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STREAM ECOLOGY

Application and Testing of General Ecological Theory

Edited by

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ORGANIC MATTER BUDGETS FOR STREAM ECOSYSTEMS: PROBLEMS IN THEIR EVALUATION

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INTRODUCTION

Since the pioneering work at Hubbard Brook (Fisher and Likens, 1972, 1973; Bormann et al., 1969, 1974; Bormann and Likens, 1979), there has been ever increasing interest in watershed budgets, both for total organic matter, usually expressed as carbon (Wetzel et al., 1972), and various ions (Fisher and Likens, 1973; Johnson and Swank, 1973; Swank and Douglass, 1975; Fisher, 1977; Webster and Patten, 1979; Fahey, 1979; Mulholland and Kuenzler, 1979; Gurtz et al., 1980; Mulholand, 1981). The primary interest in stream dynamics within a budget context has been in the rate of loss of organic matter from the land as well as storage and biological conversion of organic matter in the stream. Impetus for most studies has come from the realization that energetics of small streams (generally orders 1 to 3 [Strahler, 1957]) are heavily dependent on organic nutritional resources of terrestrial origin (Ross, 1963; Hynes, 1963; Cummins, 1974; Hynes, 1975). New insights into the structure and function of running water ecosystems and terrestrial-aquatic linkages (Waring, 1980) are based on the changing terrestrial dependence with increasing channel size (Cummins, 1975, 1977; Vannote et al., 1980; Minshall et al., 1983), varying stream-side vegetation (Minshall, 1978), and the dynamics of input, storage or processing, and output of organic matter (Vannote et al., 1980; Minshall et al., 1983; Elwood et al., 1982; Newbold et al., 1982a,b).

The role of organic matter in running waters has been documented and discussed to the point that streams and rivers are no longer viewed primarily as open export systems of terrestrial products, but rather as sites of production and processing of organic material (Hynes, 1970; Whitton, 1975). This new image has come largely from annual energy budget estimates for streams, (e.g., Odum, 1957a; Teal, 1957; Nelson and Scott, 1962; Tilly, 1968; Hall, 1972; Fisher and Likens, 1973; Sedell et al., 1974; Mann, 1975). Stream systems, from small headwaters to large rivers, import, produce, process, and store organic matter (Vannote et al., 1980). The processing and resultant partial release of organic and inorganic nutrients from one stream reach to the next has been characterized as processing along a continuum (Vannote et al., 1980) or spiraling (Webster et al., 1975; O'Neill et al., 1975; Webster and Patten, 1979; Newbold et al., 1982). Only part of this material is exported downstream to the next order or laterally to the upper bank or flood plain without significant alteration. Complex, highly specialized biological communities reside in running waters and not only alter the quantities but also the quality of organic material and inorganic nutrients exported or stored relative to that imported. An example is the alteration of the size distribution of particulate organic matter (POM i.e., detritus defined here as all particles >0.45 m plus microbial biomass; Cummins, 1974), by aggregation and disaggregation, that is exported from a reach relative to that imported. Fisher and Likens (1973) provided the initial conceptual basis for examining different lotic ecosystems using the classical two-dimensional P/R plot (Photosynthesis/ Respiration [Odum, 1957a, b]) with a third axis representing the system's import-export balance. All ecosystems, whether they accumulate materials, have net export, or are at steady state, can be located in this three dimensional space. In this mode a steady state system has its import equal to export and $P/R = 1$. To maintain a steady state when gross photosynthesis (P) and community respiration (R) are not equal, the system must either import or export energy. The mode also allows that P may equal R in non-steady state systems.

To evaluate such a model, all inputs (detritus and photosynthesis) outputs (transport and respiration), and changes in storage must be measured independently. Because this is such a laborious task, one or more parameters are routinely obtained by difference, and in no case has detrital storage been adequately examined, especially over greater than annual time periods. By assuming a steady state (i.e., inputs equal outputs and storage pools experience no net change), the annual energy budget can be balanced by attributing the difference between total energy input and output of organic matter to a single measured parameter or flux. By definition, in steady state systems, inputs which are not exported from storage compartments must be utilized or transformed. Because nutrient (e.g. organic matter) storage and turnover are considered key characteristics of stream ecosystems, an important ecological question is whether their assumed steady state is meaningful on an annual basis for the purpose of constructing such material balance budgets. Certainly none of the parameters are time invariant. Lake and terrestrial ecologists usually can place these systems within an historical perspective and view the present state of the system as a result of the past. For example, sediments in lakes and annual rings in trees provide a record of past events. Stream ecosystem history is not recorded as neatly, therefore, the history of past events has not been adequately considered in short term studies. Stream ecosystem structure and function are very much dependent on recent flood history, long term variation in runoff, and dynamics of riparian vegetation. The storage and export values commonly measured reflect past and present annual runoff, flood size and frequency patterns, vegetation, and erosional conditions in the watershed as influenced by both natural and man-induced variation. If stream organic budgets are not placed in their historical context, their usefulness for comparison with other sites and ecosystem types, as well as the significance of relationships among photosynthesis, respiration, and input/export ratio is subject to serious question.

In preparing and evaluating material budgets for running water ecosystems, it is essential to consider patterns of movement, processing, and storage in both space and time (Fig. 1). Typically, annual budget estimates have been based on sampled input and output from a stream segment or small watershed (e.g., Hall, 1972; Fisher and Likens, 1973; Sedell et al., 1974; Minshall, 1978). There are fundamental differences between segment and watershed budgets and the validity of comparisons must be carefully examined. Regardless of budget type, it is necessary to recognize the importance of episodic events, such as floods (channel), and fire (watershed) of greater than annual frequency of recurrence. In addition, if the emphasis of an investigation is biological (e.g., processing efficiency, i.e., fraction of organic inputs annually coverted to CO_2), the biological response time must be carefully evaluated relative to the period of inputs and their availability, and the source of material collected at output (Meyer and Likens, 1979).

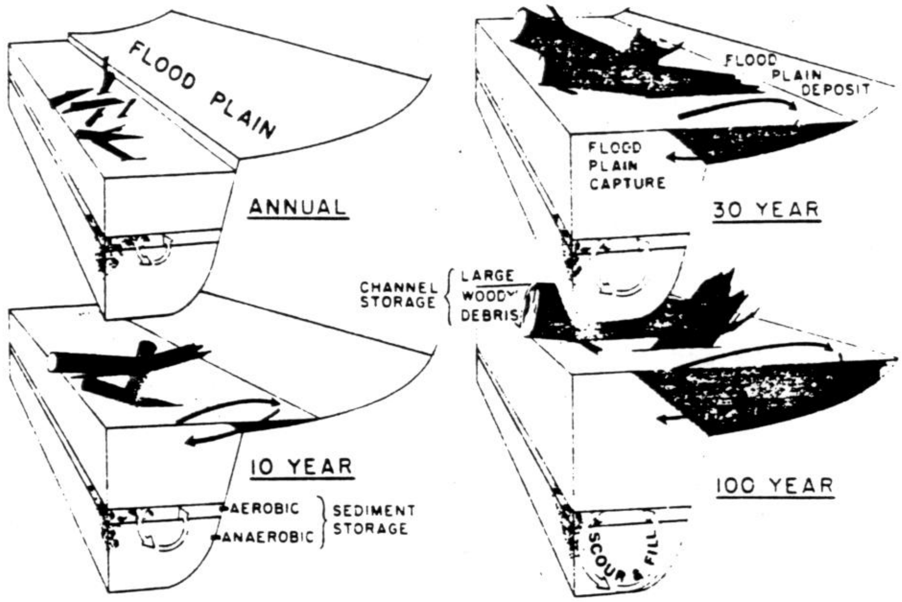


Fig. 1. Diagramatic representation of spatial and temporal relationships in the retention and displacement of particulate organic matter (detritus) in streams. The general pattern of recurrence of floods of various severities (annual, 10-, 30- and 100-year) is depicted together with: 1) depth of scour and fill = sediment storage; 2) extent of flood plain inundation = deposit onto, and capture from, the flood plain; and 3) size of channel debris dislodged or moved = channel storage of large woody debris. For example, a 100-year flood scours deeper into the sediments, extends further onto the flood plain, and moves larger debris jams than floods of lesser magnitude. Depending upon the nature and depth of the sediments, there may be an anaerobic zone where, because decomposition rates are greatly reduced, periods of organic storage are extended, unless disturbed by flood scouring.

TEMPORAL AND SPATIAL PROBLEMS IN ESTIMATING AND INTERPRETING STREAM ORGANIC MATTER BUDGETS

Ecologists commonly assume that certain natural systems are at steady state, in other words, material storage does not exhibit net changes over a study period (Morisawa, 1968; Fisher and Likens, 1973). The appropriateness of a steady state model in stream ecology or geomorphology depends largely on the time span and the area considered (Schumm and Lichty, 1965). Generally, the smaller the stream area and shorter the time period, the more applicable should be the steady state assumption. Some geomorphologists (Trimble, 1975; Schumm et al., 1975; Maddock, 1976) argue that a drainage basin can not be considered as being at steady state at any particular point in its history. Leopold and Maddock (1953) proposed that a tendency toward steady state existed for certain physical properties of streams, and that adjustments between changing streamflow variables could be defined by power function equations. They considered stream channel morphology to be in "quasi-equilibrium" because the substantial scatter about regressed relationships made it uncertain as to whether steady state had been attained. To these geomorphologists, the dynamic equilibrium of a stream channel involves adjustments to the history of water and sediment discharge (Megahan and Nolan, 1976) over the previous 5-10 years or more and does not represent a steady state condition at any one particular year of water discharge. Because channel and streamflow conditions are constantly changing, the equilibrium is described in a statistical rather than absolute sense (Maddock 1976).

However, organic matter budgets are commonly viewed as absolute, not statistical, although during any given year in which a budget is developed, steady state is probably not a valid assumption (e.g., Welton, 1980). During any single year, increase or decrease in storage dominates a budget depending on water discharge and POM input.

The assumption of steady state of organic matter storage in a stream is further complicated by variation in storage characteristics over a greater than annual time scale (e.g., Welton, 1980). Major storms may alter the volume of material in storage to such an extent that return to pre-storm channel characteristics occurs only over a period of years to decades. Furthermore, channel storage capacity of forest streams may vary over the history of the adjacent forest, because periods of tree mortality leading to inputs of large woody debris increase both the total standing crop and the channel capacity for storage of fine organic detritus. Therefore, even if a stream experiences no net change in storage for a year, that year may not be "typical" of long-term conditions which are constantly changing in response to previous storms and the history of the riparian zone.

Discharge History of Streams

The importance of flooding to stream organic matter budget studies over annual and longer cycles has been largely ignored. For example, the recurrence interval of peak flows for the study period is not standard information in stream ecology research papers. As much as 80% of the particulate organic matter (POM > 0.5 μm) exported by a stream over a year can be discharged during one or two storms (Hobbie and Likens, 1973; Bormann and Likens, 1979; Crisp and Robson, 1979). Because the origin of this material, whether it be within sediments, channel bed or banks, or the flood plain, and its residence time in the stream system are unknown, the biological significance of such events to the community has yet to be determined. High water capture of a boardwalk placed in the riparian zone along a reach of Augusta Creek, Michigan provides a specific example. Exclusion from an organic budget of the lumber which collected at the downstream weir during the storm seems logical, but what about the many other pieces of organic matter with similar histories from the same location? Clearly, both the source of the inputs and time scale in which they enter the channel and are transported are important if the emphasis is on stream biology.

Few published studies (e.g. Dawson, 1980) have placed the field sampling period in the context of either the annual flood cycle or longer term discharge patterns. It is clearly important to know the relationship of the study period to major flood or drought events. At a minimum, material or energy budget measurements should be placed in general perspective of flood return frequencies of the study year and several preceding years. Figures 2A and B present recurrence frequencies (Leopold et al., 1968; Morisawa, 1968) of peak discharge, maximum temperature, and annual degree days for the North Santiam River, near Detroit, Oregon. Such long term flow-temperature perspectives allow comparison of a study year to overall averages and conditions prior to sampling. This issue is further complicated because the history of sediment movement into and through mountain stream systems has probably been in large part keyed to major storms. In forested areas of the H. J. Andrews Experimental Forest, Oregon, for example, significant debris avalanches, a major supplier of sediment to channels, and debris torrents which flush steep channels, have been triggered by storms with a 5 year and greater return period (Swanson and Dyrness, 1975). For example, many of the mass movement events occurring over a 30 year sample record were triggered by a December 1964 storm that took place within the period but had a return interval greater than 100 years.

