e colonized and metabolically utilized by the microbial community (Triska 970).

TABLE 10.1 *Comparison of leaves and wood debris as components of small coniferous forest stream ecosystems.*[a]

Substrate	Standing crop (% of partic-ulate matter)	Season-ality of inputs	Impact on stream morphology	Carbon/ nitrogen ratio	Total fiber (%)	Degra-dation time	Microbial coloniza-tion pattern	Inverte-brate component	Invertebrate utilization
Leaves	< 5	Pulsed autumnal	Minor	25 to 100:1	20 to 40	2 to 12 mo	Surface and matrix	High (mg/g)	Food, shelter
Wood debris	> 60 (excluding boles)	Erratic	Major (stabilize and destabilize)	300 to 1000:1	70 to 80	5 to 200 yr	Primarily surface	Low (mg/kg)	Shelter, substrate, ovipoposition, pupation, emergence, food (direct and indirect)

[a] From Anderson et al. 1978.

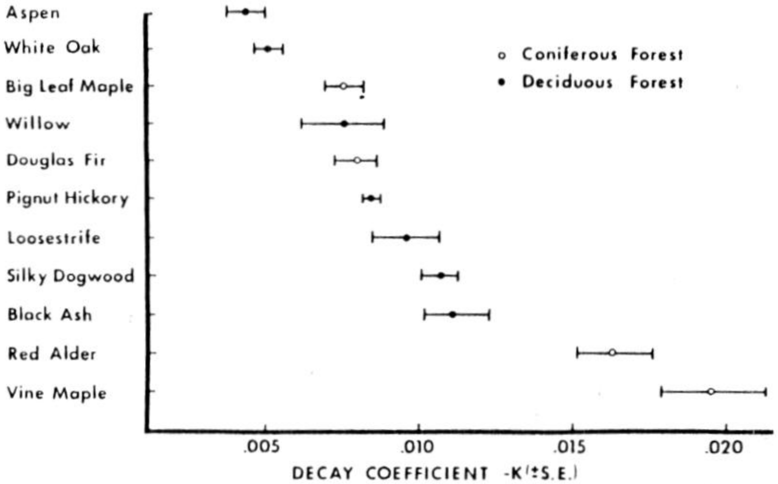


FIGURE 10.2 *Decay rates for major litter inputs to a coniferous forest stream (Mack Creek) and a deciduous forest stream (Augusta Creek, Michigan).*

Although the mechanism of conditioning is unknown, its occurrence has been verified by both field and laboratory studies. In a laboratory experiment Anderson and Grafius (1975) used leaf litter of red alder *(Alnus rubra)*, a common riparian species. Alder is low in fiber and high in N, and hence decomposes rapidly. It was conditioned for periods up to fifty days and then presented to larvae of the caddis fly *(Lepidostoma quercina)*. Consumption rate was very low on leaves of less than thirty days' conditioning time. After about thirty days litter was readily consumed at a rate related to length of conditioning time (Figure 10.3). A similar pattern, but with much longer conditioning times, was also observed for needle litter of Douglas-fir conditioned up to three hundred days prior to ingestion by larvae of *Lepidostoma unicolor* (Anderson and Grafius 1975).

Long-term microbial conditioning of refractory litter was also demonstrated in field studies at Mack Creek (Figure 10.4). There Douglas-fir litter was ignored by invertebrate larvae for approximately one hundred and fifty days. After that period, litter was readily consumed, as demonstrated by dramatic weight loss of leaf packs and weight gain by shredders. Most needle consumption occurred during spring as temperature warmed, larvae reached their final instar, and after most deciduous litter had decomposed. Although riparian species vary from stream to stream, the continuum of processing rates required for diverse allochthonous inputs mitigates the effect of large autumnal input and guarantees the availability of conditioned detritus at all seasons. In this way invertebrate life cycles can be geared to quality of litter inputs and activity of the microbial community.

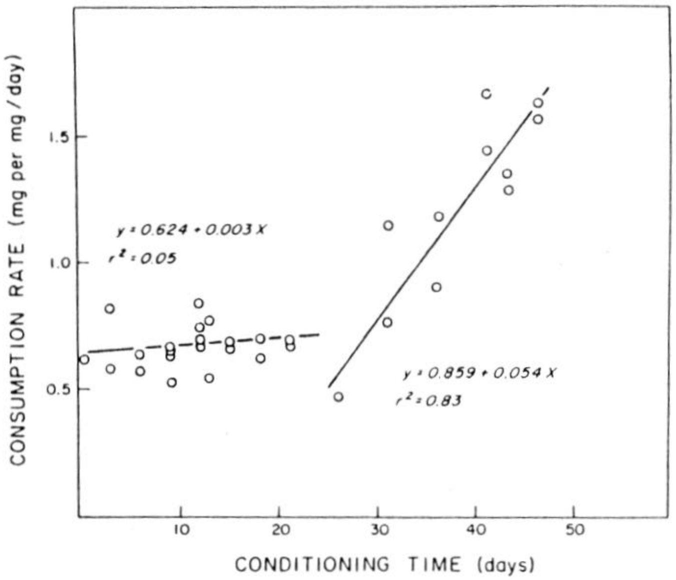


FIGURE 10.3 *Consumption rates of leaf litter of red alder* (Alnus rubra) *fed to larvae of the caddis fly* (Lepidostoma quercina) *after being conditioned for periods of 0 to 50 days in a laboratory stream (Anderson and Grafius 1975).*

One major benefit of microbial conditioning for the shredder community is the increase in protein content, first demonstrated by Kaushik and Hynes (1968). This factor may be particularly important for litter with an extremely high carbon/nitrogen ratio such as Douglas-fir needles (C/N = 93). Data from six streams in Oregon and Washington (Triska and Buckley 1978) illustrate change in absolute N content of needle litter based on leaf packs with a normalized starting weight of 10 g (Figure 10.5). Such a 10-g leaf pack had a N capital of about 59 mg prior to incubation. Leaching lowered the N capital to approximately 20 mg during the first few days. Thus, while total weight loss due to leaching amounted to 20 percent, loss of N capital exceeded 50 percent. From this base of approximately 20 mg, N capital increased rapidly as decomposition proceeded. Nitrogen content was greatest between the periods of 30 to 60 percent weight loss. At some state of decomposition, an absolute increase in N capital was observed in all six streams. After peaking, N capital declined steadily as C was mineralized. Similar gains in absolute N content have previously been reported for lotic ecosystems (Mathews and Kowalczewski 1969; Iverson 1973; Hodkinson 1975; Triska and Sedell 1976). Although the mechanism is complex and not well established, the gain in N capital does demonstrate how particulate organic matter and associated microflora serve as an N pool for stream biota.

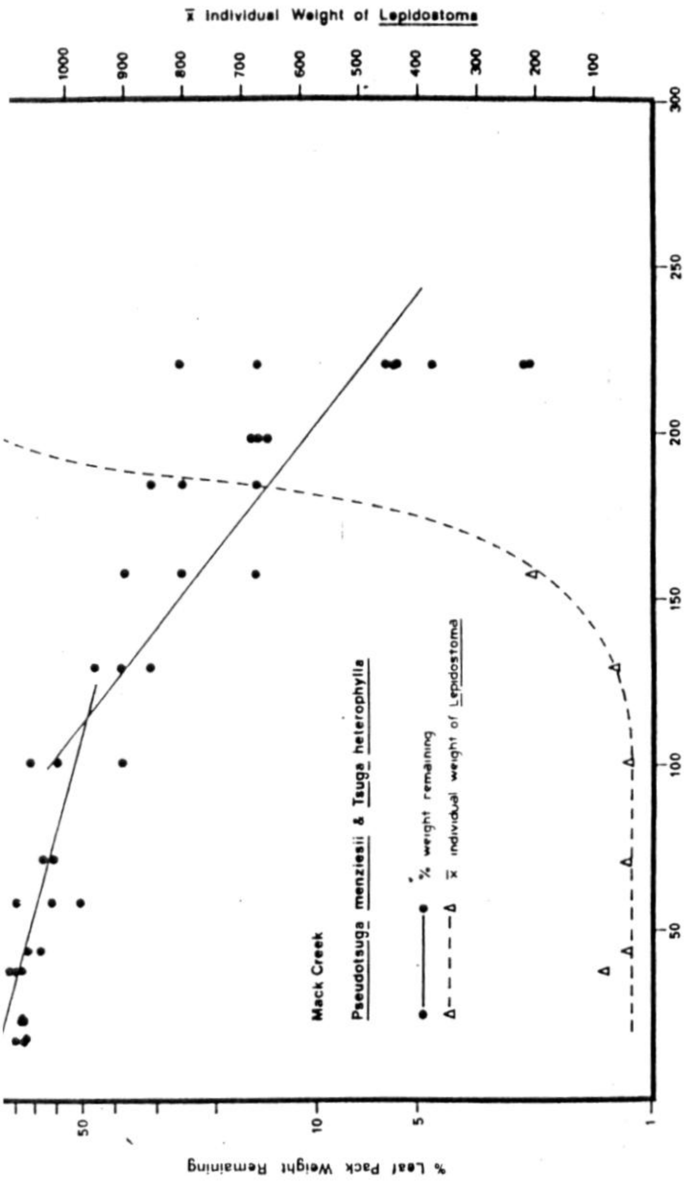


FIGURE 10.4 *Leaf-pack weight loss and mean individual weight of larvae of* Lepidostoma unicolor. *as leaf litter of Douglas-fir underwent decomposition in Mack Creek (Sedell et al. 1975).*

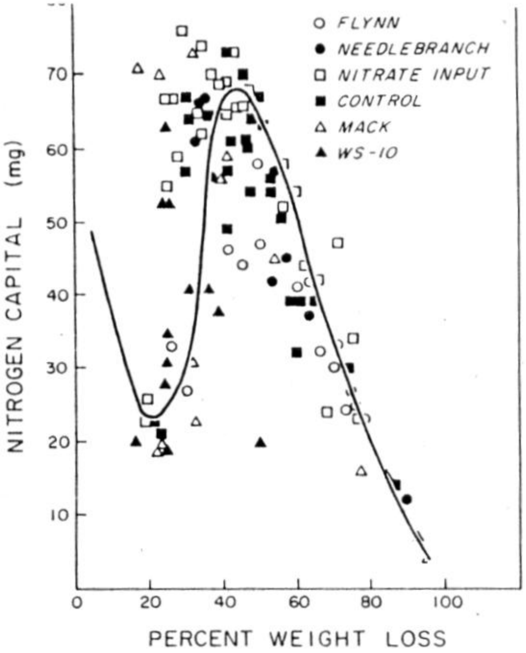


FIGURE 10.5 *Nitrogen capital of Douglas-fir needle litter as decomposition proceeds in six streams of the Pacific Northwest. Data are based on a normalized starting weight of 10 g.*

