Elemental dynamics in streams*

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Abstract. We discuss elemental dynamics in streams and seek to identify areas where there are critical gaps in our understanding. Both landscape-level processes (e.g., geology, land-use practices, vegetation) and heterogeneous in-stream processes influence the supply and availability of elements to the stream biota. Stream ecologists need to consider the relative availability of different compounds or groups of compounds to the biota rather than lumping all forms of an element into operationally-defined units such as dissolved organic nitrogen or carbon. The impact of short-term events like storms on the elemental dynamics in streams needs to be assessed and compared with other controls. The relative importance of longitudinal (upstream), lateral (riparian zone, floodplains), and in-stream controls of supply and availability of elements needs to be compared in a variety of streams. Availability of essential elements is a key factor controlling rates of primary productivity and decomposition in streams. Whole system manipulations offer a valuable tool for understanding the interactions between elements and all components of the stream food web. We include an action plan of developments that would assist researchers in addressing some of the critical gaps we have identified in our understanding of elemental dynamics in streams.

Key words: nutrients, elements, streams, spiraling, dissolved organic carbon, nitrogen, phosphorus.

In this paper we discuss ideas on elemental dynamics in streams and point out critical gaps in our understanding of the dynamics of dissolved organic carbon (DOC) and dissolved and particulate forms of nutrients such as nitrogen and phosphorus in both streams and rivers. We first discuss controls on the supply and availability of elements in streams and then examine processes that are regulated by supply and availability. We conclude with some suggestions for new programs that could stimulate progress in stream ecology. This paper is not intended as a comprehensive review of elemental or organic matter dynamics in streams; our intent is to stimulate further discussion and new research.

There are several compelling reasons for considering cycling of elements in streams. First, to the extent that nutrients are limiting in streams, they regulate the rates at which important ecological processes such as primary productivity or decomposition proceed; changes in these rates result in alterations of stream community structure (e.g., Elwood et al. 1981, Peterson et al. 1985). Changes in macroinvertebrate community structure will also have an
Elemental Dynamics in Streams

Effect on elemental dynamics; e.g., the maintenance of high algal productivity but low biomass by grazers will influence rates of nutrient uptake. The interaction between elemental and community dynamics is a major focus of this discussion.

A second reason to consider elemental dynamics in streams is that elements link aquatic and terrestrial ecosystems, and in-stream processes are sensitive to watershed alterations. The supply of elements to streams in all latitudes varies with the geologic setting of the watershed and with its plant community (e.g., Bott et al. 1984, Furch 1984, Lay and Ward 1987, Sioli 1975, Stallard 1985, Stallard and Edmond 1983). The role of riparian vegetation in regulating the nutrient economy of streams deserves special study. Natural and anthropogenic disturbance of the terrestrial ecosystem leads to changes in the amount of nutrients entering streams (e.g., Correll et al. 1984, Dillon and Kirchner 1975, Jordan 1987, Likens et al. 1970, Peterjohn and Correll 1984, Webster et al. 1983, Weller et al. 1986). These watershed-stream interactions have been documented in numerous reports, and this paper provides only a broad summary.

A third reason is that within-stream processes can alter the timing, magnitude, and form of elemental fluxes to downstream ecosystems (Meyer and Likens 1979, Rigler 1979), thereby influencing the availability of the element to biological communities downstream in rivers, lakes, and estuaries.

A fourth, DOC dynamics are included here because of the importance of DOC in stream energy budgets. In most streams and rivers allochthonous inputs of carbon are important energy resources for the stream community. DOC is often a major form of allochthonous carbon (e.g., Fisher and Likens 1973), but can also be derived from autochthonous sources (Kaplan and Bott 1982). Allochthonous and autochthonous DOC fuel a microbial food web in streams (e.g., Edwards and Meyer 1987b, Lock et al. 1984, Meyer et al. 1987a, 1987b, Rounick et al. 1982), and the importance of that food web relative to other energy flow pathways needs careful study.

Fifth, many of the anthropogenic assaults on streams have been nutrient additions leading to major alterations of the stream community (e.g., Ball and Bahr 1974, Hynes 1969, Wurmann 1972). In addition, streams supply the water needed by many communities and industries, and the suitability of that water is often dependent on the capacity of streams to remove nutrients added as wastes upstream, or in other words, on the elemental cycling in the stream.