The preceding discussion points up the difficulty in accounting for infrequent episodic events that strongly influence sediment transport and channel morphology. When a major event having a return period greater than the sample period occurs during a study, it dominates the record. If such an event does not occur within the time of the study, a major part of the long-term system behavior is missed. Further, the

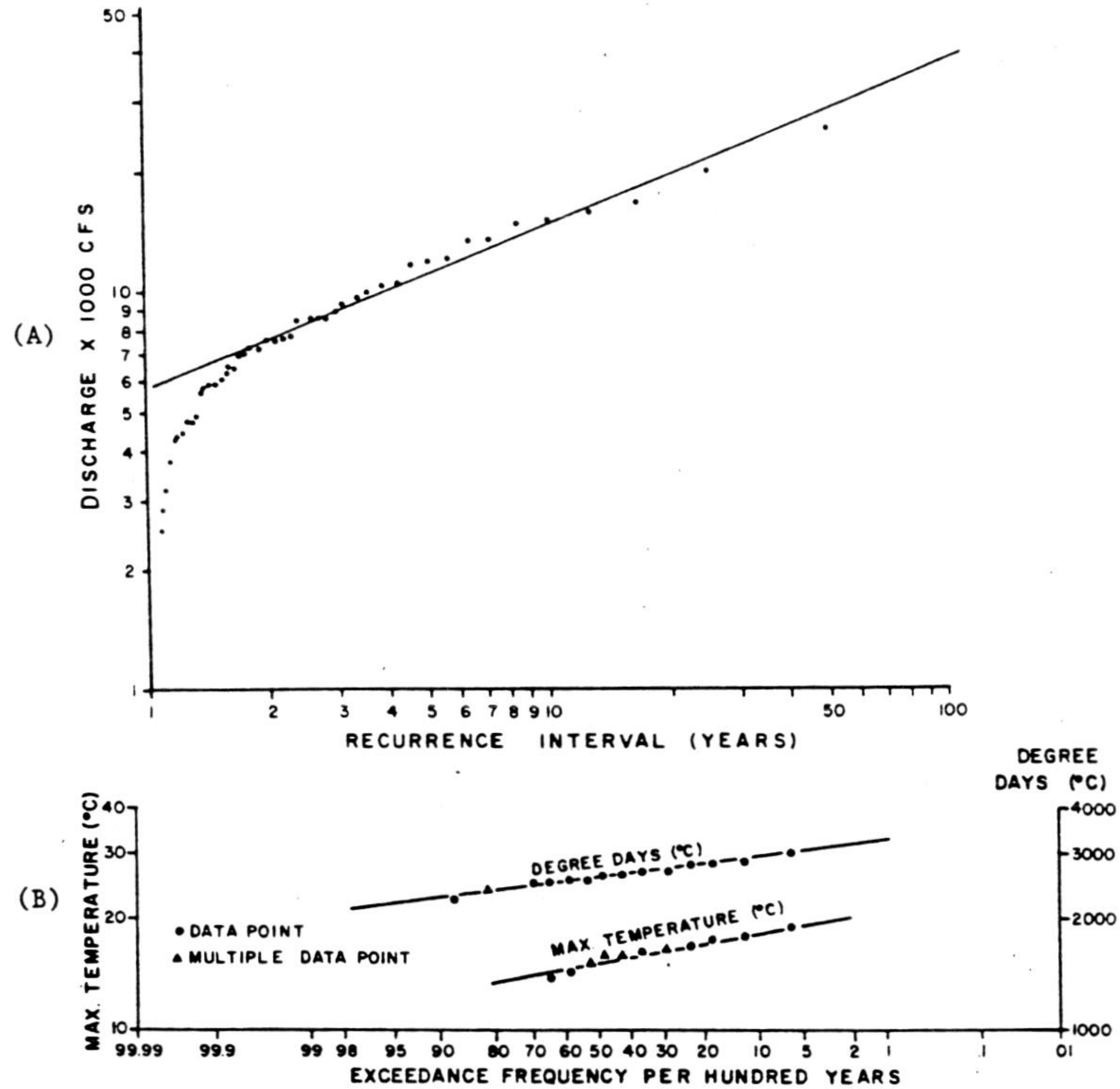


Fig. 2. North Santiam River (5th order), Oregon, recurrence intervals for maximum yearly floods (A) and temperature (B) based on a 20 year record. Degree days calculated as mean daily temperature times number of days having that mean and summed over the water year (October 1 - September 30). Recurrence interval $(T_R) = \frac{1 + n}{m}$, where n = number of years of record and m = rank of discharge or temperature for each year. (The reciprocal of T_R is the probability of occurrence of a discharge or temperature of that magnitude in any given year.)

interdependence of material transfer during successive peak flow events poses problems in framing a particular study period within a longer term perspective. Return periods of stream flow are calculated assuming independence of successive events. However, the amount of organic and inorganic material carried by a given discharge depends on a variety of factors, such as magnitudes and timing of preceding events (Paustian and Bestcha, 1981; Bilby and Likens, 1981). Consequently, return periods calculated for a sequence of peak flows do not necessarily reflect the relative magnitude of those events in terms of organic matter transport.

The record of runoff for the McKenzie River at McKenzie Bridge, Oregon, offers an indication of historical variations in precipitation, runoff, and peak annual flow in the area of a major stream ecology research site (Fig. 3). The runoff record is plotted as cumulative departure from the mean runoff for the 62 year period (Fig. 3) to show historic trends in runoff. There is no evidence that annual precipitation totals in the Northwest are serially correlated (Dowdy and Matalas, 1969). The negative slope of cumulated values from 1928 to 1945 reflects a period of lower than average runoff while a positive slope between 1947 and 1958 indicates above average runoff. Runoff during the dry period, which was 14% less than mean conditions, also exhibited average peak annual discharges of only 69% of peak flows during the wet period. 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 both a year, and during a two decade period, of average runoff. This long term runoff record suggests that during periods of dry years flushing of the stream can be considerably reduced. Although there are no organic matter budgets for these early wetter and drier periods, it is likely that accumulation of refractory organic materials in the stream was appreciably greater during dry years and there may have been an annual net loss from the watershed during the wet periods, which involved both higher total annual and peak flows.

Two annual organic budgets constructed for a small watershed (WS10) in the H. J. Andrews Experimental Forest, Oregon are an example of the importance of runoff history; the budgets include an extremely dry year, with 167 cm precipitation in water year 1973 (Oct. - Sept.) and a wet year with 303 cm in 1974 (Franklin et al., 1981). Precipitation is typically seasonal, totaling approximately 240 cm and falling mostly as rain between October and March. Water year 1972 had 3 of the 10 highest storm flows recorded in the 24-year records of runoff for the Experimental Forest. Thus, these budgets were constructed at a time when storage of organic materials probably was relatively low. Wet-year (1974) organic inputs by litterfall and lateral

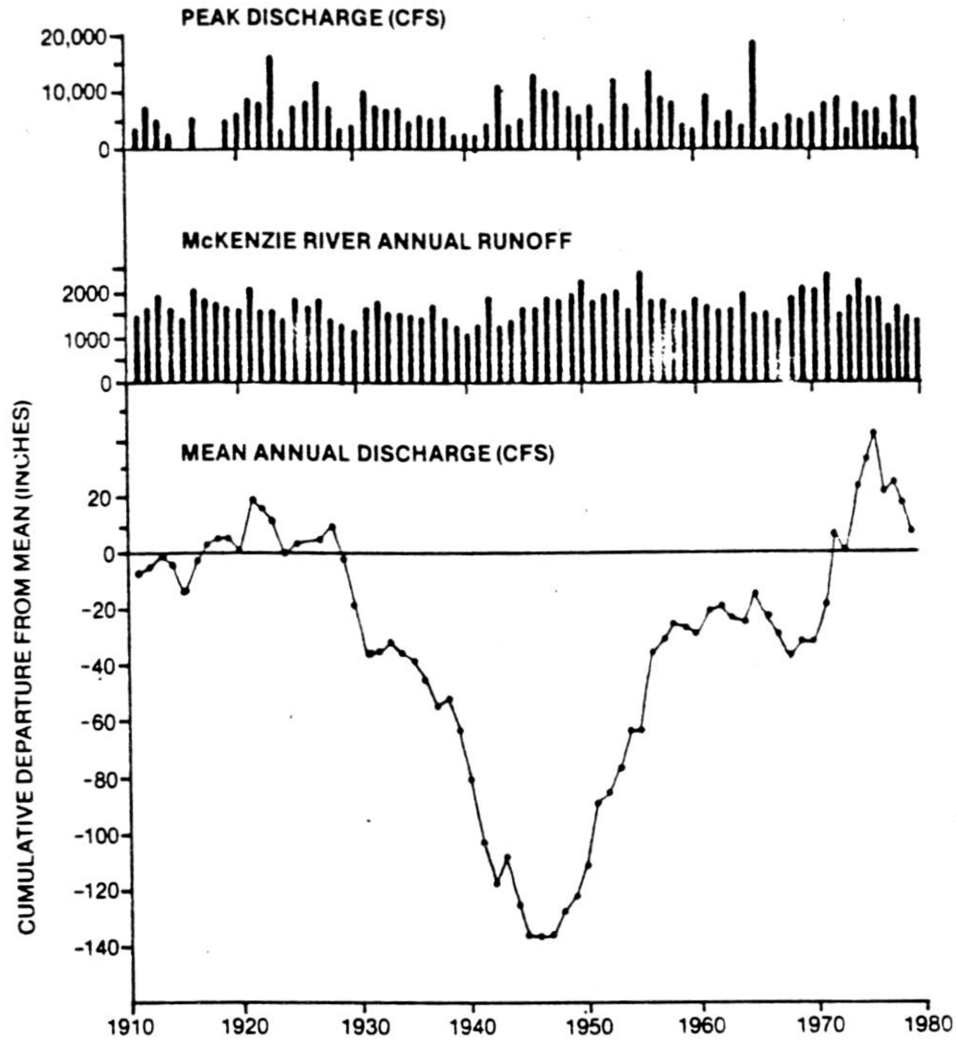


Fig. 3. Runoff history of the McKenzie River, Oregon, showing peak discharge, mean annual discharge, and cumulative departure from the mean (Dalrymple, 1965) of the entire 62 year round record. (That is, the record for each year is subtracted from the mean, keeping track of sign, and these differences cumulated and plotted through time.)

(surface) movement exceeded dry-year (1973) inputs by 5% and 65% respectively. Clearly, inputs change significantly with runoff. The dissolved organic matter (DOM < 0.45 μm) loss was 246% higher in 1974 because solution loss is related to runoff. Even though the annual runoff for 1974 was the second highest in the 63-year record for the upper McKenzie drainage, the peak discharge had a one year return period, and on that basis, POM export could be considered average or below. Therefore, the various elements of an organic budget for streams are extremely responsive to the magnitude and frequency of storm events. Although inputs (except landslides) may be relatively less variable, storage, export, and biological processes must all be evaluated in relation to runoff and return frequency if valid comparisons within and between running water systems are to be made. The discussion above has emphasized the effects of peak flows, but it is also important to consider the role of other episodic events, such as high winds without appreciable precipitation, which can result in major pulses of POM input without significant export.

Organic Export Rating Curves

Although rating curves (suspended load vs discharge) for inorganic particulate losses from a watershed have proven useful for calculating sediment transport, relationships between stream discharge and organic matter concentration are approximations at best (Fisher and Likens, 1973; Bormann et al., 1974; Brinson, 1976; Bilby and Likens, 1979; Bormann and Likens, 1979; Schlesinger and Melack, 1981). Even the best regressions of particulate organic concentration vs water discharge explain only about 50% of the POM concentration from discharge data (Bormann et al., 1974). When corrections for differences in the percent organic matter relative to total particulates at various flow rates are included, errors in calculating POM losses from a watershed are even greater. Studies of inorganic and organic components of transport have revealed different patterns for each of the rising and falling limbs of a peak flow hydrograph (Paustian and Bestcha, 1981).

Rating curves for coarse particulate organic matter (CPOM, > 1mm) are particularly poor. Fisher and Likens (1973) obtained an R^2 of 0.05 for their rating curve and rejected its use on that basis. Sedell and co-workers (Oregon State University, unpublished data) obtained a CPOM rating curve for a first order Oregon stream (WS10) with an $R^2 = 0.14$, based on samples collected over a full year by passing the entire discharge through an 80 ml net. These results indicate the high degree of uncertainty in using rating curves for calculating CPOM export.