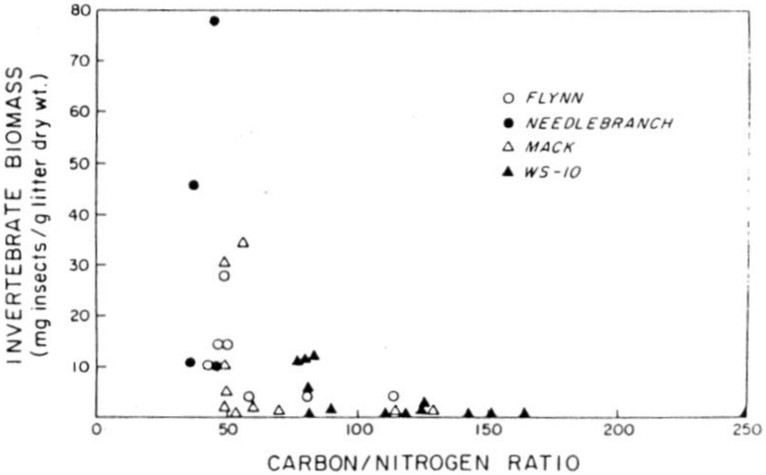


FIGURE 10.6 *Invertebrate biomass associated with decomposing needle litter of Douglas-fir as a function of C/N ratio from four streams in the Pacific Northwest.*

If N content is a major factor in conditioning, then utilization of organic matter by invertebrates should be maximum near the lowest C/N ratio (Figure 10.6). Watershed 10, which had the least gain in N concentration and the highest C/N ratio, also had least invertebrate biomass associated with needle packs. Maximum invertebrate biomass (11.2 mg/g leaf pack) was found at the time of lowest C/N ratio (80). In Mack Creek, the lowest C/N ratio was approximately 50 and occurred about three weeks before maximum invertebrate biomass was observed on the litter. Once discovered by the invertebrate community, a maximum of 35 mg invertebrate biomass occurred per gram of needle pack. This compares favorably with data for Flynn Creek, where a maximum of 28 mg invertebrate biomass/g needle pack was collected at a C/N ratio of 49. Higher invertebrate biomass was associated with litter packs at Needle Branch Creek, which also reached the lowest C/N ratio (42). In that stream highest invertebrate biomass was 76 mg invertebrates/g of needle pack, on a sample with a C/N ratio of 50. This overall invertebrate response suggests how a simple trophic function such as consumption of litter by invertebrates is a complex interaction between quality, quantity, and timing of terrestrial inputs; physical processes; nutrient regime; microbial community; and invertebrate shredders. It is through a large series of such complex interactions at each level of processing that the heterotrophic component of the stream functions as an ecological unit.

Autotrophic Function

Besides allochthonous detritus, autochthonous primary producers such as attached algae, mosses, and vascular plants constitute the second source of organic matter processed by stream invertebrates. In heavily shaded streams, primary production is dominated by bryophytes with a slight contribution by attached diatoms. In larger, unshaded streams most primary production shifts to benthic diatoms with seasonal inputs by filamentous green algae. Thus community structure of primary producers in Pacific Northwest streams varies depending on both season and canopy density (Table 10.2). The seasonality of green algae and diatom communities results from increased photoperiod and light intensity in early spring and subsequent senescence and sloughing of algae during late autumn periods of high flow. The drought year of 1976 demonstrated the role of high discharge in controlling community structure. Since no storms occurred until March 1977, an abundance of filamentous or thallus algal forms persisted until March, whereas this community is normally depleted by scouring between October and December (J. Rounick, pers. comm.).

Shading by terrestrial vegetation influences both autotrophic community tructure and the rate of primary production. Gross primary production generlly increased in the McKenzie River drainage from headwater to higher order rivers with maximum production in the fifth-order stream (Figure 10.7). The role of light in this progression is shown by the substantial increase in primary production in the open third-order site in contrast to the forested third-order site. One complicating factor in this trend, however, is low concentration of inorganic N in headwater streams, which might account for low production rates. In fact, during summer, inorganic N is undetectable in first-order streams while concentrations of 30 to 100 μg/liter NO_3-N occur in higher orders.

TABLE 10.2 *Community characteristics and patterns of growth of the periphyton communities at four study sites in three streams of the Cascade Mountains, Oregon.*

Community type	Characteristic plant	Location	Pattern of growth
Pennate diatom	*Achnanthes*	Upper Mack Creek Lower Mack Creek Lookout Creek Watershed 10	Year-round
Thallus green algae	*Prasiola*	Upper Mack Creek Lower Mack Creek	March to August
Filamentous green algae	*Ulothrix zygnema*	Lower Mack Creek Lookout Creek	April to July June to November
Centric diatom	*Melosira*	Lookout Creek	July to January

To test the hypothesis that light rather than nutrients limited primary production, a section of a first-order, old-growth forest stream was artificially lighted (Gregory 1980). Halfway through the lighted section NO_3-N was added to achieve a concentration of 100 μg NO_3N/liter. Four treatments resulted: (1) natural light; (2) increased light; (3) increased light plus nitrate; and (4) natural light plus nitrate. After twenty-eight days, gross primary production, community respiration, and diatom community structure were measured. Gross primary production was lowest in the natural light and natural light-plus-nitrate section and no difference was detected between the two (Figure 10.8). Only in the light sections did gross primary production approach a balance with community respiration. Primary production was appreciably greater than respiration in the light-plus-nitrate section. In the natural light sections, primary production was far less than respiration. This does not imply that algae were not compensating for their own respiration in these sections, but rather that algae were not able to supply all the energy needed to support the epilithic communities of algae, bacteria, and fungi. In lighted sections, however, autotrophs were able to produce enough energy to account for respiration of the entire epilithic community.

As a result of this experiment, it is evident that light rather than nutrients is limiting primary production in headwater streams of coniferous forests. Once streams are sufficiently lighted, nutrient inputs become a critical factor in

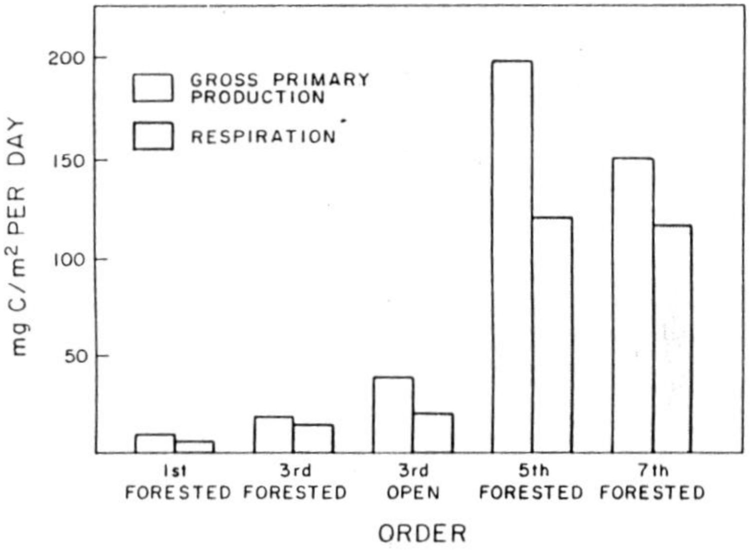


FIGURE 10.7 *Gross primary production and epilithic community respiration (mg C·m^{-2}·day^{-1}) in selected first- through seventh-order streams of the McKenzie River drainage.*

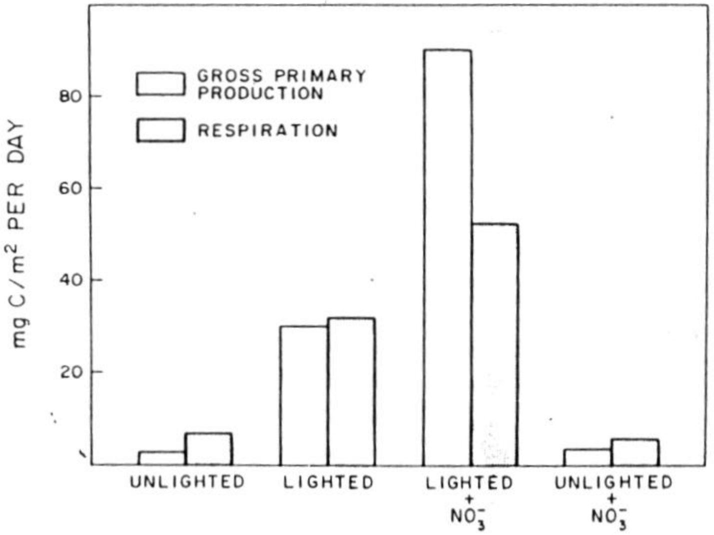


FIGURE 10.8 *Gross primary production and epilithic community respiration (mg C·m^{-2}·day) in watershed 10, resulting from experimental manipulation of light and nitrate input.*

primary production. This explains the greater production rate found in fifth-order streams, which are richer in inorganic N than less productive but unshaded third-order streams (Figure 10.7). Influence by the surrounding terrestrial ecosystems is demonstrated by regulating not only detrital inputs but also solar energy for driving primary production within the stream ecosystem.

Besides changes in primary production with light addition, changes in relative abundance of individual species of algae were observed. *Achnanthes lanceolata, Cocconeis placentula lineata, Eunotia pectinalis,* and *Meridion circulare* were dominant species in lighted areas but were found in small concentrations in natural lighted sections. *Diatoma heimale mesodon, Gomphonema intricatum pumila, G. parvulum, G. subclavatum,* and *Navicula radiosa tenella* were the most abundant of those taxa in unlighted areas and showed little response to increased light intensity. Diatom community structure in the light-plus-nitrate section was similar to that in the lighted section. Therefore there appears to be no species response to added nitrate after increased lighting.

Not only can nutrients affect primary production in open streams, but primary production affects the nutrient regime of streams. Stream chemistry has been traditionally interpreted as a function of bedrock-soil geochemistry and terrestrial nutrient cycling of the watershed, but under certain conditions stream biota may also alter stream water chemistry. Primary production creates a demand for critical elements, particularly inorganic N. Therefore, as primary production increases, the potential for alteration of stream chemistry also increases. Nitrate concentration was monitored throughout a day for a series of streams ranging from a forested, first-order stream to a fifth-order stream. Midday reduction of nitrate was greatest for the fifth-order, the most productive stream (Figure 10.9). No significant nitrate reduction was observed in the first-order stream. The open section of the third-order stream, however, had a significant reduction of nitrate, though not as great as the more productive fifth-order stream. Further evidence to relate observed changes in nitrate concentrations to primary production was provided by concentrations of inorganic C throughout the day in these same streams (Figure 10.10). Essentially the same relation was found for inorganic C as for nitrate concentrations, the fifth-order stream displaying greatest diel variation and the first-order stream showing least. Therefore the biota of stream systems are not merely existing within their ecosystems but rather interacting extensively to affect the chemical nature of streams.