Controls on elemental supply and availability

In this section we discuss factors that influence the rate of supply of nutrients and organic carbon to streams. We begin with processes operating at the level of the landscape and then consider the potential significance of short-term events like storms in determining supply and availability of elements. We then discuss the relative significance of longitudinal and lateral linkages as well as internal recycling as processes influencing elemental dynamics. We conclude this section with a discussion of the spiraling concept. The major processes considered in our discussion of elemental dynamics are diagrammed in Figure 1.

Throughout this discussion we emphasize factors that control the availability of elements to the biological community. It is critical that stream ecologists move beyond lumping all organic forms of an element together (e.g., as DOC or dissolved organic nitrogen [DON]), and recognize that only a small portion of the compounds composing the DOC, DON, or dissolved organic phosphorus (DOP) pools in a system are available to the biota. We should be considering those compounds that will have the greatest influence on the biotic community. As ecologists, we need to approach chemistry from the perspective of stream organisms and develop ways to characterize the bioavailability of compounds or classes of compounds. Organic forms of critical elements are the most abundant form in many streams. In Walker Branch, Tennessee, 30–50% of dissolved P does not react with molybdate and hence is assumed to be DOP (Segars et al. 1986), and 50% of the dissolved N export is DON (Henderson and Harris 1975); in the Kuparuk River, Alaska, 92% of dissolved N is DON (B. J. Peterson, unpublished data); DOP accounts for 45–55% of the total P in streams draining forested watersheds in the U.S. (Omernik 1977). Despite their predominance, we know little about the relative abundance of those organic compounds that stimulate biological
growth, those involved in allelopathic interactions, and those which are recalcitrant or essentially inactive. This knowledge is crucial to an accurate assessment of elemental interactions with the biotic community.

Landscape processes and in-stream heterogeneity influence elemental supply and availability

The major controls on element supply to a stream include watershed geology and hydrology, soil processes, land-use practices, landscape vegetation, and atmospheric loading. These factors vary both within and between latitudes. Considerable information about these influences exists for temperate streams, but less is known about arctic or most tropical systems. For the Amazon basin, the effects of watershed geology have been well-documented (e.g., Sioli 1984). In the Arctic, dramatic (ten-fold) differences in nitrate supply are observed in similar-sized tributaries draining different types of tundra ecosystems (B. J. Peterson, unpublished data). In North American streams, total phosphorus content of streamwater is greater in watersheds draining sedimentary rocks than in those with granitic geology, and considerably greater in streams in urbanized and agricultural rather than forested watersheds (Dillon and Kirchner 1975, Omernik 1977). Clearcutting forests has resulted in increased concentrations of nitrates in streamwater in a variety of watersheds (e.g., Likens et al. 1970, Swank and Douglass 1975). Increased atmospheric loading of hydrogen ions has resulted in decreased pH of streams in North America and Europe (Cosby et al. 1985, Kramer et al. 1986, Mason and Seip 1985). In highly weathered tropical soils, the influx of elements from the atmosphere may be the major net source of elements; the amount of elements reaching the stream will depend upon the utilization capabilities of the vegetation (Kellman et al. 1982). Despite the potential significance of atmospheric deposition of elements to many tropical ecosystems, there are as yet few data with which to determine its importance.

These watershed- or landscape-level processes define the overall supply of elements to a stream and provide the framework within which other processes operate on smaller spatial scales and shorter temporal scales to regulate supply and availability. A stream represents a spatially diverse nutrient environment, which is a reflection of landscape processes, the patchy na-
ture of streambed habitats, and in-stream biological activity. Numerous studies have demonstrated changes in concentrations of nutrients and DOC over short distances in streams (e.g., Johnson et al. 1981, Kaplan et al. 1980, Meyer and Tate 1983, Segars et al. 1986). In addition, patches of nutrient- or DOC-rich sediment may develop in response to localized concentrations of organic matter or seepage of groundwater; algal and bacterial communities respond to these (Crocker and Meyer 1987, Meyer et al. 1987b, Pringle 1985, Pringle and Bowers 1984, Pringle et al. 1986). Hence it is inappropriate to consider only the nutrient environment of the water when evaluating the nutrient supply of a stream.