A rating curve for fine particulate organic material (FPOM, < 1mm > 0.45 μm) also was developed for the Oregon stream Watershed 10 (Fig. 4). High FPOM export at moderate flows of 18-23 L/s (Fig. 4) represents the first storm in the fall, indicating the importance of timing as well as magnitude of discharge. Various curve forms produce poor fits to the data in

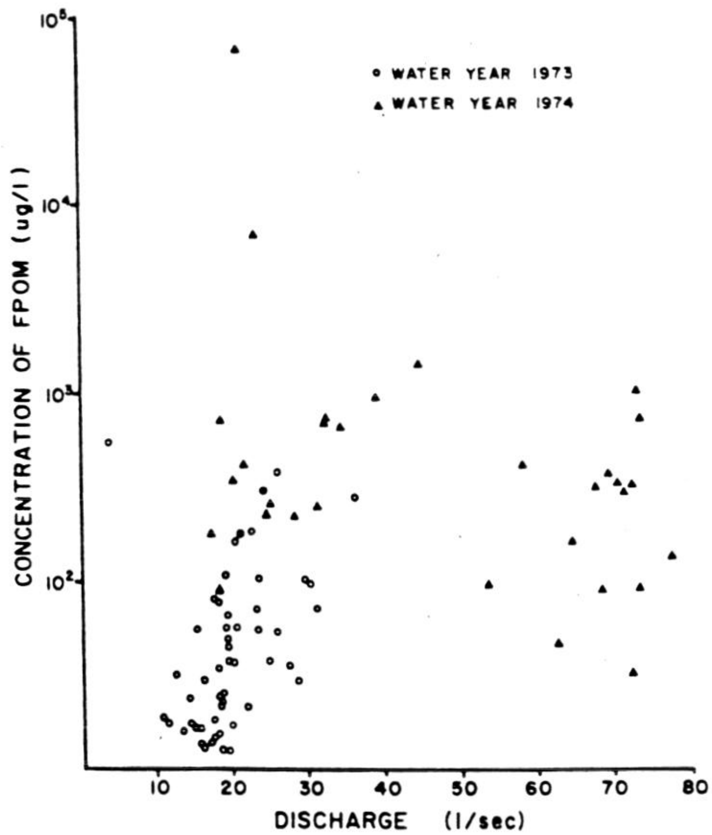


Fig. 4. Fine particulate organic matter (FPOM) vs discharge relationship for Watershed 10, Oregon, over two water years. The high value of FPOM at low discharge levels represent the first storm of the fall-winter rainy season.

Figure 4, particularly at high flows when the greatest percentage of annual POM transport occurs. Thus, peak discharge, the interval between storms, and storm sequence are all important factors in determining the total export of organic matter from a watershed during a storm event and a myriad of other factors such as time of year, amount of litterfall, decomposition rates of POM, etc.

In an effort to obtain a better fit of peak discharge to total organic export, 30 storms creating discharges >20 L/s in Watershed 10 were examined (Table 1). Linear regressions of total export against peak discharge, interval between storms, and interval between storms times peak discharge were calculated. All yielded similar results for this area of variable precipitation, but in mesic areas with fairly even precipitation regimes, the combination of interval between storms, magnitude of

Table 1. Various linear regression analyses of particulate organic matter (POM) export (> 75 μm) recorded for Watershed 10, Oregon, during all storms producing discharge peaks >20 liters sec^{-1} in water years 1973 and 1974.

X (independent variable)	Y (dependent variable)	N	R^2	Slope	Intercept	S.E. of Y	S.E. of Slope	S.E. Intercept
Peak discharge ($1\ sec^{-1}$)	Kg POM export over duration of flood	28	0.57	3.35	0.01	0.37	0.34	0.54
Peak discharge times day interval between floods	same	27	0.51	4.87	0.14	0.39	0.13	0.30
Day interval between floods	same	27	0.43	5.98	1.51	0.43	1.20	0.89

the previous storm, and peak discharge may be useful for estimation of total POM transport as well as inputs to a reach.

In general, then, the relationship between discharge and the export of organic matter from small stream watersheds is non-linear, time dependent, and site specific (i.e., dependent on retention characteristics). Such serial correlation relationships are likely to be represented best by hysteresis curves (Paustian and Bestcha, 1979; Whitfield and Schreier, 1981) and sampling needs to be continuous rather than by conventional grab-samples (Dawson, 1980; Whitfield and Schreier, 1981).

Relationship Between Organic Matter Export and Decomposition

Loss of organic material from a stream bed can result from both export (downstream and to the upper bank or flood plain) and decomposition. Decomposition rates for assumed steady state systems have been calculated by Fisher and Likens (1973) and Borman et al. (1974) from a modified equation by Olson (1963):

$$X = I/\ (k+K_1),\ \text{where,}$$

X = size of organic pool in the stream bed at steady state, in kg

I = input rate in kg of organic matter yr^{-1}

k = fractional loss rate of X due to decomposition yr^{-1}

k_1 = fractional loss rate of X due to export yr^{-1}

For a forested watershed (WS6) in the Hubbard Brook Experimental Forest (New Hampshire) a dynamic equilibrium was assumed and five years of export data were averaged to derive a mean decomposition value (k) of 0.43 per year (Bormann et al., 1974). An energy budget can be calculated for 1965-1966 using export and storage data from Bormann et al. (1974), litter input data from Gosz et al. (1972), and blow-in data from Fisher and Likens (1973), k = 0.46 and k_1 = 0.021. For year the 1966-1967, which included several large storms, k = 0.40 and k_1 = 0.088. These calculations of k and k_1 values over the five year period show that even in a year with a large storm only 8.8% of the estimated particulate inputs is exported as POM and in the year of smallest discharge events it is only 2.1%. Assuming no net change in storage, the resultant POM decomposition ranged from 82 to 96% of inputs. These calculations portray stream ecosystems as: 1) retentive and affording ample opportunity for biological processing of detrital inputs and 2) highly variable annual transport systems, with export varying more than 400% while decomposition rates varied only 14% over the 5 year period of study. Therefore, it is probable that in a wet year with no large storms, the DOM fraction would be emphasized; in a year having a 10-20 year storm, POM losses would dominate a budget.

In the modified Olson (1963) equation, decomposition of detritus is independent of temperature and dependent upon the size of the storage pool. Decomposition of detritus in streams, however, has been shown to be strongly related to temperature (e.g., Bolling et al., 1975a; Suberkropp et al., 1975) and, therefore, k is a function of temperature. For example, 90-95% decomposition of leaf litter, composed of species which are processed at medium to fast rates, takes about 1000 degree days (Petersen and Cummins, 1974). The annual accumulation of degree days, and variations between years are extremely important in determining annual losses due to microbial respiration. A maximum year-to-year variation of approximately 1000 degree days was observed over a 20 year period in the North Santiam River (Fig. 2B). This represents a potential annual fluctuation of 30 to 40% in decomposition losses attributable to temperature alone, which would influence the time of depletion of higher quality inputs as well as conditioning and use of lower quality litter. Therefore, even if storage were adequately measured and related to storm events within a given annual cycle and between years, this budget approach cannot be used independent of temperature.

Sampling schemes used to determine parameter values X, I, and k_1 in Olson's equation must deal with scales in time (turnover frequency) and space (storage pool dimensions) appropriate to characterize each parameter. Failure to do so will lead to spurious decomposition rate (k) estimates. For example, Olson's equation is dependent on definition of storage pool size under circumstances commonly encountered in budget calculations. That is, for two streams with identical I and k_1, but with twice as much POM storage (X) in one, apparent fractional loss from storage due to decomposition (k) would be 57% lower in the stream with lower standing crop (using data for I, k_1, and X from Bormann et al., 1974). Therefore, for a given stream, k will vary with the definition of X. If the storage term is considered to include logs, deep sediment, and bank storage, then input and export terms must take into account events which alter these components. Ideally each storage compartment should be characterized in terms of its particular X, I, k, and k_1 values, so that decomposition rate is more realistically a function of temperature, substrate quality, and oxygen environment and not obtained by difference. Thus, although the Olson (1963) model is a starting point, it must be significantly modified, and conditions carefully specified in order to be appropriate.

Detrital (POM) Storage

As stated previously, the assumptions of annual steady state in stream budget work has been perpetuated by failure to adequately measure storage and the input-output balance is misleading and primarily a function of physical retention or release rather than biological activity. In addition, the importance of, and interaction between, POM storage pools change with increasing stream size, from headwater tributaries to large rivers. For example, channel woody debris is particularly significant in small streams lacking sufficient hydraulic force to move large jams while flood plain deposition of POM is more significant for large rivers.

Storage in and associated with stream channels is apportioned among several sites (compartments) which are identifiable spatially and on the basis of turnover rates (Fig. 1). Although the compartments intergrade, three are sufficiently discrete to make their distinction useful: 1) in the channel sediments; 2) in the channel on or above the sediments - primarily in pools and in coarse woody debris jams; and, 3) on the flood plain or upper bank (Fig. 1). Rates of POM processing are controlled by such factors as dissolved oxygen concentration; size and degradability (quality) of the organic matter; temperature; and extent, frequency, and persistence of wetting (Merritt and Lawson, 1979). The major detritus processing sites are the aerobic sediment layer and exposed portions of POM accumulations in debris jams. The processing rates are much slower in the deeper, anaerobic sediment layers, and large woody debris accumulations have processing times much greater than an annual cycle. On the flood plain (upper bank), processing is slower during cold or dry periods than in the stream (Fig. 1). Large wood is processed more rapidly out of the stream channel during warm periods because of significantly higher fungal and invertebrate activity.

The organic storage of Bear Brook (Fisher and Likens, 1973) was assumed to be at steady state, with a detritus reservoir of about 80% of the annual input or output of energy. A standing crop less than the annual organic flux supports the assumption of steady state. However, detrital storage would be particularly important in budget calculations when it is large in relation to the other terms of the material balance equations. The storage component can be large when 1) channel conditions are conducive to retaining a large amount of organic material, and/or 2) a high proportion of the total sediment yield consists of bedload including organics. The potential for greater channel sediment storage increases with decreasing stream order, particularly in forested streams of mountainous areas. These streams are characterized by high erosion and litter production rates, and slope profile irregularities, but have channel obstructions such as logs and boulders for which there is usually insufficient hyraulic force for movement. Since slope irregularities, and obstructions create a stairstep effect, deposition of organics behind these obstructions must be considered in addition to physical processes such as scour and fill of the channel bottom.

Sediment storage. Detritus in sediment is subject to aerobic or anaerobic processing (Fig. 1). Depth of the aerobic zone is dependent upon the size and heterogeneity of sediment particle sizes, rate of microbial oxygen consumption, channel gradient, average flow conditions, and seasonal and annual flood patterns. In the cases in which total standing crop of particulate organics (excluding large woody debris) has been measured, sampling was generally in the aerobic portion of the sediment profile subjected to annual scour and fill (Fig. 1). POM is generally assumed to be available annually for biological processing to CO_2 and conversion to dissolved organic matter (DOM) and living biomass. Provided the organics and associated biota remain aerobic, at least for significant periods during the warmer portion of the annual cycle, processing can be accomplished within a year (Petersen and Cummins, 1974; Boling et al., 1975a,b). POM that remains buried in anaerobic zones is processed at significantly slower rates than that which remains aerobic over the annual cycle, as evidenced by intact, sulfide-blackened leaves excavated from deep sediments in the spring. On the other hand, since invertebrates have been recovered to depths of 45 cm or more into the substrates in streams with loose, heterogeneous beds (Coleman and Hynes, 1970; Hynes, 1974; Hynes et al., 1976), the depth of this aerobic processing zone needs to be carefully examined for each stream.

Concentration of CPOM and FPOM stored in the beds of two old-growth forest streams in Oregon was greatest in the sediments below the 10 cm depth normally sampled (Figs. 5 and 6). Studies will scour chains in such streams indicate that the depth of scour and fill (Fig. 1) for a 10-year storm is 15 to 20 cm (Moring and Lantz, 1975). Thus, storms could mobilize from storage two to four times the particulate detritus recovered in surface sediments by usual sampling techniques. Similar to flood scour, POM may be depleted from deep sediment storage or buried under new deposits through scour and fill that frequently occurs following forest clearcutting (Fig. 6) or channelization.