PARTICULATE ORGANIC MATTER BUDGETS

One tool used by stream ecologists to view overall ecosystem function has been calculation of material or energy balance. Most often the budget process has been used to examine patterns of energy flow (Odum 1957; Mann et al.

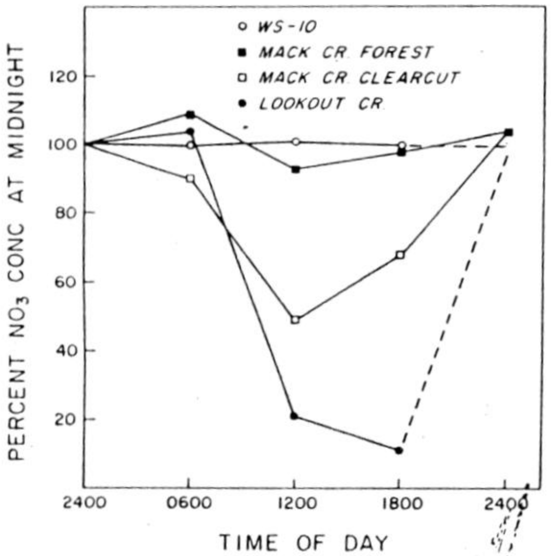


FIGURE 10.9 *Percentage change from midnight concentration of nitrate in a summer-derived sample from first-order (watershed 10), third-order (Mack Creek), and fifth-order (Lookout Creek) streams.*

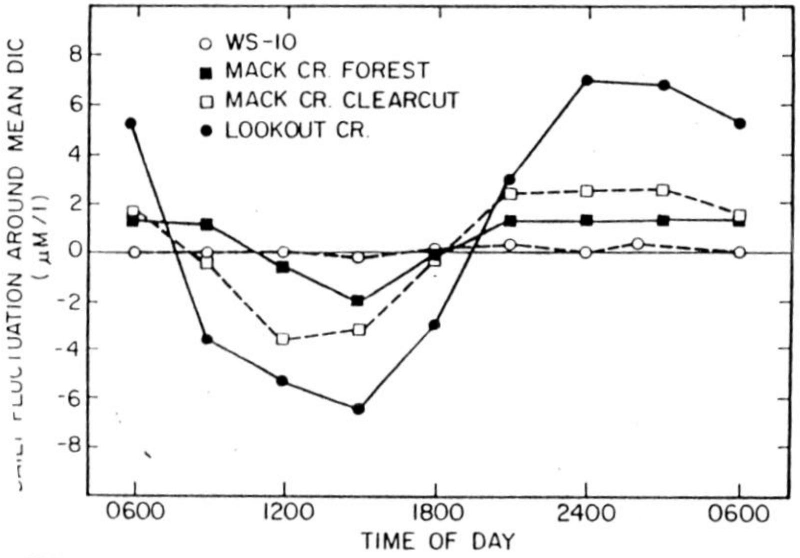


FIGURE 10.10 *Daily fluctuation of dissolved inorganic carbon (DIC) concentration in a first-, third-, and fifth-order stream.*

1972; Hall 1972; Fisher and Likens 1973; Sedell et al. 1974), although patterns of N cycling (Triska et al. in press) also provide a suitable base. The budget process encourages a holistic view of the stream ecosystem by defining the relative importance of various fluxes and pools. Extension of the budget process over more than one year also helps define variation in ecosystem behavior. Through examination of internal fluxes, organic matter and nutrient budgets provide significant insight into processing capabilities of small streams on an annual basis and their contribution to downstream communities. Measurement of these same parameters also provides an index to quantity and quality of the energy base in small streams. Measurement of production/respiration (P/R) ratios indicates allochthonous versus autochthonous influences and indexes a stream reach as either autotrophic or heterotrophic. Comparison of amount and quality of litter inputs with exports provides an index of the stream's ability to process organic debris. Estimates of detrital standing crop provide an index of retention capacity and identify physical and metabolic buffers operating in streams. Budgets allow a comparison of particulates with the dissolved components passing through the system. Once a holistic view is achieved and the importance of various fluxes is determined, budgets help set priorities for future research effort.

Organic matter budgets were constructed for WS 10 to estimate nutrient and energy flow in a small coniferous forest stream. The organic matter fluxes and standing crop were measured for a dry year 1973 (160 cm precipitation) and a wet year 1974 (300 cm precipitation). The approach was to construct a material balance budget by tallying hydrological and biological (terrestrial and aquatic) inputs minus hydrological and biological export and changes in particulate organic storage. For the C budget the major hydrological and meterological input was dissolved organic C, which entered in groundwater. Samples were taken at sites where major seeps drain into the stream and were compared with export samples taken at a gauging station at the bottom of the watershed. Terrestrial biological inputs were throughfall, litterfall, and lateral movement of particulate organic matter along the ground from the adjacent terrestrial forest (Sedell et al. 1974). The "in-stream" biological input was primary production. Since the stream was small, export was measured by collecting all particulate organic matter in excess of 80 μm during 1973 and 1 mm in 1974 in a net located at the base of the watershed. Export of particles between 80 μm and 0.45 μm was not estimated. Standing crop was determined monthly by coring, using a 15-cm pipe sampler. A Gilson respirometer was used to determine microbial respiration of benthic organic matter.

Once major inputs, outputs, and standing crops had been measured, organic budgets for 1973 and 1974 were calculated (Tables 10.3 and 10.4). Total organic input was 490 kg/yr for the dry year 1973 and 789 kg/yr during the wet year 1974. Total litterfall and lateral movement dominated inputs for both years at 361 kg/yr or 75 percent of inputs in 1973 and 503 kg/yr or 65 percent in 1974. Throughfall, both particulate and dissolved, constituted less than 10 percent of *water year 1973 (1 Oct 1972 to 30 Sept 1973).*

Inputs			Standing crop			Outputs		
	(kg/yr)	(%)		(kg)	(%)		(kg/yr)	(%)
Litterfall	161	33	Large detritus (> 10 cm diam)	8698	83	Particulate organic	37	11
Throughfall	41	8	Small detritus (< 10 cm to 1 mm diam)	1382	13	Microbial respiration	186	55
Lateral movement	200	41	Fine particulate organic matter (FPOM) (< 1 mm to 75 μm)	87	1	Macroinvertebrate respiration	2	1
Gross primary production:			Ultrafine detritus (> 75 μm to 0.45 μ)	233	2	Primary producer respiration:		
Algae	< 1	0.2				Algae	< 1	0.3
Moss	23	5				Moss	15	4
Dissolved organic matter	64	13	Primary producer biomass	31	0.3	Dissolved organic matter	96	28
			Macroinvertebrates	1				
Total	490		Total	10,432		Total	337	

TABLE 10.4 *An annual organic budget for watershed 10, H. J. Andrews Experimental Forest, for water year 1974 (1 Oct 1973 to 30 Sept 1974).*

Inputs			Standing crop			Outputs		
	(kg/yr)	(%)		(kg)	(%)		(kg/yr)	(%)
Litterfall	170	22	Large detritus (> 10 cm)	8692	82	Particulate organic	245	32
Throughfall	57	7	Small detritus (< 10 cm to 1 mm)	1535	15	Microbial respiration	183	24
Lateral movement	333	43	Fine particulate organic matter (FPOM) (< 1 mm to 75 μm)	87	1	Macroinvertebrate	2	0.3
Gross primary production:			Ultrafine detritus (< 75 μm to 0.45 μm)	233	2	Primary producer respiration:		
Algae	< 1	0.1				Algae	< 1	0.1
Moss	23	3				Moss	15	2
Dissolved organic matter	206	26	Primary producer biomass	31	0.3	Dissolved organic matter	310	41
			Macroinvertebrates	0.8				
Total	790		Total	10585		Total	756	

the budget in both years. Input of dissolved organic matter constituted about 13 percent of organic output in 1973 and 26 percent in 1974.

Massive accumulations of large detritus, primarily boles, dominated the stream and constituted 85 percent of standing crop. Small detritus, which includes leaf litter, was dominated by fine wood debris since leaf material was easily mineralized by the microbial community and lost via microbial respiration and conversion to FPOM. In fact, more than half the estimated output of WS 10 in 1973 (56 percent) occurred as microbial respiration. The large pool of fine detritus (87 kg/yr) was especially significant since it is a degradation product of large detritus and constitutes a refractory pool available to collector invertebrates. The size of the fine detritus pool was underestimated by absence of measurements for ultrafine detritus (< 75 μm). Subsequent estimates during 1974 and 1975 indicate the ultrafine detritus pool is 2.5 times as large as the fine detritus pool on WS 10. This ultrafine detritus is the product of both breakdown of large organic debris and flocculation of dissolved organic matter (Lush and Hynes 1973; C. H. Dahm, pers. comm.).

Capacity of large debris to retain detritus and permit litter processing by biota was established in several ways: (1) during 1973 less than 10 percent of the particulate organic input was exported; (2) respirometry measurements estimated some 186 kg/yr of particulate organic matter could be accounted for by microbial respiration due to retention within the reach; and (3) existence of a large pool of fine detritus verifies an extensive processing capability since the pool itself (particularly in the 250-μm to 1-mm size class) is a residue of that process.

The budget also reflects the paucity of primary production in these small forested streams. Gross primary production was low at 24 kg/yr, less than 1 kg/yr of which was by algae. Of the 24 kg/yr of gross primary production about 8 kg/yr was calculated as net primary production; the remainder was lost as plant respiration. As a result, net primary production provided only about 2 percent of the organic budget, indicating the heterotrophic nature of these first-order streams.

The refractory nature of many inputs prevented microbial degradation within one year. In addition, low streamflow during 1973 and retention structures in WS 10 effectively prevented export of detritus. The result was a large storage of small detritus (Table 10.4). Comparison of the amount and quality of debris input with export indicates that labile litter such as leaves and needles were effectively retained and only a minor proportion was exported in a recognizable state in either year (Figure 10.11).