A temporal perspective: the relative importance of short-term events

Much of the emphasis in studies of elemental dynamics in streams has been on those processes that release nutrients and DOC and supply them to streams. Variation in rates of elemental supply to streams occurs on temporal scales ranging from hours to decades. We know most about seasonal and annual patterns and least about longer term (e.g., decade) and diel changes. Because stream chemistry reflects the landscape which it drains, long-term changes in the landscape may result in changes in stream chemistry. On a geologic time scale, weathering of a watershed is likely to alter the element economy of drainage systems. On a shorter time frame, anthropogenic impacts such as acidification of precipitation may also result in changes in elemental concentrations in streams. Such changes are difficult to detect owing to the need for a long-term continuous data base. Long-term changes in stream chemistry have been observed in New Hampshire; for example, magnesium concentration has decreased ~20% in 20 years (Likens et al. 1985). Although the cause of this decrease is not certain, it is likely related to acidic deposition and associated changes in ion exchange and/or weathering in the watershed.

The rates of terrestrial processes such as rock weathering, elemental uptake by the vegetation, and leaching of soil organic matter, and in-stream processes such as excretion of organics by algae may vary seasonally leading to changes in elemental supply rates. For example, in streams at Hubbard Brook Experimental Forest, New Hampshire and Walker Branch, Tennessee, nitrate supply to the stream is greater during the winter because of the absence of uptake by the terrestrial vegetation (Elwood and Turner 1988, Likens et al. 1977). In White Clay Creek, Pennsylvania, spring algal growth leads to diel pulses of DOC (Kaplan and Bott 1982). The Caroni River, Venezuela, exhibits large seasonal fluctuations in DOC concentration (Paolini et al. 1983), whereas in the Caura River, Venezuela, DOC, total N, and total P concentrations show little seasonal change despite major seasonal changes in discharge (Lewis 1986, Lewis et al. 1986). The proportion of the total element standing stock available to the biota also probably varies seasonally, but this is an area where more work is needed. Examination of changes in the proportion of element standing stock available to the biota over a variety of temporal scales will be a fruitful area for future research.

How important to the biota of streams are the less dramatic but longer-lasting seasonal shifts in supply of elements relative to the more dramatic but short-term changes seen during pulsed events like storms? We don't have sufficient data to provide a good answer to that question. In one sense, concentration at baseflow is what supports production, and hence slight seasonal changes in concentration may have a major effect. On the other hand, storms may serve as an element subsidy by mobilizing previously unavailable nutrient sources, and nutrients taken up during short periods of elevated concentration may support growth over several days. The distinction between a disturbance and a subsidy is unclear. Increased flows of low magnitude but short recurrence interval may provide elemental inputs that subsidize the community between major events. Larger storms with longer recurrence intervals may be disturbances because they scour the community and remove much of the nutrient capital associated with benthic organic matter. Are there thresholds for spates above which the short- and long-term system productivity is decreased, but below which it is enhanced? This question of the role of storms on the elemental dynamics of streams is part of the larger group of questions on the impact of disturbance on streams addressed by Resh et al. (1988—see this issue). It is a question requiring further research.

Changes in element concentration with stream discharge have been documented in nu-
merous studies. In Table 1 we summarize data on element relationships with discharge for 13 constituents in 12 drainages in latitudes ranging from 68°N to the equator. There are no consistent changes in the relationships with latitude. One of the most striking features of the table is the variation observed between elements and streams. In most streams NH$_4$ concentration does not change with discharge, whereas DOC, particulate organic carbon (POC), total phosphorus (TP), and suspended sediments consistently increase. The increases in POC, TP, and suspended sediments are a consequence of increased ability to erode and to keep particulate matter suspended at higher flows. Depending on the stream being sampled, soluble reactive phosphorus (SRP), Mg, Ca, SO$_4$, and NO$_3$ concentrations either increase, decrease, or remain constant as discharge changes. In two streams, the relationship between NO$_3$ concentration and discharge varies between storms; Na and K also show between-storm variability. In general, Na concentration and pH either are constant or decrease with increasing discharge. Potassium concentration is either constant or positively related to discharge.

The variability in relationships between concentration and discharge that is clearly shown in Table 1 is to be expected because data collected from several streams in the same basin vary considerably (D. L. Correll, Smithsonian Environmental Research Center, personal communication). Within the Rhode River watershed the pattern changes with magnitude of the storm, season, year, and even time since last rainfall. Adjacent watersheds exhibit different patterns based on differences in topography or land use. Even the method of sampling (e.g., grab vs. flow-weighted) alters the apparent pattern. Thus, although we may see general patterns emerging within data sets, the variation is large. Some of the variation is also associated with the different flow paths of water through the watershed. For example, in Walker Branch calcium and magnesium concentrations decline with increasing discharge because of dilution of groundwater that has been in contact with the dolomitic bedrock by quick-flow soil water that has not. Sulfate increases as a result of the input of soil water flowing through the upper soil horizons where the sulfate adsorption capacity is low, sulfate retention is minimal, and water soluble sulfate levels in soil are high (Elwood and Turner 1988).