Channel debris. Until recently (Froehlich, 1973; Keller and Swanson, 1979; Bilby and Likens, 1980; Bilby, 1981) large woody debris has been ignored in stream budgets. The assumptions, for budget purposes, that the amount of large woody debris in channels was small and its processing rates insignificant were

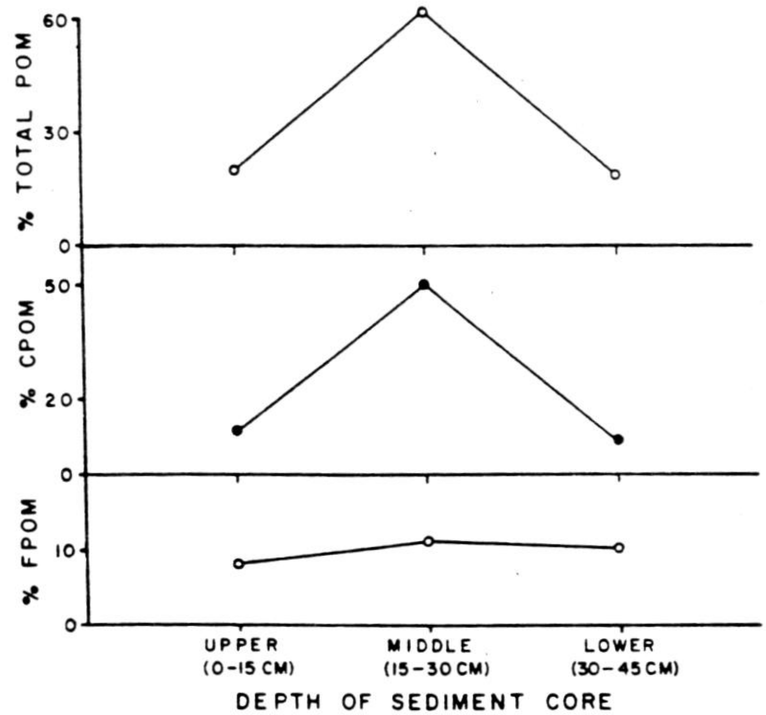


Fig. 5. Changes in relative % storage of total (POM; >75 μm), coarse (CPOM; >1 mm) and fine particulate organic matter (FPOM: <1 mm >75 μm) at three riffle sediment depths. Based on ash free dry weight of seven, approximately 20 cm diameter, frozen cores in Flynn Creek, Oregon, August 5, 1975. Total POM ranged from about 450 gm^{-2} to 1600 $g\ m^{-2}$, CV's as % ranged from 20-50. Unpublished data, Hess and Brown, Dept. of Forest Engineering, Oregon State University.

untested. It is obvious that the assumption of insignificant quantities of debris is not valid, particularly in debris-laden headwater channels of the Pacific Northwest (Fig. 7A). The amount of woody debris in first and second order Oregon streams has been measured at 8-25 kg/m^2 organic dry weight (Froehlich, 1973; Keller and Swanson, 1979; Anderson et al., 1978; Anderson and Sedell, 1979; Triska and Cromack, 1979). Assuming a maximum 100+ year processing time to convert woody debris to finer particulates, the annual contribution of large wood-derived FPOM to the mean aerobic sediment standing crop would be about 5 to 10% based on data available for Oregon and Michigan streams (Sedell and Cummins, unpublished data). Furthermore, a leaching rate (assuming gradual conversion of cellulose and lingin to more

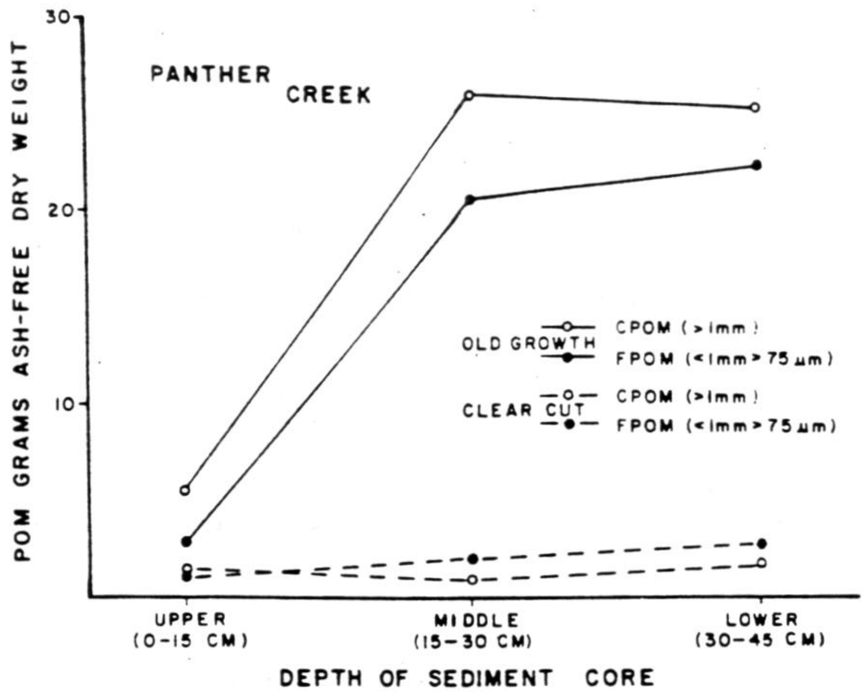


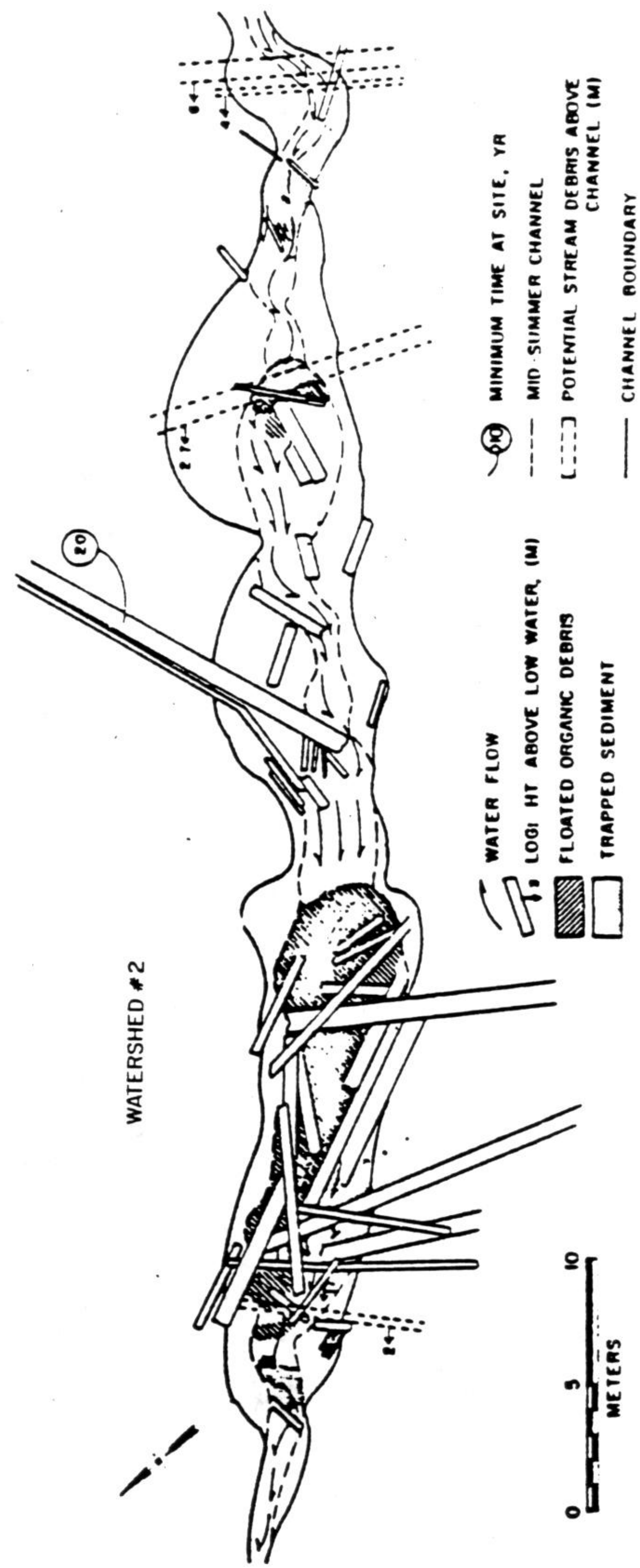
Fig. 6. Comparison of coarse (CPOM; >1 mm) and fine (FPOM; < 1 mm >75 um) particulate organic matter in riffle sediments of Panther Creek, Oregon, a 2nd order tributary of the Alsea River. Old-growth Douglas fir (120 year) and clear cut (two years after cutting) are compared. Samples were three to five frozen cores, approximately 15 cm in diameter, taken in each section September 9, 1973. CV's and % ranged from 30-50. Unpublished data, Sedell (Dept. of Fisheries and Wildlife) and Brown (Dept. of Forest Engineering), Oregon State University.

labile substrates) of only 0.1% per year from large debris would be sufficient to account for the entire annual measured DOM export from Watershed 10 (Oregon). Processing of large wood is apparently continuously concentrated in the outer millimenter or so (Aumen, Oregon State University, unpublished data). Input of large woody debris, which varies greatly from year to year, can not be assessed by litterfall or bank traps. For example, in a 100 m reach (about 1 m wide) of Watershed 2 in the H. J. Andrews Experimental Forest the blow-down of several tree tops doubled the standing crop of organic debris in a single storm. All the large (> 10 cm diameter) woody debris was measured in a 260 m reach of a third-order section of Augusta Creek, Michigan, which appeared to have a low concentration of wood (Fig. 7B). Even in this stream, the measured loading of woody debris--approximately 1.2 kg/m^2 organic dry weight, was about 15 times the mean annual detrius standing crop of the aerobic sediments, excluding the large wood measured by conventional traps. Assuming a 30 year processing time for large wood (hardwoods are processed more rapidly than wood of conifers; data from experimental streams yield estimates of 10 years for medium [approximately 10 cm] and smaller wood) the breakdown of this CPOM would yield the equivalent of about 14% of the FPOM standing crop annually. Because the amount of large woody debris in the particular study reach was probably below the average for streams in the area due to land use practices, and processing rate is probably greater, this estimate is conservative.

Another important feature of large woody debris is its role in retention of finer CPOM and FPOM and DOM (Bilby and Likens, 1980). Retention of FPOM in debris jams and associated sediments may result in its storage for periods of more than a year and the FPOM may require several years for processing. Whether the channel is in a period of loading of large debris, and whether large woody debris is retaining or releasing finer particulates, are critical assessments in compiling a budget.

Flood plain. Food plains are areas of river valley bottom inundated when bankfull channel capacity is periodically exceeded (Maddock, 1976). During overbank flow the flood plain or upper bank can serve as both a source and a sink for POM (Fig. 1). The organic content of flood plain and upperbank deposits has not been considered in budget determinations for lotic systems, nor has the movement of organic matter from the flood plain back into the channel. the rates of rise and fall of water level, peak discharge, channel and flood plain geometry, and flood plain vegetation all interact to determine the POM dynamics of a flood plain during overbank flow. Exposed and buried living and dead vegetation can be used to evaluate the balance between deposition and erosion on the flood plain, as well as the extent of inundation from floods of various magnitudes. Sigafoos (1964) reconstructed the depositional history of about 75 cm of sediment in the flood plain of the Potomac River which resulted from a mix of deposition and erosion over a 30-year period - the net effect being deposition.