Although water year 1974 had twice as much precipitation as 1973, overall conclusions remained the same. The largest budget difference was a threefold increase in DOM. Even during the wet year the organic budget was still dominated by particulate organic matter, which constituted 65 percent of organic inputs. A major change was also observed in particulate export, which was dominated by woody debris not effectively transported the preceding year

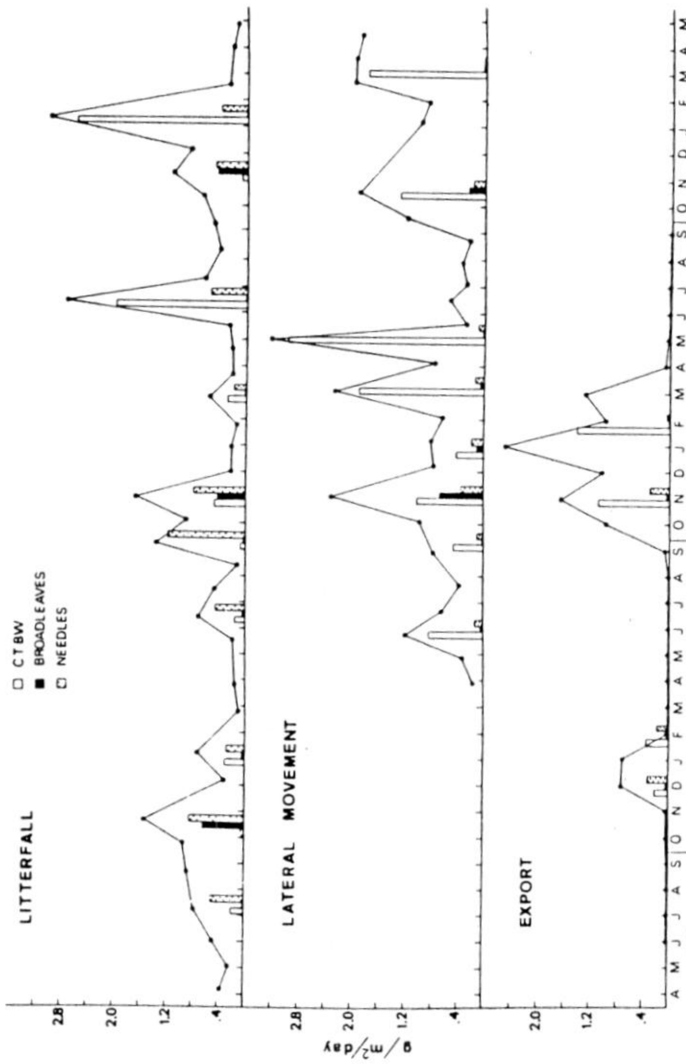


FIGURE 10.11 *Three-year record of total particulate organic input and export (solid line) in g/m⁻²/day⁻¹. Histograms are provided for major litter components. The designation CTBW is combined input of wood litter (cones, twigs, bark and wood). Data from watershed 10, H. J. Andrews Experimental Forest.*

Figure 10.11). The role of the microbial community was reduced from 56 ercent of organic output to 25 percent, because of increased transport. Despite creased transport relative to retention, significant particulate storage was bserved during both years, 136 kg/yr in 1973 and 75 kg/yr in 1974. Particulate torage was derived by difference between particulate inputs (litterfall + lat-ral movement) minus outputs (respiration + particulate). Some storage was bserved despite massive increase in particulate export, partially because of a 5 percent increase in lateral movement. Although not measured directly, loss f 0.45- to 75-μm particles (Frederiksen 1975) would not significantly affect he organic budget of 1973. As data from 1974 are analyzed, ultrafines may rove to be a significant export component.

Construction of the organic budgets provided insight into the functioning of a small stream as an ecosystem. It provided estimates of the magnitude, type, quality, and timing of various inputs to a small coniferous forest stream. It led to elucidation of the role of large debris as retaining structures. Finally, the organic budget resulted in discovery of a large pool of fine detritus, which is the product of debris processing and flocculation and quantified the role of FPOM as a major export and a refractory organic pool for the biota. The capacity of biota to mineralize debris was also quantified. Construction of budgets for two very different years allowed observations of various shifts in outputs, and introduced a temporal perspective to the inputs and overall functioning of a stream ecosystem.

TEMPORAL ASPECTS

Lake and terrestrial ecologists are often able to place their systems in historical perspective, to view the current state of their systems as a result of past events. Sediments in lakes and annual rings in trees both provide a historical record. Because history is not neatly recorded for streams, past events rarely have been considered in studies of stream ecosystem behavior. Stream ecosystem energetics are greatly dependent on recent flood event history, long-term variation in runoff, and adjacent vegetation. Storage and export values measured today reflect past and present annual runoff, flood size and frequency patterns, vegetation, and erosional conditions of a watershed. If organic budgets are not placed in a historical context, their usefulness in terms of comparing other sites, understanding processes at a site, or deriving relationships among photosynthesis, respiration, and input/export ratio is subject to serious question. Unfortunately, data are not available to directly evaluate the magnitude of historical variation in organic matter storage or transport; however a number of sources of information may be used to assess long-term variation indirectly and to evaluate the magnitude of short-term variation.

One indirect measure of export and long-term storage capacity of a stream channel is discharge, which has largely been ignored by biologists. As much as 80 percent of particulate organic matter exported annually is discharged during one or two storms (Bormann et al. 1969, 1974; Hobbie and Likens 1973; Fisher and Likens 1973; J. R. Sedell, pers. comm.). The history of sediment movement into and through a stream community has yet to be determined. Presently there are no published studies in which field sampling for organic matter budgets has been placed in the context of either annual flood cycles or long-term discharge patterns. It is important to know if study periods involved a major flood and, if not, what effect such a flood would have. At a minimum, material or energy budget measurements should be placed in a general perspective of flood return frequencies of the preceding year and the year of the measurements. Otherwise, there is no basis on which to determine if outputs of a given hydrologic year are related to inputs for the same year or different years.

Within the past century there have been periods of distinctly higher- and lower-than-average precipitation, mean annual discharge, and peak annual discharge. The record of discharge for the McKenzie River at McKenzie Bridge, Oregon, offers an indication of the historical variations in mean and peak annual flow in the Pacific Northwest (Figure 10.12). Occurrence of major floods is not restricted to generally wet periods. The flood of December 1964, the largest well-documented historic flood of a regional scale in the Pacific Northwest and California, occurred during a year of otherwise average discharge.

In Figure 10.12 the record of annual discharge at McKenzie Bridge is also plotted as cumulative departure from the mean of the mean annual discharges for a sixty-two-year period. A negative slope, such as shown for the period from 1928 to 1945, reflects a period of lower-than-average mean discharge; a positive slope, like that between 1947 and 1958, indicates above-average runoff. Annual mean discharge during the dry period was 14 percent less than mean conditions and exhibited average peak annual discharges only 69 percent of peak flow of the wet period. Thus, during dry seasons, flushing capacity of a stream would be considerably reduced. Although there are no organic budgets for these early periods, it is likely that storage of refractory organic materials in the stream occurred during dry years, with annual net loss or reduced net accumulation during wet periods.

Importance of discharge history can be seen in the two annual organic budgets presented earlier. Figure 10.13 presents return frequencies of peak discharge for twenty-five years of record at WS 2, H. J. Andrews Forest. The year prior to initiation of the budget study (1972) had three of the ten highest storm flows recorded (second, seventh, and ninth). As a result, these budgets were initiated at a time when storage of organic materials should have been low. Wet-year organic inputs by litterfall and lateral (surface) movement exceeded dry-year inputs by 5 percent and 65 percent, respectively. Clearly, inputs change significantly with the pattern of precipitation and discharge. The dissolved organic matter (DOM) loss was 323 percent higher in 1974 since solution loss is related to mean annual discharge. Although annual mean discharge

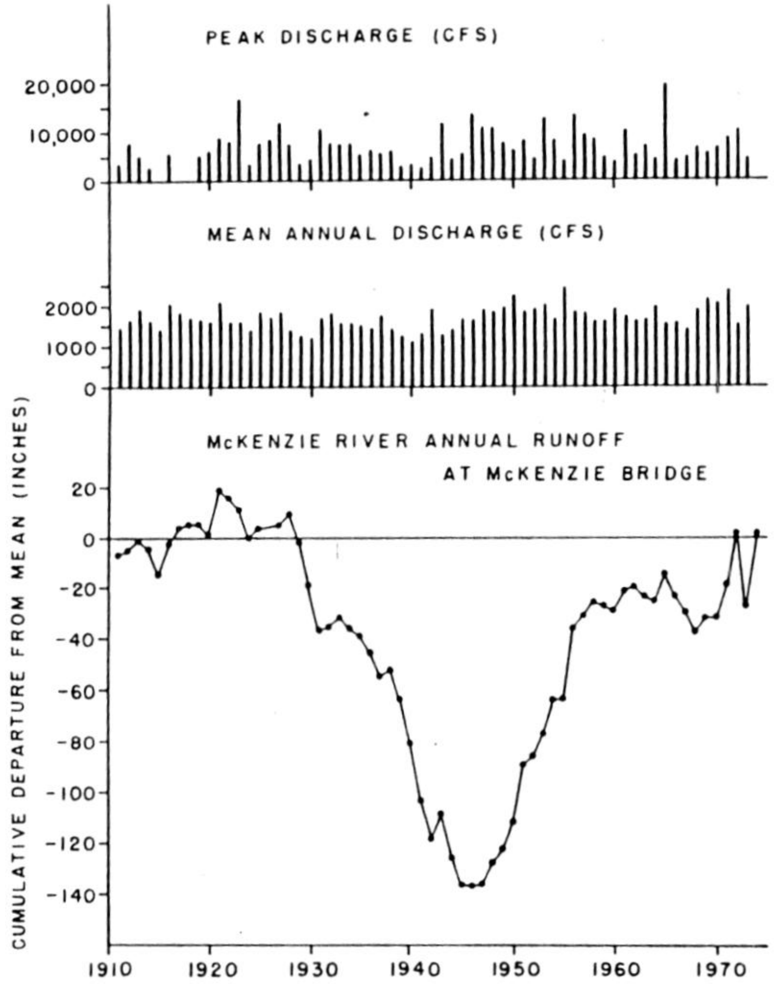


FIGURE 10.12 *Sixty-year discharge record of the McKenzie River measured at a gauging station at McKenzie Bridge, Oregon.*

for 1974 was second highest in the sixty-three-year discharge record of the upper McKenzie drainage, peak discharge had a one-year return period, and, on that basis, capability to export particulate organic matter could be considered average. Thus parameters measured to construct an organic budget for streams are extremely responsive to magnitude and frequency of storms. Storage, export, and biological process rates must be evaluated in terms of mean discharge and flood return frequency for temporal understanding of interaction between processes at the ecosystem level.