Although our data base on variation of elemental concentration with discharge is extensive, we know little about how changes in discharge affect concentrations of biologically available forms of critical elements. For example, although the concentration of DOC increases with discharge in 11 of the 12 streams listed in Table 1, we do not know if all forms of DOC increase or if, for example, the refractory forms increase to a greater extent than the more labile ones. In Bear Brook, New Hampshire, carbohydrate concentration did not increase as rapidly as total DOC with discharge, suggesting dilution of labile DOC during storms (McDowell and Likens 1988). We need to clarify the relationship between the pool of biologically available elements, the total element pool, and the elements washed downstream during storms. This area of stream ecology will likely benefit from the application of new analytical methods, such as measuring specific forms of DOC and speciation of key elements. To understand linkages between elements, biota, and suspended particles, it will be important to assess how the biological availability of elements varies with stream discharge.

We also know little about the effect of storm-induced fluxes of elements on the biological community. Do storm-generated nutrient pulses initiate important processes such as algal reproduction? Are storms a nutrient subsidy for the community or a nutrient loss? The answer probably varies with both the intensity of the storm and the season in which it occurs. A low magnitude storm will probably not scour the streambed, but can supply or mobilize nutrients in the channel; a high magnitude storm can erode nutrient-depleted surface layers of rock or organic matter, but may also destroy most of the biotic community. For example, in White Clay Creek, Pennsylvania, a light rain on freshly fallen leaves increased DOC concentration from <2 to >5 mg C/L, stimulating bacterial production; but heavy rains scour the streambed community (T. L. Bott and L. A. Kaplan, unpublished data). The exchange of materials between the channel and interstitial zone is often controlled by the volume of water in the channel (i.e., the pressure head); hence at higher flows, the flux of materials to the hyporheos will probably increase. A small storm may have little impact on the hyporheic zone, a moderate storm may pump more material into it, but an
TABLE 1. The relationship between element concentration and stream discharge in a variety of streams over a range of latitudes. A "+" indicates that element concentration increases with increasing discharge, "−" indicates that concentration decreases, and "0" indicates that there is no change in concentration with discharge. More than one symbol is used when the relationship between concentration and discharge varies between storms.

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<thead>
<tr>
<th>Stream order</th>
<th>Latitude (°N)</th>
<th>Nitrate</th>
<th>Ammonium</th>
<th>Soluble reactive phosphorus</th>
<th>Total phosphorus</th>
<th>Dissolved organic carbon</th>
<th>Particulate organic carbon</th>
<th>Suspended sediments</th>
<th>Sodium</th>
<th>Potassium</th>
<th>Magnesium</th>
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* Data set from grab samples during storms.

† Asymptotic above 1.1 m/s.

3. Lewis and Grant 1979.
eroding storm will wash out pockets of organic matter and nutrients that have accumulated since the last storm in protected sediment environments. The impact of storms on the sediment community will depend on the depth of scour relative to the extent of the hyporheos.

The effect of high discharges on element dynamics will vary depending on the major pathways for element uptake in the stream. For example, the uptake length for phosphorus in Walker Branch varies seasonally with the standing stock of coarse particulate organic matter, and generally increases after storms owing to the loss of organic matter from the stream bed during the storm (Mulholland et al. 1985b). This organic matter is the dominant sink for dissolved phosphorus in this stream. Uptake length is not very responsive to changes in epilithic algal standing stock in Walker Branch; the mass-specific uptake rate of epilithic algae is high, but their biomass is low (Newbold et al. 1983). In an unshaded stream where the algal component of phosphorus uptake may be more important, the algal response to storms should regulate changes in nutrient dynamics. We need more information on these types of storm effect for a range of elements and streams.