Detritus exchange between the channel and flood plain is likely to involve important qualitative changes with respect to


WATERSHED #2
WATER FLOW
LOG: HT ABOVE LOW WATER, (M)
FLOATED ORGANIC DEBRIS
TRAPPED SEDIMENT
MINIMUM TIME AT SITE, YR
MID-SUMMER CHANNEL
POTENTIAL STREAM DEBRIS ABOVE CHANNEL (M)
CHANNEL BOUNDARY
0
5
10
METERS

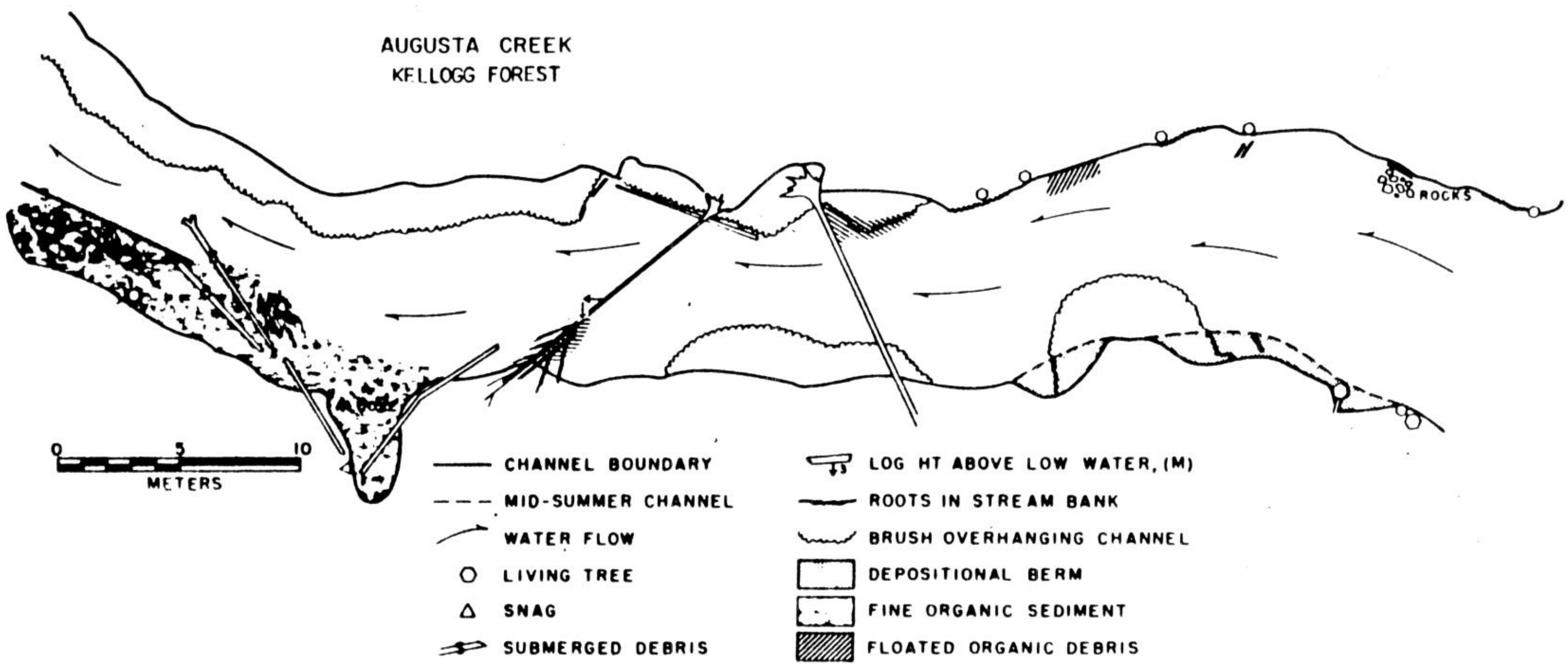


Fig. 7. Detailed reach maps showing wood debris in Watershed 2 (H. J. Andrews Experimental Forest) in the Cascades of Oregon (A) and Augusta Creek (Kellogg Forest, Michigan State University) in southwestern Michigan (B).

particle size, biochemistry, microbiology, and degree of conditioning in the terrestrial system (Merritt and Lawson, 1979; Triska and Cromack, 1979). Furthermore, as stated above, when temperatures are lower on the flood plain than in the stream and/or conditions are dry, biological processing of particulate detritus can be slower than in aerobic zones of the stream (Merritt and Lawson, 1979). Consequently, leaf litter deposited on the flood plain in the autumn and captured during spring high water, enters the stream in a less processed condition than litter that remained in the aerobic stream sediments over the same period.

Quantitative and qualitative data are required on the export from and import to the channel to and from the flood plain over annual and longer periods. However, typical litterfall and ground surface movement trap techniques are not adequate to characterize flood plain dynamics and other methods (e.g., some sort of mark and recapture procedure) would be required for assessment of organic matter input and output from flood plains.

Changes in POM storage along river continua. Input, storage, biological processing, and export of organic matter vary through a drainage basin from headwater streams to larger rivers. In the River Continuum concept described by Vannote et al. (1980), it was suggested that the size distribution of POM changes with increasing stream order such that both transport and surface sediment storage are generally characterized by decreasing amounts of CPOM as the influence of the riparian vegetation decreases with increasing channel width. This trend of decreasing CPOM to FPOM ratio in transport and storage (Sedell et al., 1978; Naiman and Sedell, 1979a, 1979b; Cummins et al., 1982), which more adequately characterizes the latter, is modified by tributaries and the CPOM generated from macro-algae (Minshall et al., 1983; Wallace et al., 1982). The changes in relative importance of certain size classes, which reflect different input, physical retention, and biological processing along the river continuum, necessitate modifications in the sampling methods applied to organic budget studies in streams and rivers of various size. For example, channel storage in debris jams would be most significant in first through about third order headwater streams, while upper bank, off channel pools, along banks and on point bars, and flood plain sites become more significant with increasing river size. The importance of deep sediment storage in organic budget calculations in a particular water year and the action of scour and fill along the river continuum are presently unknown. The problem of comparison among streams of different sizes is compounded because budgets for headwater streams typically approached on a watershed basis, differ significantly from analysis of individual reaches which is more feasible for larger rivers.

COMPARISON OF WATERSHED AND REACH (SEGMENT) DERIVED ORGANIC BUDGETS

Theoretical Considerations

The components of watershed and reach organic budgets are summarized in Figure 8. The watershed approach covering all channels in a basin is appropriate for small first-, to about third-order watersheds. For stream orders greater than about three, however, a "representative" reach, or river segment, usually is selected, preferably with few tributaries. An initial step in either case is the determination of a water balance. When the entire watershed is included, ground water inputs, overland flow, and precipitation directly into channels should

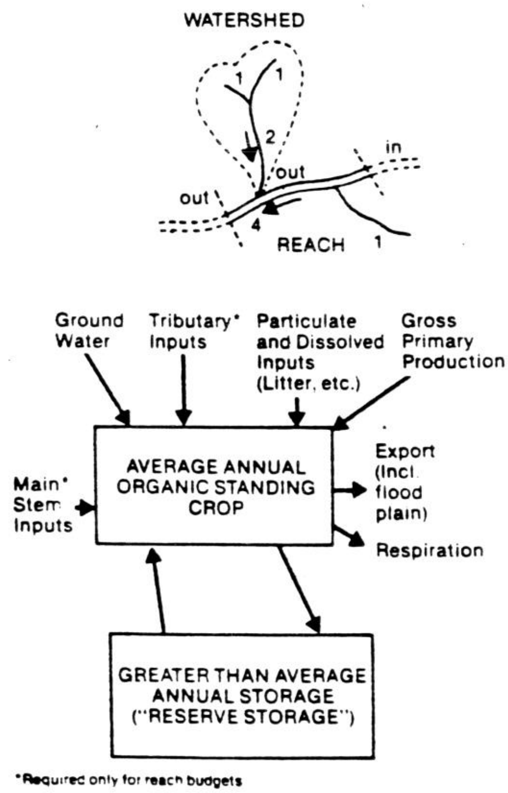


Fig. 8. A comparison of components of watershed (A) and reach or segment (B) organic budgets. Examples of stream orders (numbers) and input and output measurement points are shown in the top portion of the figure.

equal mainstem output plus evaporation and channel related transpiration. The usual method to determine POM and DOM fluxes has been based on relationships between organic matter concentrations in grab samples of input and output at different rates of water discharge. Total organic fluxes are then calculated on the basis of transport rating and flow duration curves (e.g., Fisher and Likens, 1973). Storage is frequently the most poorly documented element of budgets (Fig. 8), because both spatial and temporal sampling problems may lead to significant over- or underestimates of this parameter for a given annual budget.

Budget comparisons. Data from seven study sites across the United States provide examples of broad trends and problems in comparing organic matter budgets for different streams (Tables 2-5). Tables 2 and 3 summarize background information on the study streams and methods used to estimate the organic budgets. The sites differ significantly in watershed area, stream slope, and other geomorphic characteristics. Differences in riparian vegetation represent important sources of variation among streams of a given order in different basins. For example, first-order streams in arid regions are bordered by sparse vegetation, so particulate inputs from surrounding areas are lower than in-stream primary production (Table 4). In Deep Creek, POM generated from aquatic macrophyte breakdown is the major component of the fraction. In contrast, a coastal coniferous forest stream may flow through a 70 meter high forest and receive low light inputs and abundant litterfall from canopy and understory vegetation of riparian plants (Campbell and Franklin, 1979). This variation in the degree of coupling between terrestrial and aquatic components varies predictabilty along the river continuum, even within a particular vegetation biome (Vannote et al., 1980).

Although obvious differences exist among the organic budgets of the lotic ecosystems compared (Tables 4 and 5), POM constituted a major component (25 to 71%) of the total organic matter input. Except for Deep Creek and Fort River, the amounts of POM imported, expressed on an areal basis, are similar. Of the approximately 2300 to 3200 kcal m^{-2} yr^{-1} POM delivered to WS10, Augusta Creek, and Bear Brook, 7 to 37% was exported, the remainder being converted to DOM, biomass, respired to CO_2 and stored. POM exports significantly exceeded imports only in Deep Creek and White Clay Creek. Values of gross primary production for the systems cluster into two groups at approximately 10 to 90 kcal m^{-2} yr^{-1} (0.2 to 2.5% of total inputs of their respective budgets). As expected, the small, heavily shaded streams had low primary production. In all but Deep Creek and Fort River,

Table 2. Selected geomorphic, hyrologic, meteorologic, physico-chemical and ecological data for the stream systems for which data are presented in Tables 3 and 4.

Parameters	Bear Brook	Watershed 10	Rattlesnake Creek	Augusta Creek	Deep Creek	White Clay Creek	Fort River
Stream Order	2	1	1	1	2	3	4
Biome	Deciduous (New Hampshire)	Coniferous (Oregon)	Arid (Washington)	Deciduous (Michigan)	Arid (Idaho)	Deciduous (Pennsylvania)	Deciduous (Massachusetts)
Geology	Stillimanite gneiss	Basalt	Basalt	Glacial till	Lacustrine sediments	Mica schist gneiss	Metamorphic Paleozoic rock
Waterhsed area Km^2 (Acres)	1.3 (321)	0.1 (25)	350.0 (86,485)	3.3 (815)	447.0 (110,453)	7.2 (1,779)	105.0 (25,946)
Dominant Watershed Activity	protected	protected	protected	grazing	grazing	farming, grazing	farming, grazing
Drainage, density (length/basis area)	1.31	5.00	0.01	1.10	0.09	2.79	--
Stream gradient (%)	14	47	2	0.2	0.2	1.0	0.2
Base flow discharge M^3/sec (cfs)	0.002 (0.07)	0.003 (0.01)	0.011 (0.40)	0.013 (0.45)	0.09 (0.12)	0.068 (2.40)	0.28 (10)
Annual precipitation (cm)	123	245	17	152	41	107	110
Maximum Temp (°C)	18	16	22	20	27	22	27.5
Annual cumulated degree days	3285	3165	5547	3256	6695	4398	--
Total alkalinity (mg/l)		10	127	185	233	52	--
NO_3 (mg/l)		<0.1	0.3	3.3	0.2	2.8	0.2
Total P (μg/l)		80	0.15	30	40	--	25
Water (detritus year(s) for which budget is presented (Table 4)	1968-1970	1972-1973, 1973-1974	1969-1970	1972-1973	1970-1972	1972-1974	1972-1973

Table 3. Methods used for determining organic budgets for six North American streams.