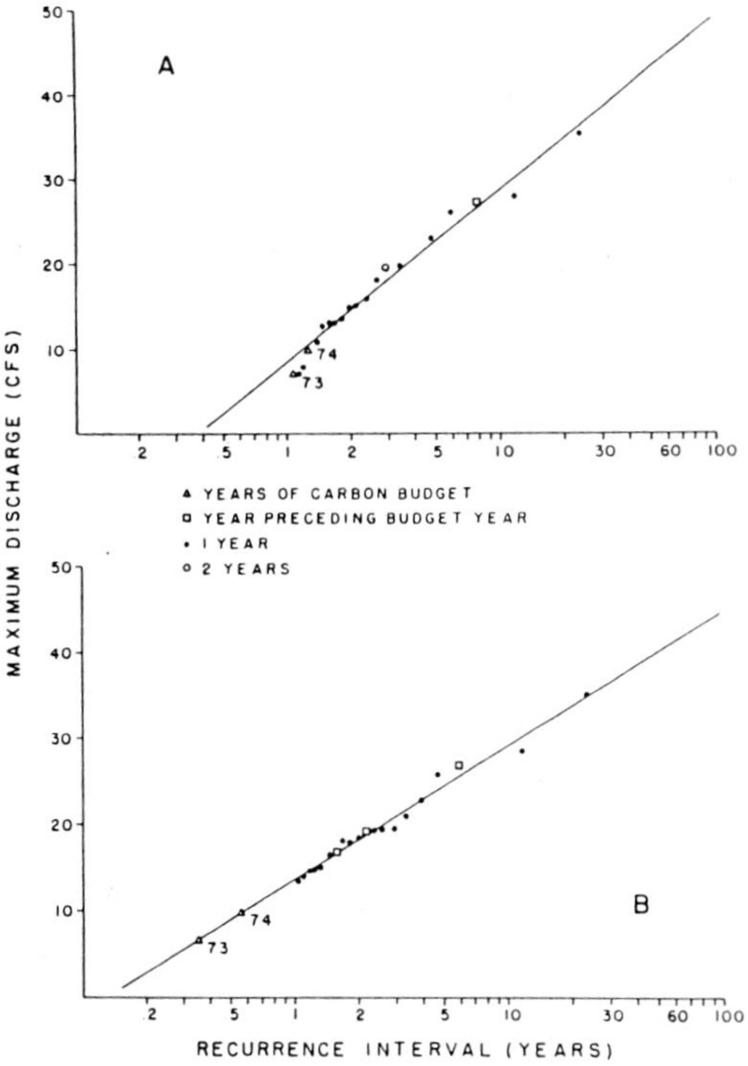
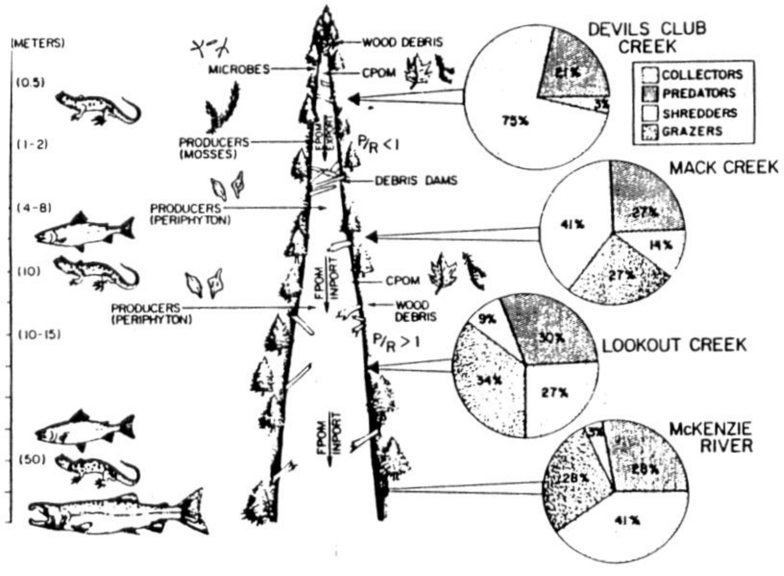


FIGURE 10.13 *Return frequencies of peak discharge (A) and partial return frequencies (B) from a twenty-five-year discharge record at watershed 2, H. J. Andrews Forest.*

A SPATIAL PERSPECTIVE

With the exception of arid regions, streams generally increase in size and discharge as they flow into higher order streams. As streams become larger, influence of the terrestrial system diminishes (Figure 10.14; Vannote et al.



GURE 10.14 *A simplified schematic diagram of a river network reflect- g the response of biotic community structure to modified input of water, rticulate organic matter, and light.*

80, Cummins 1976, 1977). A natural river system, from headwaters to outh, can be considered a gradient of process zones ranging from a strongly trital system in headwater streams to an annual autotrophic regime in derate-sized streams, followed by a gradual return to predominantly het- trophic processes in large river systems. Biotic structure shifts from a stem dominated by shredder and collector processes to one where shredder nctions are diminished and grazer functions increase. As streams flow into ger rivers, benthic algae are often replaced by more planktonic forms. Col- tor organisms shift from a major component of insects to a system domi- ted by such organisms as sponges, mussels, and worms. These patterns of ange in both the hydraulic geometry of streams and nature of organic inputs pear predictable throughout natural river systems. As a result a spatial per- ective can be obtained by examination of parameters related to physical ucture, stream chemistry, and biological processing capabilities down a er system. Chemical and biological parameters measured in the McKenzie ver drainage include: (1) heterogeneity of soluble organic matter; (2) ounts and ratio of coarse particulate organic matter to fine particulate or- nic matter on the stream bottom (CPOM/FPOM); (3) spatial aspects of ention and transport; (4) ratio of primary productivity to total community spiration; and (5) shifts in invertebrate functional groups.

Heterogeneity of Soluble Organic Matter

A river continuum hypothesis outlined by Vannote et al. (1980) predicts that the composition of DOM undergoes change in a downstream direction. As water passes through the lotic network, DOM becomes available for biotic uptake, as well as for physical-chemical processes such as flocculation or ultraviolet degradation. As a result, DOM transport exhibits a fractionation pattern reflecting loss of the most labile components and a decrease in heterogeneity of DOM through a spatial continuum.

In the McKenzie River system, total DOC concentration in our small headwater stream was always higher than in third-, fifth-, or seventh-order streams and also showed a difference in fractionation pattern.

Table 10.5 summarizes some data obtained from Sephadex G-25 analyses conducted by R. Larson, Stroud Water Research Center (pers. comm). Residual "humic acid" was low in all streams. This is to be expected in streams of low color; some southeastern streams of high color have 1 to 10 mg humic acid/liter (Martin and Pierce 1971). The bulk of colored material in the four systems appeared to be similar to fulvic acid, as shown by the Sephadex patterns. Total color decreased downstream from first- to third-order sites. Analyses of dissolved carbohydrate showed the highest concentration in first- and third-order streams, as had been observed previously in other river systems (R. Larson, pers. comm.). In each system, the percentage of DOC that could be classified as carbohydrate, phenolics, or amino acid generally decreased from first- to sixth-order streams.

If stream microorganisms degrade low-molecular-weight organic fractions in preference to those of larger size, Sephadex fractionation patterns for a stream system should show progressive decreases in the size of later eluting peaks (small molecular size) relative to those eluting earlier (large molecular size) as stream order increases. This decrease was observed spatially at the

TABLE 10.5 *Stream water concentration of total dissolved organic matter (DOM) fractionated into major organic subcomponents in four Oregon streams.*[a]

Stream system	Humic acid content (mg/l)	Total color	TOC (mg/l)	Carbo-hydrate (mg/l) C	Phenol (mg/l) C	Amino acid (mg/l) C	Σ last 3 as % of TOC
Devil's Club Creek	—	4.14	2.87	0.81	0.22	0.02	37
Mack Creek	0.25	0.68	1.81	0.47	0.06	0	29
Lookout Creek	0.90	0.52	1.20	0.64	0.05	0	58
McKenzie River	0.08	0.28	1.70	0.27	0.05	0	19

[a] R. Larson, personal communication.

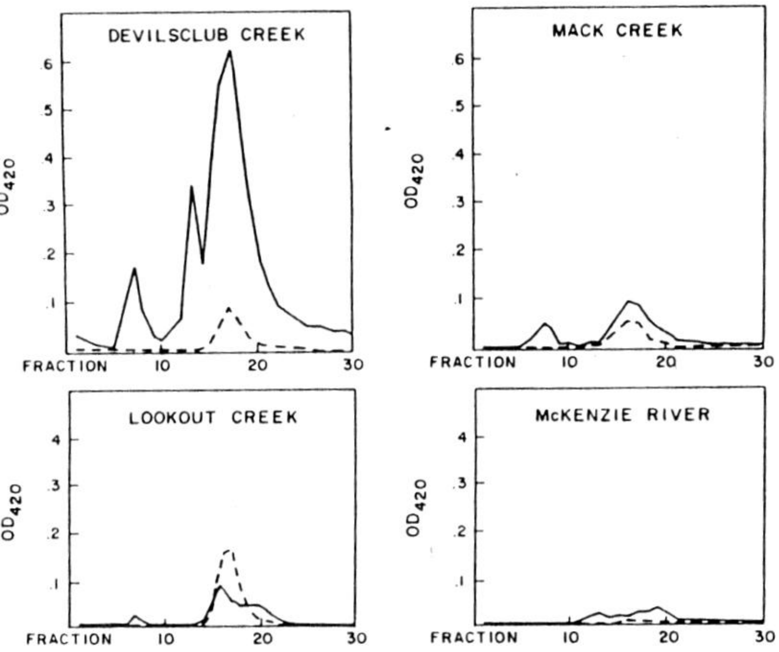


FIGURE 10.15 *Sephadex fraction pattern of dissolved organic matter from four streams of increasing size: Devil's Club Creek (first-order); Mack Creek (third-order); Lookout Creek (fifth-order); and McKenzie River (sixth-order): Solid line = color, dashed line = fluorescence (data from R. Larson, pers. comm.).*

regon sites (Figure 10.15); DOM in Devil's Club Creek displayed greater lor maxima than other sites, with a large contribution of medium-sized lymers. At Mack Creek and Lookout Creek sites, most colored DOM had sappeared. McKenzie River DOM was virtually free of colored or fluorescent aterial. R. Larson (pers. comm.) suggests that DOM from different water-eds will have characteristic fluorescence distributions, probably related to incipal leaf and wood litter, soil constituents, or both, supplied to the stream each area. Although data at hand are very limited, it appears that much cessing of DOM in Cascade river systems occurs rapidly in very small eams.