The effect of storms will also vary depending on the relative importance of particulate and dissolved forms of the element of interest. Particle concentration increases during storms in most streams (Table 1). Hence an element like phosphorus, which is found primarily in the particulate phase, will be lost disproportionately during storms (e.g., Meyer and Likens 1979). Storms may also have important consequences for particle-associated microbiota. For example, in the Rhode River, most bacteria in the water column are not attached to particles (Rublee et al. 1984) and about three orders of magnitude lower in concentration than in the underlying silty sediments where bacteria are mostly attached to particles (Rublee et al. 1983). When sediment resuspension occurs during storms, significant bacterial biomass and activity are then associated with particles (Rublee et al. 1984). Similar changes in particle-bound bacteria have also been observed in headwater streams (Palumbo et al. 1987). In contrast, in a subtropical blackwater river with an extensive floodplain, the proportion of particle-associated bacteria remains small even during floods, presumably because large numbers of unattached and inactive bacteria are washed from floodplain soils during inundation (Edwards 1987, Edwards and Meyer 1986). Thus in streams without extensive floodplains, storms may inject particle-bound and metabolically active bacteria into the water column and subsequently displace them downstream or wash them out of the system.

Geomorphology has a major impact on particle transport and hence also on elemental dynamics in streams. Retention devices like debris dams are critical in retaining particulate organic matter in streams (e.g., Bilby and Likens 1980), and the amount of organic matter is a key determinant of the stream's ability to remove dissolved elements from solution (Mulholland et al. 1985b). But are these sites of organic matter storage also major sites of nutrient regeneration? And how do geomorphic features such as gradient or riffle:pool ratio influence particle transport and hence organic matter storage and the capacity for retention of dissolved elements in flowing waters? These questions are as yet unanswered.

The effects of storms on elemental cycling will also be influenced by the season in which they occur and by the extent and nature of the floodplain. Floodplains can increase the retention of the system for dissolved and particulate nutrients as a consequence of the larger storage volume, more circuitous routing, and greater biotic and abiotic sorption than occurs in the stream itself.

Although many questions still remain about the influence of increases in discharge on elemental dynamics, we know considerably more about the influence of these events than about the influence of drought. Studies on intermittent streams have shown that drying will have a profound impact on the insect community. Immediately after rewetting, the invertebrate community of a seasonally dry stream is different from that of the perennial stream, but converges to that of the perennial stream with time (Delucchi 1988). We know little about the impact of drying, rewetting, and changes in the invertebrate community on the nutrient economy of these streams; yet a periodic drought may be a greater disturbance than a spate.

A spatial perspective: longitudinal vs. lateral controls on elemental dynamics

A central tenet of the River Continuum Concept is that community structure and function
are dominated by upstream processing, i.e., longitudinal linkages in the ecosystem are strong (Minshall et al. 1983, Vannote et al. 1980). However, the relative importance of lateral influences (floodplain or riparian zone), upstream linkages, and internal recycling (e.g., within biofilms or between deep and surface sediments) have not been sufficiently well examined to provide a real test of the concept. For example, does retention of elements in upstream reaches lead to nutrient limitation downstream? If lateral inputs from the riparian zone or regeneration of nutrients within the reach are important sources of biologically available nutrients at a point in the stream, then the retention of nutrients upstream will have only a minor impact. In that case the structure of the upstream community will have little influence on processes occurring downstream.

Strong longitudinal linkages have been demonstrated in some streams. For example, in Sycamore Creek, Arizona, uptake of nitrogen upstream leads to blue-green algae dominating the algal community downstream (Fisher et al. 1982). In Walker Branch, SRP concentration declines downstream from major groundwater seeps because of uptake or conversion of SRP within the stream channel in fall and winter (Segars et al. 1986). Hence the supply of P to downstream communities is reduced by the uptake of P in upstream reaches. If the P taken up by detritus upstream is regenerated into the water, then retention may act as a stabilizing influence on the P supply. However, if the P taken up by the detritus is washed out or released back to the water in a less available form, it represents a permanent sink of P for upstream communities and a potential source of P to downstream communities if it is converted to an available form downstream. The temporal and spatial scales at which one considers the question of elemental uptake, storage, and transport thus become important. The relative importance of lateral vs. longitudinal vs. internal controls on available nutrients will also vary temporally. For example, under drought conditions, internal recycling of elements in a reach would presumably become a more important source of available nutrients than upstream sources.