	INPUTS			OUTPUTS			
Stream System	Particulate Organic Matter (POM)	Dissolved Organic Matter (DOM)	Net Primary Production (Net PP)	POM	DOM	Respiration	Storage
Bear Brook	Litter fall (irregular intervals) and lateral transport traps (weekly intervals, branches >1cm diameter not included); non-winter drift and bottle samples, irregular intervals	Throughfall ground water and stream grab samples, irregular intervals (DOC <0.45 µm)	Light and dark bottle (mosses), three determinations	CPOM pending basin, FPOM (<1mm) bottle samples, irregular intervals	Stream grab samples, irregular intervals	Microbial respiration by difference; mosses dark bottles (3 determinations); macroconsumer respiration (calculated)	None detected-steady state standing crop in ponding basin
Watershed 10	Litter fall and lateral transport traps, monthly intervals (>0.45 µm)	Throughfall, storm event, groundwater seep and stream grab samples, monthly intervals, (DOC < 0.45 µm)	Circulating chambers in summer months	Continuous whole stream seiving with 80 µm net. Irregular grabs	Same as inputs	Gilson respirometer of detritus quality and particle size, monthly intervals	By difference of the POM inputs to outputs
Rattlesnake Creek	Litter fall traps, Irregular intervals and weekly bottle samples (> 0.5 µm)	Weekly grab samples (< 0.5 µm)	Upstream-downstream pH	Weekly bottle samples (> 0.5 µm) plus loss of standing crop of insects and water cress flushed out by floods	Weekly grab samples (< 0.5 µm)	Upstream-downstream pH	Not measured

Stream System	INPUTS: Particulate Organic Matter (POM)	INPUTS: Dissolved Organic Matter (DOM)	INPUTS: Net Primary Production (Net PP)	OUTPUTS: POM	OUTPUTS: DOM	OUTPUTS: Respiration	OUTPUTS: Storage
Augusta Creek	Mean monthly detritus standing crop for the detritus year	Difference (magnitude checked against biweekly DOC grab samples)	Circulating chambers, monthly intervals	By difference (magnitude checked against standing crop changes less respiration)	Weekly grab samples (< 0.5 μm)	Gilson respirometer of detritus by particle size and circulating chambers, monthly intervals	Not measured (assumed to be different than standing crop)
Deep Creek	Litter fall and blow in (irregular intervals) and drift (monthly)	Monthly grab samples (< 0.5 μm)	Upstream-downstream O_2 or pH	Drift (monthly)	Monthly grab samples (< 0.5 μm)	Upstream-downstream O_2 or pH	Coring and various measures of deposition and accrual
White Clay Creek	Litter fall and lateral transport traps (weekly intervals for 2 yrs.) POM standing crop, random transects equivalent to $1m^2$ FPOM $0.1m^2$ core samples	Weekly grab samples (DOC < 0.45 μm)	Circulating chambers, 2-5 sample runs per week	CPOM (7 mm) wier on stream orders 2 and 3 before and after storm events in fall and winter, irregular spring and summer samples. FPOM (< 7mm > 50 μm) 24 hour pump samples, 2-5 per week	Weekly grab samples (DOC < 45 μm)	Circulating chambers 2-5 sample runs per week	Not measured
Fort River	Litterfall traps (biweekly) and drift (every 3 days: CPOM 1mm mesh net at timed intervals; FPOM grab samples)	Grab samples every 3 days (< 0.1 μm)	Diel O_2 curves (23 measurements over 18 months)	Drift (same as Inputs)	Same as Inputs	Diel O_2 curves	None detected-steady state standing crop

Table 4. Energy budgets for 7 North American Streams (POM = particulate organic matter, > 0.45 m particle diameter; CPOM = coarse particulate organic matter, > 1-2 mm; FPOM = fine particulate organic matter, < 1-2 mm > 0.45 μm; DOM = dissolved organic matter, < 0.45 μm; GPP = gross primary production). All values kcal $m^{-2}yr^{-1}$ calculated by conversion of organic matter ash free dry wt using Cummins and Wuycheck (1971).

Parameters	Bear Brook	Watershed 10	Rattlesnake Creek[1]	Augusta Creek	Deep Creek	White Clay Creek	Fort River
Order	2	1	1	1	2	3	4
Budget Type	Reach (1700 m)	Watershed	Watershed	Watershed	Reach (Station 3)	Reach	Reach (1700 m)
INPUTS							
POM	3226	2633	2728	2317	142758	3030	36000
CPOM	(2733)	(2369)	(1215)	(355)	(2490)	(2153)	(2250)
FPOM	(493)	(263)	(1513)	(1962)	(140268)	(878)	(33750)
DOM	2807	979	3699	1974	149085	4117	100125
GPP	10	90	5000[3]	38	14245	3782	2700
SUBTOTAL	6033	3701	11427	4328.5	306088	10929	138825
OUTPUTS EXPORT							
POM	1201	176	2726	858	169099	3286	31500
CPOM[4]	(927)	(116)	(1213)	---	(2469)	(1894)	(900)
FPOM	(274)	(60)	(1513)	---	(166639)	(1392)	(30600)
DOM	(2797)	(1476)	(3201)	(1022)	(149085)	(4117)	(101700)
Respiration	2035	1053	3611[3]	2449	12124	3031	5625
SUBTOTAL	6033	2704	9538	4329	330308	10434	138825

Parameters	Bear Brook	Watershed 10	Rattlesnake Creek[1]	Augusta Creek	Deep Creek	White Clay Creek	Fort River
Storage	0	806	0	0	0	0	0
TOTAL	6033	3510	9538	4329	330308	1043.	138825
Difference in Input-Output Balance[2]	0	191	1889	0	-24220	495	0

[1] Cushing and Wolf, 1982

[2] No difference reported in some because values obtained by difference.

[3] Does not include aerial respiration of emergent vegetation.

[4] Vascular hydrophyles plus benthic organic matter.

Table 5. Organic budget components, expressed as percent, for 7 North American streams.

Parameters	Bear Brook	Watershed 10	Rattlesnake Creek[1]	Augusta Creek	Deep Creek	White Clay Creek	Fort River
Order	2	1	1	1	2	3	4
Budget Type	Reach (1700 m)	Watershed	Watershed	Watershed	Reach (Station 3)	Reach	Reach (1700 m)
INPUTS							
POM	53.5	71.1	23.9	53.5	46.6	27.7	25.9
CPOM	(45.3)	(64.0)	(10.6)	(8.2)	(0.8)	(19.7)	(1.6)
FPOM	(8.2)	(7.0)	(13.2)	(45.3)	(45.8)	(8.0)	(24.3)
DOM	46.3	26.4	32.4	45.6	48.7	37.7	72.1
GPP	0.2	2.5	43.7	0.9	4.7	34.6	2.0
TOTAL	100.0	100.0	100.0	100.0	100.0	100.0	100.0
OUTPUTS							
Exports	66.2	26.6	62.1	43.4	96.3	71.0	95.9
POM	19.9	6.9	28.6	19.8	51.1	31.5	22.6
CPOM	(15.4)	(4.6)	(12.9)	---	(0.7)	(18.2)	(0.6)
FPOM	(4.5)	(2.3)	(15.9)	---	(50.4)	(13.3)	(22.0)
DOM	(46.3)	(19.6)	(33.6)	(23.6)	(45.1)	(39.5)	(73.3)
Respiration	38.8	41.6	37.9	56.6	3.7	29.0	4.1
Storage	0	31.8	0	0	0	0	0
TOTAL	100.0	100.0	100.0	100.0	100.0	100.0	100.0

community respiration was a significant portion (29 to 56.6%) of the organic budget output.

Many of the differences in budget characteristics are artifacts of system delimitation, thus in reaches of larger streams such as Deep Creek and Fort River, fluvial import of organic matter assumes greater importance relative to inputs measured on an area basis such as litterfall. Respiration, per unit area exhibits a twelve-fold range in the various systems when reported on a $kcal/m^2$ basis, and an eleven-fold range on the basis of percent of total output which is not areally based. The heavy macrophytic producing streams (Fort River and Deep Creek) have the highest absolute rates of community respiration yet the lowest percent output by respiration. The remaining output is by fluvial export which is naturally high in these rivers.

The hydrologic data shown in Table 2 should be interpreted in the context of the long term patterns in each watershed. Because the U.S.G.S. water year covers the period of October 1 through September 30, stream discharge records correspond well with the "detritus year", conveniently defined in the temperate zone as extending from one period of leaf fall to the next. Peak 24-hour flows for the budget years compared (Tables 4 and 5) are in the range of 1 to 5-year flood recurrence intervals of annual maximum daily discharge, based on 8-24 year records. Although similar flood years allow for more legitimate comparisons, the absolute organic budget values given for each site are not necessarily representative of the long term.

The ratio of export to import (E/I) and primary production to community respiration (P/R) for the seven streams are compared in Table 6. First-order streams (except Rattlesnake Springs) and second-order Bear Brook had P/R ratios less than one. Watershed 10, Augusta Creek, and Bear Brook are all heavily shaded systems with significant allochthonous inputs, and measured organic matter export was two-thirds or less of imports in these streams. In Rattlesnake Springs, Deep Creek, and Fort River systems with $P/R > 1$, and E/I near to or >1, the majority of POM particulate export was derived from extensive beds of aquatic macrophytes. The seven study streams' relationships shown in Table 6 follow the prediction of Fisher and Likens (1973) that in systems having $P/R < 1$ (heterotrophic) imports exceed exports, when $P/R > 1$ exports exceed imports, and they balance when $P/R = 1$ (see Fort River, Table 4). However, the ratios given in Table 6 are only approximate, because of problems in accurately measuring detrital export and derivation of major budget items by difference, which essentially makes them a function of export.

Table 6. Comparison of primary production/community respiration (P/R) and organic matter export/organic matter import (E/I) ratios for the seven flowing water systems (United States) compared in Tables 2-5)

Ecosystem Parameters	Watershed 10 (Oregon)	Augusta Creek (Michigan)	Rattlesnake Springs (Washington)	Bear Brook (New Hampshire)	Deep Creek (Idaho)	White Clay Creek (Pennsylvania)	Fort River Reach (Massachusetts)
Stream Order	1	1	1	2	2	3	4
E/I	0.26	0.44	0.83	0.66	1.09	1.04	0.98
P/R	0.09[1]	0.50	1.38	0.01[1]	1.18	1.25[1]	0.96[1]

[1]Minimal estimates calculated assuming gross primary production equals twice net.

Comparison of reach and watershed methods of budget calculations. It would be useful to be able to compare hydrologically and geomorphically diverse stream ecosystems in terms of over-all biologic functions with some index of efficiency of organic matter processing. The desired index must be applicable to both reach and watershed stream budgets and should be insensitive to such arbitrary features as ecosystem size. Fisher and Likens (1973) suggested that Respiration per Total Input (R/I), termed ecosystem efficiency, may be an index of general utility in this regard.

For stream ecosystems studied on a reach basis, for example Bear Brook, inputs such as litter and primary production, as well as respiratory output, occur on an areal basis. If the size of the study reach were increased, these parameters would increase proportionately (on a whole system basis). However mainstream input (transport from upstream) is constant, regardless of the study reach length below the input site. Therefore, to arbitrarily increase reach length is to automatically increase efficiency since R increases while mainstem input declines in importance on a unit areas basis. Thus, ecosystem efficiency, as originally defined by Fisher and Likens (1973), is of no utility in comparing diverse stream ecosystems.

For whole watershed stream studies, however, mainstem and tributary inputs are irrelevant since all channels are designated as part of the system. Inputs of organic matter in flowing water occur only as groundwater or, in some cases, overland flow directly from the terrestrial system. To increase system size by considering all channels in a watershed does not automatically alter the ratio of R to total input, since all fluxes can be calculated on an areal basis. Groundwater input to stream channels is a function of watershed area, and if drainage density remains constant as system size is increased, so does areal groundwater input (baring groundwater losses). Therefore, watershed budget studies can be compared legitimately, regardless of size.

We suggest two efficiency indices of general utility:

Ecosystem Efficiency (EE) = R/(P+L+G)
Retention Efficiency (RE) = (R$\pm$ ΔS)/(P+L+G)
where R = ecosystem respiration; P = gross primary production; L = litter input; G = groundwater input; and S = organic matter storage.

All units can be expressed as kilocalories $\cdot$ m^{-2} $\cdot$ yr^{-1} (or as grams organic matter $\cdot$ m^{-2} $\cdot$ yr^{-1}).

Ecosystem efficiency (Fisher and Likens, 1973) indicates the extent to which all organic matter inputs are respired by the system per unit time (e.g., annually). Retention efficiency indicates the extent to which all inputs are either respired or stored and is the preferred general expression for handling non steady-state systems. At steady state, the expressions are equivalent, although the difference between fast processing and low retention needs to be carefully distinguished.

Bear Brook data can be converted to a watershed basis and compared to Bear Brook reach data (Table 7). Since all channels are now included, ecosystem area increases 2.4 fold as do all areal fluxes. Tributary and mainstem inputs become zero and DOM input declines per m^{-2}. Ecosystem efficiency (EE) for Bear Brook as a watershed is then 0.61 as compared to 0.37 for Bear Brook as a reach ecosystem. The latter value is unique to the arbitrarily defined reach studied and has no general applicability.

Ecosystem efficiency for the other apparently steady-state watershed stream, Augusta Creek, is 0.56. Rattlesnake Creek and Watershed 10 are not at steady state and must be described with Retention Efficiencies. RE's for these two systems are 0.22 and 0.49 respectively compared to 0.56 and 0.61 for Augusta Creek and Bear Brook.