tal Amounts and CPOM/FPOM Ratios of Benthic ganic Material

Old-growth western Cascades forests (>400 years) have trees that are e (>50 cm diam) and often infected with heartrot, which increases susceptibility for windthrow into streams. The result is episodic input of large wood debris. Accumulation of debris in dams is less likely to occur in large channels than in small streams, regardless of gradient. Instead, larger streams deposit bole wood on bends and flood terraces inundated only briefly during the year. Debris in these larger streams functions as food or habitat to only a limited extent. In smaller streams, large boles are not moved by water except during debris torrents. Debris clumped into dams traps small organic debris and sediments and helps shape and stabilize the channel. Because of forest age, large tree size, and resistance to decomposition and export, bole wood overwhelms the amount of small wood in Cascade streams (Table 10.6). Table 10.7 reflects the influence of bole wood (>10 cm diam) in benthic standing crop. Even if bole wood is excluded, Devil's Club Creek and the stream at watershed 10 have a greater year-round standing crop of detritus than Lookout Creek or the McKenzie River because of capture of fine organic particles by large debris dams. Neither the fifth-order section of Lookout Creek nor of McKenzie River has significant accumulations of large woody debris, because of the transport capacity of these larger streams. Consequently, detritus standing crops are

TABLE 10.6 *Estimated quantities and surface areas of wood debris in four Oregon streams.*[a]

	Large branch and bole wood			Small branch wood[b]	
	(> 10 cm diam.)			(< 10 cm diam.)	
Stream system	Biomass (kg/m²)	Surface area (m²/m²)	Surface to vol ratio (m²/m³)	Biomass (kg/m²)	area (m²/m²)
Devil's Club Creek	140.89	0.43	8.62	1.11	0.14
Mack Creek	28.50	0.16	9.94	0.61	0.08
Lookout Creek	11.65	0.04	5.37	0.08	0.01
McKenzie River	0.08	0.003	19.28	0.08	0.01

[a] From Anderson et al. 1978.
[b] Surface:volume ratio of small branch wood measured only for Lookout Creek = 27.96

TABLE 10.7 *Mean standing crop of benthic organic matter (g ash free dry weight · m^{-2}). Estimates exclude large woody debris (>10 cm dia.).*

	Winter	Spring	Summer	Autumn
Devil's Club Creek	3242	1640	2296	1040
Mack Creek	173	564	1706	87
Lookout Creek	62	285	85	58
McKenzie River	128	76	52	79

[a] Anderson et al., 1978 and Naiman and Sedell, 1979.

BLE 10.8 *Percent composition of benthic detritus by size class and season from a spatial continuum of four Oregon streams.*[a]

		Percentage of total organic storage[b]		
am system	Season	> 1 mm	1 mm to 53 μm	53 μm to 0.45 μm
il's Club Creek	Winter	96.9	3.1	—
	Spring	66.8	29.7	3.5
	Summer	59.4	26.2	19.2
	Autumn	38.2	37.6	24.1
	Mean	65.3	24.2	15.6
ck Creek	Winter	74.2	25.8	—
	Spring	67.2	26.7	6.1
	Summer	62.3	32.4	5.3
	Autumn	41.9	47.0	11.1
	Mean	61.4	32.9	7.5
kout Creek	Winter	41.8	18.5	38.7
	Spring	69.2	29.7	1.1
	Summer	47.8	41.7	7.2
	Autumn	41.2	45.3	13.5
	Mean	50.0	33.8	15.4
Kenzie River	Winter	50.4	13.8	39.7
	Spring	52.9	43.4	4.0
	Summer	26.2	61.3	12.5
	Autumn	31.9	56.9	11.1
	Mean	40.4	43.7	16.8

om Naiman and Sedell, 1979.

es not include large woody debris > 10 cm diameter.

atively low, ranging from 62 to 285 ash-free dry g/m^{2}in Lookout Creek and om 52 to 128 ash-free dry g/m^2 in the McKenzie River.

Excluding bole wood, there is a progressive decrease in percentage of total ganic storage contributed by the > 1-mm fraction as stream order increases able 10.8). Mean percentage of the > 1-mm size class ranges from 65 per- nt in Devil's Club Creek down to 40 percent in the McKenzie River. Corre- ondingly, importance of the 1-mm to 53-μm fraction increases as stream der increases. This fraction composes a mean of 24 percent in Devil's Club eek and 43 percent in the McKenzie River. The 53-μm to 0.45-μm fraction generally a minor component of benthic standing crop, although at Lookout eek and the McKenzie River it constitutes 39 and 40 percent, respectively, detritus during winter. In smaller streams the percentage remains nearly nstant (8 to 17 percent range) with no discernible trends in response to eam order.

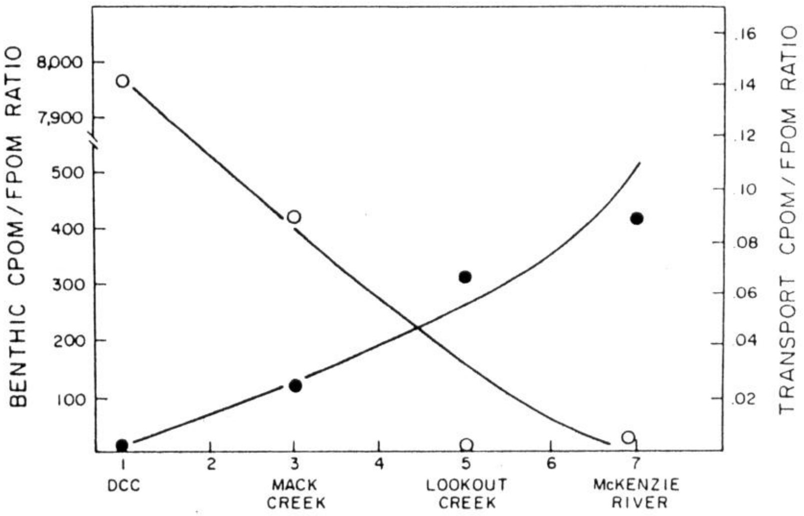


FIGURE 10.16 *Ratio of coarse to fine particulate organic matter (CPOM/ FPOM) in benthic standing crop (○), and transport (●) in the first through seventh orders of a stream system.*

In Devil's Club Creek the CPOM/FPOM ratio in benthic standing crop ranged annually from approximately 95:1 to 6500:1 (Figure 10.16). The amount of coarse particulates remained nearly constant but fine particulates varied enough during the year to cause the wide range. In Mack Creek the ratio ranged seasonally from less than 96 to about 477. Again, most variation was caused by fluctuations in the standing crop of fine particulates. In both Lookout Creek and the McKenzie River the CPOM/FPOM ratio was always less than 10 and nearly constant throughout the year.

The general downstream decrease in the ratio of CPOM to FPOM is due to decreased quantity of large woody debris (Table 10.6), while fine particulates < 1 mm become a dominant component of benthic detritus (Table 10.8). Although the percentage of FPOM as a component of benthic standing crop increases in the downstream direction, the amount decreases, because in very small streams such as Devil's Club Creek retention structures effectively trap fine detritus. These small streams can be envisioned as a transition between terrestrial and aquatic ecosystems, which are efficient in retaining and processing organic inputs (Fisher and Likens 1973; Sedell et al. 1974; Naiman 1976; Webster and Patten 1979). When stream order increases, as in Mack Creek, storm flows become sufficient to overcome some retention structures and transport fine particles downstream, but not powerful enough during normal years to move large woody debris. Hence the capacity for retention and time for biological processing within a reach decreases in a downstream direction as the capacity for transport increases in large stream orders.

patial Consideration in Material Transport

The decrease in wood-generated habitat at each step in the continuum aries the amount and composition of small organic residue. As retention apacities decrease, transport mechanisms previously buffered by organic deris begin to operate. The resultant capacity to move particulate organic mateial is reflected in the quality and quantity of organic transport. Initially, one night suspect coarse materials from first-order streams, with most intimate errestrial interaction, would supply more productive third- to fifth-order treams with large quantities of leaf litter. In fact, the findings were the oppoite. First-order streams, as shown by organic budgets, are extremely retentive nd primarily transport materials previously processed to FPOM. Only in arger streams, where formation of rentention structures is prevented by the ydraulic capacity to move debris, is coarse particulate material such as leaf tter effectively transported (Figure 10.16). As a result the CPOM/FPOM atio for transport increases in a downstream direction. The transport ratio ndicates that first-order streams supply downstream reaches primarily through nput of FPOM to collector invertebrates rather than input of intact leaf litter to hredders. In fact, 75 to 90 percent of the organic particles in transport were etween 0.5 and 50 μm in diameter at all four sites in the McKenzie drainage Sedell et al. 1978). Large wood in small streams dissipates the energy of flow nd retains coarse organic particulates, while in larger streams channel morhology dissipates energy but permits transport of larger organic particles.

atio of Primary Production to Total Community espiration Rates (P/R)

The ratio of gross primary production to community respiration has been sed to assess the degree to which a stream reach is basically autotrophic or eterotrophic (Fisher and Likens 1973). A P/R ratio of less than 1.0 generally ndicates a heterotrophic energy base while a ratio greater than 1.0 indicates a asically autotrophic stream reach. In the McKenzie drainage, P/R ratio ineases through the first six orders of the river system. Devil's Club Creek is ost heterotrophic, followed by Mack Creek, which also has a P/R <1. ookout Creek has a P/R > 1 but less than the McKenzie River.