The regeneration/mineralization of nutrients in streams is an area in need of process-level work to determine the rate of regeneration, the forms of regenerated nutrients, and their biological availability. For example, approximately half the phosphorus taken up by leaf detritus in a heterotrophic laboratory stream channel was retained in the detritus and half was lost either by regeneration to soluble P, grazing, or sloughing (Elwood et al. 1988). The effect of these processes on the supply of P to downstream systems depends on the biological availability of the regenerated P and the permanence with which P is retained by detritus. Some regenerated P appears to be less available to microbes than orthophosphate (Mulholland et al. 1988), thereby reducing the supply of available P to downstream communities. This needs to be examined in a greater variety of streams and in relation to size spectra and composition of inorganic particles.

Clearly lateral input from natural or anthropogenic sources can be important for lotic communities at all scales. The potential for increased importance of lateral inputs and decreased importance of longitudinal linkages is great in rivers with extensive floodplains. Fisheries workers have documented a positive relationship between fish production and flooding intensity both within and between rivers (e.g., Moses 1987, Welcomme 1985). Less is known of the impact of floodplain extent and nature on the nutrient economy of streams. Two lines of evidence suggest that the Amazon floodplain is an important source of the carbon to the river: its tributaries do not provide adequate organic matter to support observed levels of respiration in the river (Sedell and Richey 1988), and measures of floodplain production, respiration, and decomposition suggest that 11% of carbon fixed annually is exported to the river (Junk 1985). In general, watersheds with associated floodplains and wetland export more organic matter than drainages without wetlands (Schlesinger and Melack 1981), attesting to the importance of lateral inputs in these systems. Riparian wetlands will also influence the nutrient economy of the fluvial ecosystem through their retention of nitrogen and phosphorus (Mitch and Gosselink 1986).

In rivers with extensive floodplains a greater surface area is exposed, and hence atmospheric interactions are probably of greater importance. Methanogenesis is very active in tropical floodplains such as those bordering the Amazon, and efflux of methane from these wetlands makes a notable contribution to tropospheric methane (Bartlett et al. 1988). Processes such as nitrogen fixation and denitrification can greatly influ-
ence the nitrogen economy of all flowing waters, yet we have little comparative data from a diversity of systems on rates of these processes. In Oregon headwater streams, N fixation accounted for only 5% of total N inputs (Triska et al. 1984), but in an unshaded California stream, high rates of N fixation were measured (Horne 1975, Horne and Carmiggelt 1975). In Oklahoma streams grazing activities of fishes lead to an algal community with abundant blue-greens, and hence the potential for high rates of nitrogen fixation (Power et al. 1985). Denitrification was found to be a significant nitrogen sink in southern Appalachian streams (Swank and Caskey 1982) and in a nitrate-enriched Canadian river (Hill 1979, 1983). These processes vary considerably within a single stream; hence we anticipate variation in the rates and importance of processes like nitrogen fixation and denitrification will be as great within as between latitudes.

Elemental dynamics in a stream may also be influenced by the riparian vegetation (Peterjohn and Correll 1984). The riparian forest removed 82% of dissolved N, 54% of dissolved P, and 42% of dissolved Ca draining into a Georgia Coastal Plain stream with an agricultural watershed (Todd et al. 1983). Trees with nitrogen-fixing symbionts are a common feature of many riparian zones; in southern Appalachian watersheds dominated by the nitrogen-fixing black locust (*Robinia pseudoacacia*), nitrate concentrations are higher than in adjacent reference watersheds, and leaf decomposition rates are accelerated by this additional nitrogen (Meyer and Johnson 1983). The strength of these types of lateral linkages needs to be assessed with respect to the longitudinal linkages discussed earlier.

**Recycling of elements within a stream reach**

The relative importance of external vs. internal sources of elements (regenerated nutrients) needs to be assessed in terms of the biotic community. How much of the biological demand for nutrients is met by recycling vs. external loading? This question has been central to many studies of nutrient dynamics in lake and marine systems (e.g., Eppley and Peterson 1979), but has not been adequately addressed in streams. The answer will vary depending on the element being considered and the stream. It may also vary temporally and with position in the stream network.

The extent of biotic regulation of elemental supply and availability needs to be compared with the impact of factors such as storms and seasonal changes in element supply rates. For example, how does the impact of grazers on the nutrient economy of a stream compare with the impact of the ten-year flood? Assessments of the impact of biotic and abiotic controls on stream elemental dynamics are critically needed in streams spanning a range of latitude and disturbance regimes.