These data suggest that for a variety of watershed streams (except Rattlesnake Creek), more than half of all inputs are retained and/or processed to CO^2 on an annual basis. If we extend the model unaltered to the watersheds of large rivers, we would predict that less than half of all organic matter inputs to streams enter oceans. Realized retention efficiencies of large rivers may in fact be greater than those of small watershed streams. For example, litter inputs decline per unit of channel area in wider streams and primary production may not increase compensatorily. Large rivers and small to mid-sized streams with high drainage density are quite difficult to treat directly as watershed streams and have consequently been studied as stream reach ecosystems (e.g., Deep Creek, White Clay Creek, Fort River). As previously stated, budget data for reaches cannot be used to compute EE and RE due to the problem of system size. How then might stream reaches be compared? Stream metabolism index (SMI; Fisher, 1977) can be used to compare stream reaches and is defined as:

$$SMI = (R \pm \Delta S)/(P+L+T+M+G) - (Q_f)(M)$$

Where T = organic matter input via tributaries; M = Organic Matter input at mainstem upstream site; Q_f = discharge at mainstem output site/discharge at mainstem input site. Other variables are as previously defined.

Table 7. Comparison of reach and whole system budgets for Bear Brook, New Hampshire.

	Reach		Watershed	
	(Segment)[1]		(All Channels)[2]	
Length	1704m		5174m	
Area	$5877m^2$		$14,029m^2$	
	Kg $stream^{-1}$	g m^{-2}	Kg $stream^{-1}$	g m^{-2}
Litter	3260		7791	
Lateral transport	547		1162	
Litter fall	43		103	
	(3850)	(655)	(9556)	(681)
CPOM	640	109	0	
FPOM	155	26	0	
DOM, surface	1580	269	0	
subsurface	1800	306	3380	
	(4175)	(710)	(3380)	(241)
P_G	13	2	31	2
Total Input	8038	1368	12,967	924
CPOM	1370	233	1370	98
FPOM	330	56	330	24
DOM	3380	575	3380	241
	(5080)	(864)	(5080)	(362)
Respiration	2958	503	7887	562
Total Ouput	8038	1368	12,967	924
R/Input	.37		.61	
R/Particulate	.37		.61	
SMI	1.0		.82	

1 Fisher and Likens, 1973.
2 Unpublished but calculated from data in Fisher and Likens, 1973.

As with EE and RE, SMI measures the efficiency of respiration or storage of some organic input. The denominator of the expression represents all inputs that enter the reach from all sources less mainstem input (fluvial transport) corrected for accrual of water through the reach. That is $R \pm \Delta S$ is judged relative to excess inputs which would otherwise cause organic matter concentration to increase across the system. An increase in organic matter concentration in transport across the system is termed loading in this context, thus if SMI = 1.0, output water would have the same organic matter concentration as mainstem input water, and the system would not load. If SMI < 1.0, organic matter concentration would increase across the system and if SMI > 1.0, concentration would decline. The specified performance criterion used here (zero loading) is admittedly arbitrary - the system may merely "hold its own" and prevent concentration increases linearly.

For watershed stream systems, SMI reduces as follows:

$$SMI = (R \pm \Delta S) \;/\; P+L+O+O+G - (Q_f)(M)$$

and, since M is analogous to G;

$$SMI = (R \pm \Delta S) \;/\; P+L+G) - (1.0)(G)$$

$$SMI = (R \pm \Delta S) \;/\; P+L$$

Thus any watershed stream which respires or stores organic matter equivalent to primary production and litter inputs will have SMI = 1.0 and will export water with an organic matter concentration equivalent to the DOM in groundwater. If SMI = 1.0 all the way to the sea, organic matter concentration in water entering estuaries will be equivalent to that in groundwater entering headwater streams. In fact, SMI may vary widely from headwater to estuaries, being > 1.0 in some regions (e.g., below sites of organic enrichment) and < 1.0 in others.

Reach SMI's were computed for Bear Brook and Fort River systems (Table 7). Bear Brook had an SMI of 1.0 while Fort River SMI = 0.66. If Fort River is assumed to be a steady-state system, respiration is only 66% of that required to prevent loading. As estimated, Bear Brook does not load because all "excess" inputs are respired.

Watershed stream SMI's for WS10 and Bear Brook are 0.62 and 0.82 respectively, although WS10 exhibits an almost two-fold range in two consecutive years (Table 7). Both systems load, in that SMI < 1.0. Loading in watershed streams occurs as groundwater containing only DOM rapidly picks up more DOM (Kaplan et al., 1980) and POM via litter inputs. Thus, we might expect that loading is the general rule in headwater systems as a consequence of the SMI as defined.

While all three efficiencies described here are legitimate indices for comparing different streams on a watershed basis, all are sensitive to discharge and accompanying fluvial transport of organic matter. In the two years' of budget data available for WS10 in Oregon, inputs were low in the relatively dry water year 1973, ΔS was high, and RE was 0.73 (Table 7). In wet water year 1974, input was higher, yet respiration remained constant and RE dropped to 0.34. Retention efficiency was thus generally an inverse function of discharge which in turn increased total input and ΔS was negative. Yet in both years, ΔS was positive. During years with unusually high discharges we can envisage a negative ΔS that exceeds respiration. Under those conditions, RE would be negative. In steady-state systems increased discharge lowers RE simply by increasing organic matter input at (presumably) constant R. SMI behaves similarly in both watershed and reach systems even though the absolute values are different. At relatively constant R, increased discharge lowers SMI, thus the system loads to a greater extent during wet than during dry years. For WS10, SMI's for dry and wet years are 0.84 and 0.46, respectively.

In summary, we see that while the efficiency indices proposed here are conceptually sound and can be applied to all watershed stream ecosystems, only SMI can be applied to reach systems. To date, no satisfactory analogue of RE suitable for use on reach systems, has been devised, and thus reach and watershed stream systems cannot be compared in this regard. More importantly perhaps, all efficiency indices are highly sensitive to fluctuations in discharge and decomposition rate of organic matter. Because we have shown that discharge exhibits great year to year variation, efficiency values of whatever type, are of little utility when based on data from a single year. Not only is discharge a critical variable shaping seasonal and even diel patterns in efficiency, but several other factors also greatly influence efficiency on a short-term basis. Temperature, cumulative degree days, insolation, litter input, primary production, and the heterotrophic-autotrophic status of communities, among other variables, shown much greater variation of diel or seasonal periods than from year to year. All influence efficiency. Thus the annual organic budget at best represents a temporal compromise which is too short for revealing stream function on the time scale of geomorphic change and too long for elucidating biologic control of critical processes.

Whole Basin Budgets by Stream Order

As discussed above, quantification of organic budgets has most frequently involved inputs and outputs from entire small (first order) watersheds (e.g., Fisher and Likens, 1973; Sedell et al., 1974) and occasionally from discrete reaches (e.g., Fisher, 1977). The River Continuum Concept visualizes the stream-river as a continuum of nutrient turnover processes and population assemblages which are predictably adapted to the most probable physical state of a river system along its drainage network (Vannote et al., 1980).

Comparisons of the four different biome stream-river systems studied by the River Continuum Group were made by estimating annual organic carbon budgets. Seasonal terrestrial input, primary production, respiration, storage, and transport data from the 16 sample sites were calculated by stream order using basin geomorphic and hydrologic characteristics (Table 8 and 9). The annual carbon budget gives a first approximation of absolute carbon fluxes for all channels of a given order in each basin. By comparing the inputs (litter, gross primary production, and [non-flood event] transport to order n from n-1) to outputs (respiration and transport) and the difference between them to POM storage (except large wood), each basin was evaluated with respect to changes in carbon storage as to general aggrading (storing organic carbon) or degrading (exporting) condition. Storage divided by the excess of inputs or outputs provides an estimate of the number of years of storage for the given output rate (Table 9) - that is, given the current loss/accumulation rate, the number of years required to remove/accumulate the present storage pool. About 60% of the 23 (by order) systems showed a pattern of aggradation with outputs less than inputs.

Headwater Oregon streams (orders 1 and 2) and all Michigan streams (except first-order) were characterized by large amounts of storage (Table 9). All other stream orders in all four biomes appeared to be quite active - either rapidly degrading or aggrading with estimated periods for accrual or loss of existing storage of less than two years ($<$ 0.1 to 1.7). Only one of the 23 order-systems (Oregon fifth order) was evaluated as being close to equilibrium (inputs-outputs = 5.6 Ton C). In all but one case (Idaho second order), the difference between inputs and outputs was about an order of magnitude (11 cases) or less (11 cases) than storage. At the basin level, all systems except Oregon (due to large sixth and seventh order export) appear to be aggrading. Storage in Michigan streams larger than order 1 was dominated by massive amounts of FPOM, representing between about 2 and 13 years accrual at measured input-output rates.

Inclusion of large wood (generally $>$ 10 cm diameters) in the whole basin estimates changes the input-output balance considerably. Excluding wood-dominated Oregon streams, all basins were estimated to be aggrading with enough storage to account for between 1 and 14 years of accrual at existing input-output rates. By contrast, about 60 years would be required to remove coarse wood in the Oregon basin.

Table 8. Basin characteristics used in calculating order-specific budgets. Stream length-watershed basin relationships as: Watershed area = $(\text{Stream Length})^B$.

Order	No. of Streams	Mean Watershed Area (Km^2)	Mean Length (Km)	Mean Stream Width (m)	Total Channel Area (Km^2)
OREGON					
1	346[a]	0.2	0.96	0.6	0.20
2	87	0.2	1.1	1.8	0.17
3	22[a]	5.2	2.8	3.0	0.18
4	8	0.8	3.0	7.5	0.18
5	3[a]	16.5	6.6	12.0	0.24
6	2	178.9	15.3	26.0	0.80
7	1[a]	484.6	27.9	40.0	1.10
Total	469	484.6	590.9	--	2.87
IDAHO					
1	852	0.2	0.5	0.3	0.13
2	252[a]	0.8	0.8	0.5	0.04
3	63	7.4	2.3	3.2	0.29
4	16[a]	70.6	5.0	6.0	0.26
5	2[a]	738.1	35.0	30.0	1.80
6	1[a]	1238.3	56.0	46.0	0.97
7	--	--	--	--	--
Total	1186	1238.3	728.8	--	3.49
MICHIGAN					
1	80[a]	0.4	0.6	1.5	0.07
2	13[a]	3.4	26.4	6.2	2.13
3	8[a]	3.6	23.1	8.0	1.11
4	2	103.3	148.4	27.8	8.25
5	1[a]	777.3	451.9	47.5	21.50
6	--	--	--	--	--
7	--	--	--	--	--
Total	104	777.3	1275.3	--	33.06

(Contiued)

Table 8. Continued

PENNSYLVANIA

Order	No. of Streams	Mean Watershed Area (Km^2)	Mean Length (Km)	Mean Stream Width (m)	Total Channel Area (Km^2)
1	59[a]	0.3	0.5	1.5	0.04
2	17[a]	0.8	2.5	3.0	0.13
3	6[a]	1.0	5.3	6.2	0.16
4	3[a]	24.5	9.1	11.8	0.32
5	1	37.5	17.7	17.4	0.31
6	--	--	--	--	--
7	--	--	--	--	--
Total	86	37.5	139.7	--	0.96

[a] Stream order for which a sampling site was included in the Continuum study.

[b] Upper Salmon River from headwaters to Yankee Fork.

Table 9. Watershed budgets by stream order for the basins in each of the regional biomes. All values in metric tons carbon per year for all channels of a given stream order in a basin (i.e., Ton C · order n^{-1} · yr^{-1}).

	OREGON	IDAHO	MICHIGAN	PENNSYLVANIA
ORDER 1				
Inputs				
Litter	73.6	3.3	22.7	21.9
Gross Primary Production	3.6	11.2	2.3	2.7
Total	76.6	14.5	25.0	24.6
Outputs				
Transport	39.5	459.6	180.6	38.0
Respiration	8.1	15.2	6.0	5.7
Total	47.6	474.8	186.6	43.7
Storage[a]	142.0	12.7	21.1	8.1
Input-Output[b]	29.0	-445.1	-161.6	-19.1
Years of Storage[c]	4.9	0.1	0.1	0.4
ORDER 2				
Inputs				
Litter	4.8	1.4	471.5	14.8
Gross Primary Production	39.5	459.6	180.6	38.0
Transport[d]	62.1	1.0	319.5	71.2
Total	106.4	464.4	971.6	211.4
Outputs				
Transport	24.1	220.0	27.7	18.8
Respiration	7.6	1.9	473.3	18.5
Total	31.7	221.9	504.0	37.3
Storage[a]	138.9	3.9	949.4	12.1
Input-Output[b]	74.7 (A)	242.5 (A)	476.6 (A)	174.1 (A)
Years of Storage[c]	1.9	0.1	2.0	0.1

(Continued)

Table 9. Continued.