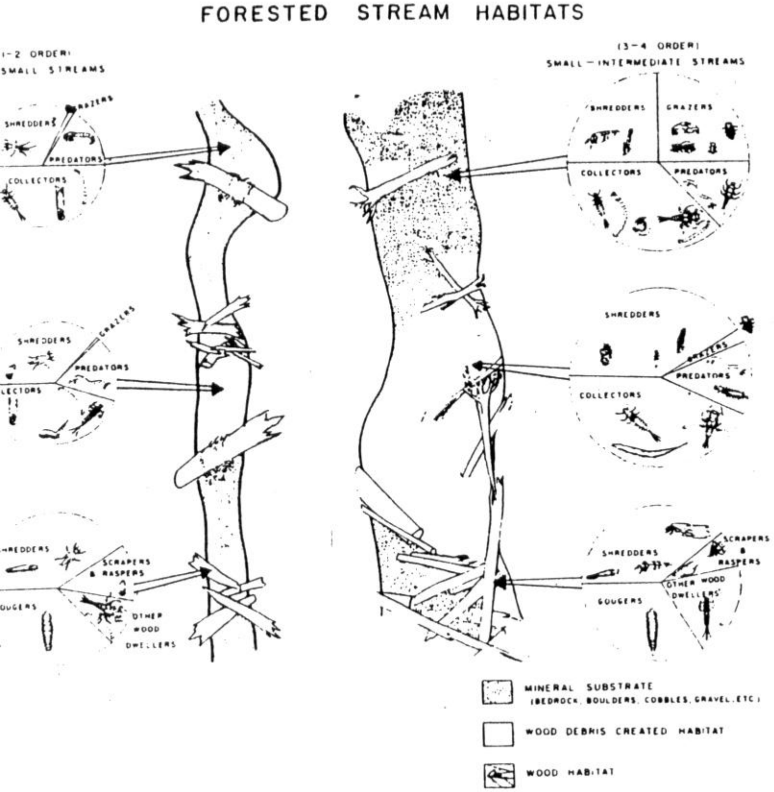
Devil's Club Creek may attain a fairly high P/R seasonally but never aches 1.0, since it is dominated by microbial activity that increases commuty respiration. Mack Creek has a P/R ratio greater than 1.0 for every season cept winter, but it still has a considerable amount of detritus (Table 10.8), hich depresses the P/R ratio. Mack Creek has both algae and detritus as an ergy base. During spring Mack Creek approaches conditions of an algal-iven, autotrophic stream, but is heterotrophic on an annual basis. Lookout eek is autotrophic during all seasons. The standing crop of detritus is relatively small and the leaf litter component is biologically available primarily during winter. In Lookout Creek microbial activity on detritus does not depress the P/R ratio to <1. The benthic algal community of the McKenzie River has the highest P/R ratio. Thus this river is definitely autotrophic at all seasons. The macrophyte community along the shores of this river has a P/R ratio between 0.7 and 0.9, which partially reduces the overall ratio; however, boulders and cobbles free of macrophytes constitute about 85 percent of the benthic area. Since both light input and P/R ratio increase in a downstream direction, the data reinforce the hypothesis of canopy control of P/R ratio over the first six stream orders.

Functional Group Shifts

The relative dominance of invertebrate functional groups also shifts spatially in response to changes in particulate organic inputs (both algal and detrital), substrate conditions, and materials in transport.

Functional groups shift in response to organic input at sites along the McKenzie River drainage (Figure 10.14). Data were from benthic samples collected in gravel areas for invertebrates larger than 500 μm. As a result the smallest invertebrates (chironimids and copepods) were not included. The diagram is based on a percentage by numbers of samples collected during summer 1976 (C. L. Hawkins, pers. comm.). In the small, first-order stream (Devil's Club Creek), with a completely closed canopy, wood retention devices, and low P/R ratio, 75 percent of collected invertebrates were classified as shredders. Only about 3 percent were classified as fine particle feeders; none of the sampled invertebrates were grazers. At the third-order stream (Mack Creek), with partial canopy and less retention capacity, the role of shredders was reduced while the grazing functional group increased significantly. In Mack Creek collectors also exhibited a far more significant role. In samples from the fifth-order stream, Lookout Creek, shredders decreased to only a minor role. With its open canopy and greater primary production, grazers represented 34 percent of sampled invertebrate organisms. The proportion of collectors also increased. In the sixth-order river, grazers continued to be important; however, collectors dominated the community. Numbers of invertebrate predators varied only between 20 and 30 percent at all four sites. Thus the downstream continuum characterized by canopy opening, decreased terrestrial inputs per square meter, and input of preprocessed fine organic material by transport results in a definite response in biotic structure and function.

In areas dominated by wood debris, the resultant habitat also influences composition of the invertebrate community (Figure 10.17). In very small streams approximately 25 percent of the stream area is wood, and a second 25 percent is organic debris and sediments stored behind wood residues. As a result, half the stream habitat is either wood or wood-created. The remainder is either bedrock or mineral sediment. In third- to fourth-order streams in the H. J.



GURE 10.17 *Schematic diagram illustrating the role of large wood de-*
s in modifying stream habitat in large and small streams, and its influence
invertebrate biota.

drews Forest, only about 12 percent of the area is occupied by wood with rly equal amounts in wood-created habitat, while 75 percent of the stream is eral substrate. As noted previously, wood in fifth-order streams is found ng or on the banks depending on flow conditions. Although the smallest ams have the greatest wood-created habitat, invertebrate biomass is lowest he smallest streams. The smallest streams also have a large proportion of all invertebrates. In larger streams, particularly those with an algal and rital base, there is greater biomass diversity of functional groups and species nvertebrates.

REST LAND-USE IMPLICATIONS

Knowledge of the stream's basic physical-biological structure through e and space can form a basis for evaluating response of lotic systems to land-use practice. In the Oregon Cascades, and indeed in much of the coniferous forest biome, timber harvest is a major land use. Therefore response of streams to typical logging practices through time has become a critical land-use consideration. As stated previously, small forest streams in old-growth forests are completely dominated by forest vegetation. This domination includes shading, input of organic litter for the biota, large debris inputs that partially regulate channel morphology, and contribution of the riparian zone (Chapter 9). Therefore, removal of forest canopy either naturally by fire or by timber harvesting critically affects the adjacent stream.

One hypothetical scenario is that canopy opening will result in a significant increase in primary production and an attendant shift in biotic structure as a result of shifting from heterotrophic to autotrophic energy pathways. This open canopy would be transient, however, since the riparian zone responds rapidly to canopy removal (Chapter 9). Within ten to fifteen years a thicket of alder and willow would occupy the riparian zone and reshade the stream. We hypothesize this would result in a decline of the temporary autotrophic base and a return to heterotrophic conditions. Quality of allochthonous inputs, primarily litter of alder and willow, is much higher (more labile) than coniferous litter of old-growth forests and is processed more rapidly by the biotic community. As the coniferous canopy recovers, shrub species in the riparian zone would be slowly shaded out and the alder/willow component of the riparian zone would die out. Mortality in the riparian zone would reintroduce wood debris to the stream. Since hardwoods are processed more rapidly, however, debris dams would not be as persistent. As alder and willow litter declined in amount, return to coniferous litter would signal a general decline in food quality for biota and overall production would decline rapidly. Finally, after about 125 years, coniferous tree mortality would increase, and debris dams capable of stabilizing the streambed would be formed. At this time, coniferous mortality in the adjacent forest would reintroduce some direct lighting and the community of the old-growth forest stream would become reestablished.

Although evidence to support this hypothetical scenario is part of our current research, shaded and unshaded sections of streams were previously examined to determine algal, insect, and fishery response to canopy removal. Aho (1976) conducted a study of cutthroat trout *(Salmo clarki clarki)* in an unshaded and a shaded section of Mack Creek. The objective of this study was to test the hypothesis that no differences existed between trout populations in the two stream sections. Periodic sampling and tagging were used to determine population levels, growth rates, and production. Movement, diet, and prey-size selection were also investigated.

Aho found the unshaded section supported higher trout biomass than the shaded section. Trout up to three years old were as numerous in the unshaded as the shaded area, but biomass (wet weight) of all trout was 12.2 g/m^2 in the unshaded and 6.2 g/m^2 in the shaded section. Mean length by year class was also greater for trout from the unshaded habitat. From 1973 to 1974, estimated production was 7.5 g/m^2 in the unshaded and 2.6 g/m^2 in the shaded section.

Higher level of trout production in the unshaded section probably resulted rom a combination of factors including the differences in diet, abundance of rey, and water temperature. A more productive food resource in the unshaded abitat was indicated by a greater abundance of multivoltine insects and grazers ı the diet of trout from this area. In the unshaded section, emergence traps aptured approximately twice the combined biomass of several insect groups nportant in the trout diet. Because of higher water temperatures, trout fry merged earlier in the unshaded section. Earlier emergence probably provided n initial growth advantage that was maintained throughout the life of the trout.

Primary production rates in the clearcut reach were more than twice as high s in the forest reach of Mack Creek (Figure 10.18). This increase in algal naterial has potential advantages for consumers. Algae have low C/N ratios (6 › 12) and are therefore high-quality food for collectors and grazers. Algae have ast turnover rates and therefore can support high standing crops of consumers elative to their own standing crop. This was evidenced both by simulation nodeling (McIntire 1973), which showed algae could support fifteen times neir own standing crop of consumers, and by experiments on grazers in labora-ory streams. In an experiment using four densities of snails, only the heaviest ensity resulted in decreased production of algae (Figure 10.19). Thus algae an sustain heavy rates of cropping and still maintain uniform standing crop. nother advantage of the autotrophic food base is that the major insect forms aat graze algae in Northwest streams are Ephemeroptera, some of which are ultivoltine and have fast turnover rates. These insects are also more prone to rift than most detrital feeders, and would therefore be more available for trout onsumption. Thus increased algal production has many attributes that would ivor higher production on invertebrates and trout.

Relative increase in autochthonous inputs is a function of shading prior to nopy removal since the degree of canopy openness determines the level of imary production in streams. We examined algal colonization rates in eight iirs of old-growth forest and clearcut sections of streams. Relative difference colonization rates between forested and clearcut sections was strongly re-ted to stream width, an indirect measure of canopy openness (Figure 10.20). ıus change in stream productivity as a result of deforestation is greatly depen-nt on physical parameters of the stream such as solar radiation and tempera-re, both of which are determined by canopy openness.

These observations suggest that clearcutting can potentially lead to en-ncement of trout production if the stream channel is maintained physically ebris dams, lack of significant erosion, lack of large temperature increases). ı a long-term basis (25 to 175 years), however, there may be no net enhance-nt in stream production due to rapid revegetation of the riparian zone.

Trout populations in small streams (old-growth, clearcut, second-growth) the western Cascades were inventoried to assess logging impacts on trout undance (Murphy 1979). Cutthroat trout *(Salmo clarki)* was the only salmo-l present in sites with gradients higher than 2 percent. Trout biomass (g/m^2 t wt) varied according to density of forest canopy (Figure 10.21). The same

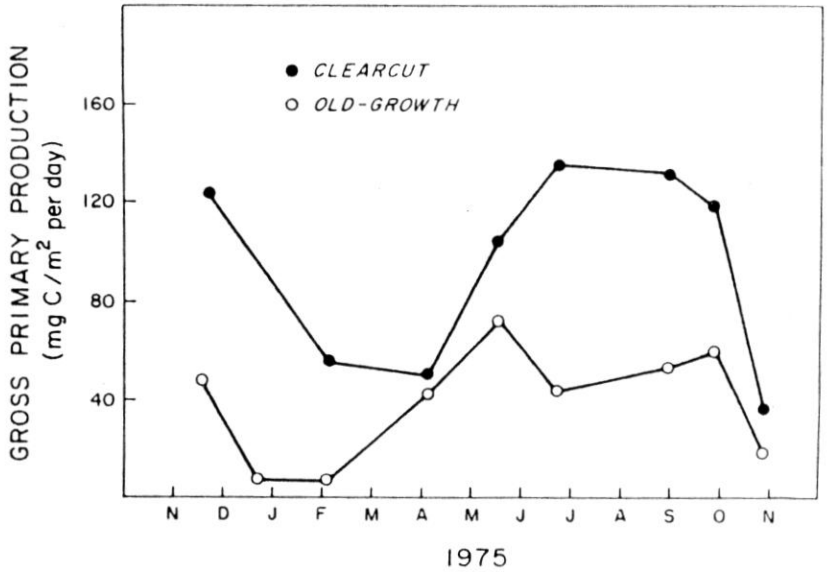


FIGURE 10.18 *Pattern of annual gross primary production in an open ten-year-old clearcut and a forested old-growth section of Mack Creek.*

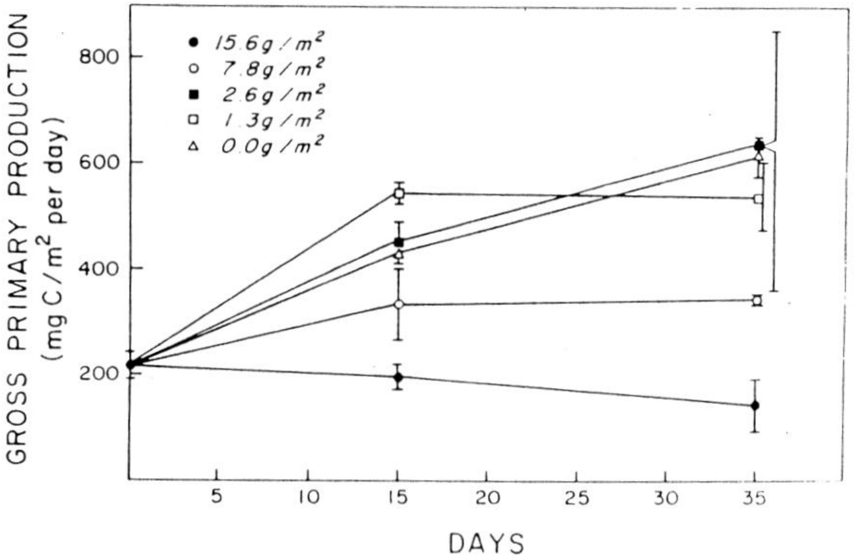


FIGURE 10.19 *Laboratory determination of gross primary production in experimental channels subjected to four levels of grazing pressure by snails. The levels of grazers' biomass (ash-free dry wt) were: 15.6 g/m^2 (•); 7.8 g/m^2 (○); 2.6 g/m^2 (■); 1.3 g/m^2 (□); and ungrazed control (△).*

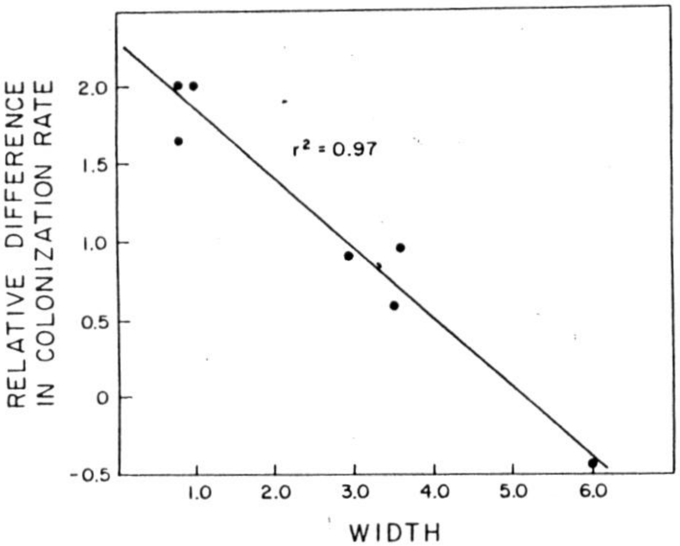


FIGURE 10.20 *Relative difference in algal colonization rate on clay tiles incubated in seven streams of the H. J. Andrews Forest in relation to stream width (m).*

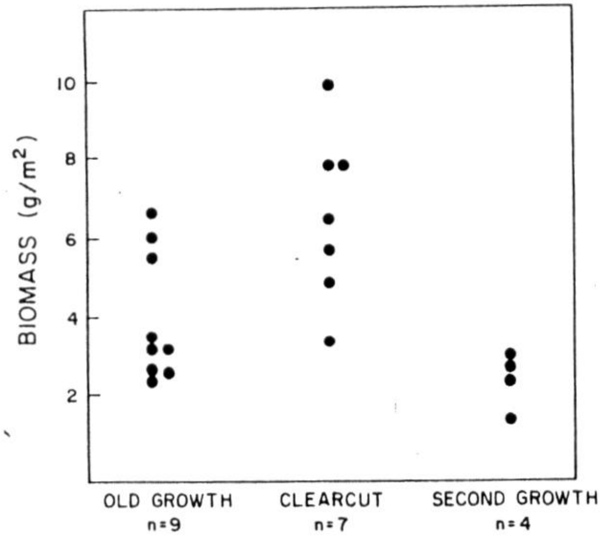


FIGURE 10.21 *Trout biomass (g/m²) in twenty streams draining old-growth, clearcut, and second-growth forests of the western Cascades.*

response was also found for insect predators (Murphy 1979). Biomass a diversity tended to be greatest in young clearcut (< 10 years) sites, intermed ate in old-growth (>450 years) sites, and least in second-growth (> 15 yea sites. After fifteen to twenty-five years the riparian zone in the western Ca cades gradually switches from deciduous to coniferous species. Although on a few stands have been studied to date, data indicate only a temporary enhanc ment of biological production in streams by opening the canopy, and perhaps long-term reduction of biological production because of heavy shading second-growth stands. With eighty-year rotations intense shading of secon growth could become a proportionally greater part of stream history tha natural rotations, which include long periods of moderate shading characteri tic of old-growth stands.

Another aspect that should be considered in a recovery perspective is th potential shift in functional groups as a result of clearcutting. Insect function groups described previously have specialist roles in the ecosystem, that i grazing, gouging, and shredding. In the coast range of Oregon most stream have a significant component of snails, which are best described as generalist That is, snails can consume leaves (shredding), graze on the surface of miner substrate (scraping), and even consume fine particulate organic matter (collect ing). Although data are scant, they indicate a shift to the generalist sna following clearcutting in the coast range (Figure 10.22). As the canopy close again in second growth, generalists begin to decline and are replaced by inve

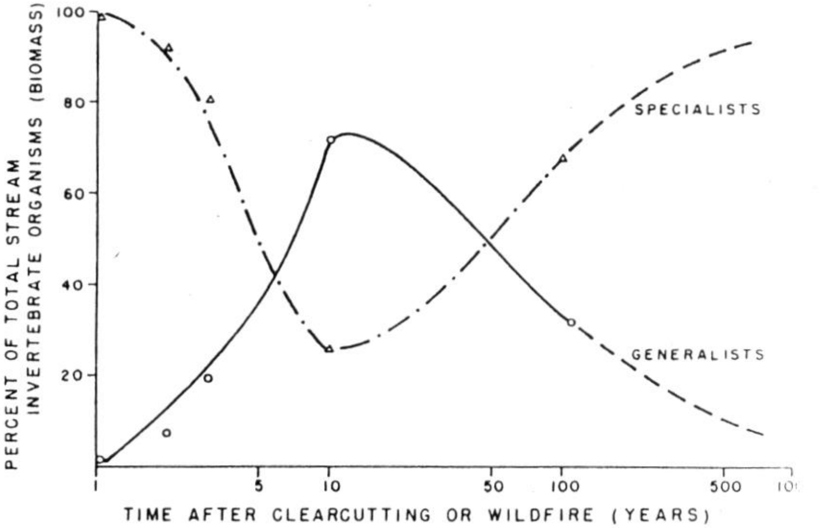


FIGURE 10.22 *Comparison of specialist and generalist compositions of th invertebrate community in five streams of the Coast Range of Oregon drain ing stands of different ages.*

tebrate specialists. The cause of this shift and its long-term influence on the diversity of biota of streams is unknown. To answer a question such as this, however, requires an appreciation for the biotic structure of streams and its interaction with the terrestrial environment through time.

A third aspect to be considered in land management decisions is the geomorphological role of wood on the biota. Streams adjust to changes in timing and amounts of water and sediment by changing width, depth, gradient, hydraulic roughness, and amount of sediment in transport. For streams in the northwest, wood greatly influences channel morphology. In terms of routing of water and sediment, wood (boles) is every bit as important to streams as the timing and quantity of sediment and water. The consequences of ignoring this third element are becoming more obvious when one considers the "historical" role of wood and how we are currently managing land and streams.

Under current management practice, extensive stream cleanup is required after logging, which results in removal of wood debris. Yet without stable wood debris in the highest gradient streams, retention of gravel and organic material for biotic habitat could not occur. The result is removal of retention mechanisms that are characteristically present and that allow the biological component of the stream to function effectively.

In the natural stream, loading with large wood debris occurs more or less evenly through time. With short-rotation timber harvesting this important morphological component may be permanently removed. Furthermore, as the last old-growth timber lands are cut, wood may diminish as a significant organic input. Eighty-year rotations, in conjunction with precommercial and commercial thinning, could gradually eliminate debris dams as a morphological feature of streams. The highest gradient streams may then erode to bedrock and become functionally depauperate in a biological sense. Sediments could be routed more rapidly and sediment load formerly retained as habitat may impact downstream fisheries. Removal of debris dams, which formerly dissipated energy of water in high gradient streams, may in the future allow high water to erode banks, promote siltation, and speed discharge to lower gradient streams with resultant flooding.

Under current land-use practices, we are effectively channeling our mountain streams and managing land to keep them so. In channeled high-gradient streams, normal sediment and organic loads are routed more quickly than under natural conditions. Retention of sediments and organics is neither large in amount or long in time. If the stream does not retain organic material and maintain a diversity of physical habitats then, biologically, it may be unable to process organic matter from the adjacent forest and large, functional and structural components in the stream ecosystem could disappear.

Wise management of streams and watersheds can prevent these problems and preserve biological functioning in streams. The development of future management strategies will best result from a basic knowledge of the biotic structure and function of streams and their interaction with physical and chemical components of stream ecosystems. Once developed, effective application of management strategies will depend on a basic knowledge of the stream ecosystem and how it functions through time and space.

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