	OREGON	IDAHO	MICHIGAN	PENNSYLVANIA
ORDER 3				
Inputs				
Litter	5.7	13.7	174.3	87.7
Gross Primary Production	7.0	26.0	233.1	72.2
Transport[d]	24.1	220.0	27.7	18.8
Total	96.8	259.7	435.1	178.7
Outputs				
Transport	21.1	531.3	96.9	50.5
Respiration	8.7	22.0	274.2	19.3
Total	29.8	553.3	371.1	69.8
Storage[a]	21.1	24.0	535.0	20.2
Input-Output[b]	67.0	-293.6	64.0	108.9
	(A)	(D)	(A)	(A)
Years of Storage[c]	0.3	0.1	8.4	0.2
ORDER 4				
Inputs				
Litter	65.7	12.3	288.9	175.4
Gross Primary Production	8.5	43.4	2498.1	60.0
Transport[d]	21.1	531.3	96.9	50.5
Total	95.3	587.0	3183.9	285.9
Outputs				
Transport[d]	2.8	131.1	466.0	269.4
Respiration	8.7	26.8	2473.4	60.4
Total	11.5	157.9	2939.4	329.8
Storage[a]	14.1	17.7	3852.8	27.9
Input-Output[b]	83.8	429.1	244.5	-43.9
	(A)	(A)	(A)	(D)
Years of Storage[c]	0.2	0.04	15.8	0.6

	OREGON	IDAHO	MICHIGAN	PENNSYLVANIA
ORDER 5				
Inputs				
Litter	87.6	11.9	850.9	115.1
Gross Primary Production	13.2	376.7	8869.6	74.0
Transport[d]	2.8	131.1	466.0	269.4
Total	103.6	519.7	10186.5	458.5
Outputs				
Transport	86.5	619.9	1245.5	91.6
Respiration	11.5	289.8	7580.9	79.6
Total	98.0	909.7	8826.4	171.2
Storage[a]	9.6	290.7	9718.0	15.0
Input-Output[b]	5.6 (A)	-390.0 (D)	1360.1 (A)	287.3 (A)
Years of Storage[c]	1.7	0.7	7.1	0.1
ORDER 6				
Inputs				
Litter	135.1	14.8		
Gross Primary Production	52.0	101.2		
Transport[d]	86.5	619.9		
Total	273.6	735.9		
Outputs				
Transport	726.4	67.8		
Respiration	43.0	71.3		
Total	769.4	139.1		
Storage[a]	63.6	102.3		
Input-Output[b]	-495.8	596.8 (A)		
Years of Storage[c]	0.1	0.2		

(Continued)

Table 9. Continued.

	OREGON	IDAHO	MICHIGAN	PENNSYLVANIA
ORDER 7				
Inputs				
Litter	120.5			
Gross Primary Production	82.9			
Transport[d]	726.4			
Total	929.8			
Outputs				
Transport	1162.3			
Respiration	65.3			
Total	1227.6			
Storage[a]	42.9			
Input-Output[b]	-297.8			
Years of Storage[c]	0.1			
BASIN TOTAL				
Storage[a]	432.2	451.3	15076.3	83.2
Input	1725.7	2466.0	14650.6	1067.8
Output	3308.3	2337.0	12175.2	680.1
Input Output[b]	-533.8 (D)	139.7 (A)	1983.6 (A)	507.3 (A)
Years of Storage[c]	0.8	3.5	6.1	0.2
Coarse Wood Storage[e]	32350	1537	5309	583
Years of Storage (including wood)	61.4	14.2	10.3	1.3

[a] Storage not including coarse wood (approximately > 10 cm diameter; also fine wood < 10 cm > 2 cm probably underestimated

[b] If output > inputs (I-O = negative value) the system was degrading (D) the year of measurement and generally storage should be small. If output < input (I-O = positive value) the system was aggrading (A) and storage should be large. Balanc inputs and outputs indicated equilibrium (E) for the sample year.

[c] When inputs (I) exceed outputs (O) (I-O) = positive) the years of storage entry indicates length of time that would be required to accumulate the observed storage at the calculated aggradation rate. When outputs exceed inputs (I-O) = negative) the years of storage entry indicates length of time that would be required to remove observed storage at the calculated degradation rate.

[d] This assumes that all transport measured in stream order n-1 is input for stream order n.

[e] Coarse wood approximately > 10 cm volumes estimated by separate inventories. Annual coarse wood export from basin assumed = 0.

ECOSYSTEM COMPARISONS

Despite the problems in calculating stream budget-derived efficiencies, lotic researchers (e.g., Fisher and Likens, 1973; Bormann et al., 1974; Bormann and Likens, 1979) have joined system ecologists in making efficiency calculations (Reichle, 1975; Reichle et al., 1975; Webster et al., 1975; O'Neill et al., 1975). The importance of allochthonous inputs and the unidirectional flow of running waters make comparisons of streams with terrestrial and lentic systems difficult, although steep sloping terrestrial systems also exhibit unidirectional "flow". Streams are not mere conduits which export terrestrial products from watersheds, but, as with other systems, are physically retentive and biologically active. Organic matter and inorganic nutrients are partially cycled within a given reach of stream or river with some portion being released to the reach below or retained in storage (Elwood et al., 1982; Minshall et al., 1983; Newbold et al., 1982). If the terrestrial community through which a stream flows accumulates organic matter over long periods of time, the stream should behave in a generally similar fashion, although specific processing rates and storage capacities would differ.

If comparisons of lotic with terrestrial ecosystems are made on the basis of net ecosystem production (NEP; Reichle, 1975; Reichle et al., 1975), particulate and dissolved organic matter inputs (I) must be included in the stream calculations. The comparative relationships would be (Batzli, 1974):

$$\text{Terrestrial NEP} = GPP - R_E$$

$$\text{Stream (aquatic) NEP} = [GPP + I] - [R_E + E] = \Delta S,$$

where GPP = gross primary production, R_E = ecosystem respiration, E = organic matter exports, and ΔS = change in storage pools Based on measurements made on WS10, net ecosystem production can be calculated as:

$$NEP = (90 + 3612) - (1053 + 1651) = 988 \text{ Kcal m}^{-2} \text{ yr}^{-1}$$

(mean of actual measurement of ΔS = 806 Kcal m^{-2} yr^{-1})

If ecosystem productivity is calculated as NEP divided by GPP + I (Reichle, 1975; Reichle et al., 1975), the value is 0.27 for WS10, higher than for various terrestrial communities (0.05 - 0.24 [Reichle et al., 1975]) and in the range for lakes (0.30 - 0.53, calculated from Wissmar, unpublished data, University of Washington). However, given the uncertainties of budget measurements in streams, particularly temporal and spatial variations in storage, the calculation of such ecosystem parameters will require very extensive data sets. Also, the range of values through the drainage net (Vannote et al., 1980) would predictably cover at least as wide a range as terrestrial systems, particularly since stream system differences are compounded by varying degrees of terrestrial (riparian) influence. Nevertheless, when adequate data permit it, within and between ecosystem comparisons of material balance budgets should provide useful insights into system function.

DISCUSSION

As pointed out initially, a primary objective of stream organic budget assessments has been the determination of ecosystem functional properties, which would allow comparisons within and between biomes. Because of the temporal and spatial problems inherent in material balance budgets for organic matter in streams, the results can be ambiguous and misleading. For example, budgets constructed primarily from export data are more a feature of physical retention characteristics than biological function. Therefore, present budget-derived perceptions of stream ecosystem efficiency are dependent on storage and export phenomena which tend to obscure the significance of biological processes. Since organic matter budgets for streams have been used in the calculation in efficiencies employed in ecosystem comparisons, the conclusions resulting from such comparisons must be evaluated carefully.

The basic problem with existing organic budgets is that the steady state, or dynamic equilibrium, that is the range over which the parameters fluctuate, is not time invariant (Botkin and Sobel, 1975) for running water systems. Depending upon the time frame of reference, flood events of different magnitude can be variously considered as perturbations that displace streams from stable trajectories or as fundamental ecosystem features and, therefore, within the boundary conditions (i.e., variance) of the trajectory. Major components of lotic ecosystems, such as organic storage, are largely dependent on the timing and magnitude of discharge events, and periodic adjustments in the size of the organic storage pool are features of the system, not perturbations (e.g., Dawson, 1980). Since any definition of a steady state or dynamic equilibrium condition for stream ecosystems is highly time dependent, so are the boundary conditions for "normal stability." Therefore, the concepts of a system's resistance to, and resilience after, a change (Webster et al., 1975, this volume), for example in storage, must be so narrowly defined for a given running water system that their general usefulness may be significantly reduced.

As we have shown, existing material balance budgets for streams reflect physical transport and storage characteristics to a much greater extent than the metabolic properties of the stream ecosystem. The large majority of materials are exported during flows which occur for less than ten percent of the time. Since flows vary from year to year, time dependent budgets are not useful unless they have been constructed over a long period (possibly ten years or more). While organic budgets have been useful in showing the retentive capacity of streams to be fairly efficient, the separation of the metabolic properties of the ecosystem from the physical hydraulic ones has yet to be done. Flood transported organic particulate matter is seldom quantified nor is the rate of decomposition of the material estimated. For example, the origin of major exports from a watershed (or basin) may be from outside the channel or in other deep storage pools that are characterized by minimal biological activity. Also, the passage of the material may be so rapid as to preclude significant biological response.

A flow-dependent analysis is available (e.g., Sedell et al., 1978) which might prove useful in characterizing organic transport between reaches and allow for the interpretation of the variability between geomorphic setting and hydrologic regime. An additional advantage is that one runoff season would be sufficient if representative flows are monitored. Since the sediment and water moving through a stream channel are the primary independent variables influencing channel morphology, quantitative relations have been established between water and sediment and all aspects of channel morphology such as dimension, shape, gradient, and pattern have been related to stream discharge. The ability of water to do work, or stream energy, combined with a measure of reach retention might serve as a suitable common denominator for comparing differences in organic transport and storage characteristics between streams (Minshall et al., 1983).

Geomorphologists and hydrologists (Leopold et al., 1968; Pfankuch, 1975) have shown a relationship between stream energy and the size of suspended and bedload inorganic material transported by streams. Stream power, defined in terms of discharge, percent channel slope, and density (or mass) of water per unit channel width (Leopold and Langbein, 1962; Langbein and Leopold, 1964; Leopold et al., 1968), seems to be a logical unit for comparing streams of different sizes. However, the power expression needs to be scaled with a roughness term to account for a stream's retention characteristics prior to plotting against biological parameters (e.g., primary production). Some empirically derived scaling system for retention is badly needed (see Minshall et al., 1983 for possible approaches).

Further evaluation of ecosystem properties will come with improved understanding of storage dynamics. Input-output dynamics of the storage pools in aquatic ecosystems need to be examined in terms of 1) the frequency and magnitude of events which reset the quantity and composition of material in storage, 2) the relationship between the source of exported material, its movement through a system and the stream biological response time (for example, if material that was rarely or ever in the channel is moved through and out of a watershed at a rate that does not allow for significant biological activity (Meyer and Likens, 1979), its inclusion in biologically oriented budget calculations is not warranted and 3) the more continuous, low level leakage in and out of a storage compartment between major turnover events, and the internal processing dynamics of each storage pool should be evaluated in relation to temperature, substrate quality, conditioning (microbial colonization and metabolism of the organic substrates), and oxygen environment.

CONCLUSIONS

Many of the problems with organic matter budgets discussed in this paper suggest that the field of stream ecology will not benefit from the development of budgets for numerous systems based on short-term (1-2 yr) records and in which some key parameters are determined by difference. Small-scale research programs should focus on comparisons of selected processes between diverse stream ecosystems rather than attempt to determine whole system budgets. What is needed is the determination of total stream ecosystem budgets at a few selected sites where existing long-term data sets can be continued and augmented by improved monitoring of storage dynamics.

These studies should view the system on scales appropriate to system behavior. For example, log dynamics must be viewed on the time-scale of decades and centuries, but this does not mean that the studies themselves must be of this duration. Using dendrochronologic and mapping methods, it is possible to reconstruct histories of debris inputs to, and catastrophic export from, streams for periods up to more than a centruy (Sigafoos, 1964; Swanson et al., 1976). Improved understanding of storage dynamics will arise from other types of studies not commonly a part of budget development. Such studies include long-term monitoring of decomposition by repeated sampling of marked organic materials placed on the stream bed and in the sediment. There is also a particular need for study of the effects of flood on the storage and biota in streams. Stream ecologists need to be opportunistic and prepared to respond to infrequent episodic events.

Floods, large debris in streams, and major changes in storage are elements of fluvial geomorphology. It is geomorphic processes and features which establish the physical template on which stream biology is developed and maintained. Future progress in stream ecosystem analysis will be dependent in large measure on the ability of stream ecologists to incorporate understanding of physical and historical processes into models of lotic ecosystem behavior and functioning.

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