The active and diverse community of macrofaunal, meiofaunal, and microfaunal consumers is likely to have a significant effect on nutrient availability in streams. This is a subject in need of further attention. For example, in streams where relatively large consumers like fish or snails are abundant, their feces may prove to be a key link in nutrient cycles (W. J. Matthews, University of Oklahoma, personal communication). Meio- and microfaunal contributions to stream nutrient dynamics will be an important area for further research. These organisms have been demonstrated to be important remineralizers in other ecosystems (Barsdate et al. 1974, Fenchel 1970, Johannes 1965); their importance in sediment-dominated systems like streams needs to be assessed. It is likely that the importance of faunal remineralization will vary with the nature of the sediments, particularly grain size, because of its impact on the composition of the fauna. In other aquatic systems, microflagellates predominate in fine-grained sediments, ciliates in coarser-grained sediments, and nematodes in sediments with high silt and clay content (Fenchel 1978).

The microbial food loop (sensu Pomeroy 1974) needs to be examined in sediment-dominated systems like streams. In some pelagic systems the microbial loop appears to be a sink for carbon (Ducklow et al. 1986, but see also Sherr et al. 1987), but a regenerator of other nutrients (Goldman and Caron 1985). In sediments, the reverse may be true. In streams most of the bacterial biomass is found in the sediments, even in larger rivers (Meyer et al. 1987b). Where the bacteria are particle-bound, the loop may be a more direct link in the food web because larger consumers can ingest small microbes as a "sandwich" of some biomass and a lot of detritus; hence microbes are available to larger organ-
isms with fewer trophic transfers. For example, bacteria on decomposing leaves are directly available to leaf-shredding insects, although their biomass does not appear to be a major carbon source for the insects (Findlay et al. 1986). Bacterivorous meiofauna such as copepods are abundant in stream sediments (O'Doherty 1985), and these copepods are found in the guts of macroinvertebrates like dragonflies (Wallace et al. 1987). In addition, many stream-dwelling, filter-feeding macrofauna (e.g., black flies) have the capacity to remove bacteria-sized particles from the water (e.g., Edwards and Meyer 1987b, Wotton 1980). Hence the bacteria are converted into larger morsels of food with few trophic transfers and therefore greater efficiency. The nutrient regenerating function of the loop will be influenced by the nature of the sediment, in particular its ability to sequester nutrients. Nutrients regenerated in the sediments are vulnerable to abiotic sorption processes, and hence a smaller portion may be available to supply biotic needs than in the water column. These ideas need to be pursued.

Critical interfaces for the control of elemental dynamics in streams appear to be floodplains or riparian zones, biofilms (e.g., epilithon), and the sediment–water interface. Because of sharp gradients in physical and chemical parameters (e.g., pH, \( E_h \), oxygen) that can exist at these interfaces, they can be exceedingly important in regulating elemental flux. Work needs to be done in these ecotones (cf. Naiman et al. 1988 and Pringle et al. 1988—both in this issue). For example, the relative importance of sediment and overlying waters as sources of elements for epilithic and epipsammic biofilm communities has been examined (Bott et al. 1984, Pringle 1987, Pringle and Bowers 1984) and deserves further attention. The intimate relationships between primary producers, heterotrophic microorganisms, and consumers within the aufwuchs suggest that within-biofilm interactions as well as biofilm–water column exchanges will have an impact on elemental dynamics in streams.

The hyporheos constitutes an important reservoir of nutrients and organic matter, and its role in the nutrient economy of streams is worthy of further investigation. The hyporheos is a patchy environment, as discussed earlier; variation in nutrient and DOC concentration, oxygen content, and flow regime is considerable (Hynes 1983, Rutherford and Hynes 1987). The abundant organisms in this habitat are supported by allochthonous organic matter processed by an active biofilm community of bacteria and fungi rather than primary producers (e.g., Bretschko and Leichtfried 1988, J. A. Stanford, University of Montana, unpublished data); these organisms will probably be more significant than algae in nutrient dynamics in this zone. The hyporheic biofilm community appears to be surface-area limited (Leichtfried 1985). Lateral inputs of dissolved substances from the watershed or riparian zone frequently pass through the hyporheic zone; in some instances DOC seems to be largely consumed in the hyporheos before it reaches the overlying water (Wallis et al. 1981). Exchanges of dissolved and particulate substances between surface water and hyporheos are probably discharge dependent, although this is a subject on which more research is needed. Metabolic activity is considerable in the deep sediments of some streams (e.g., Grimm and Fisher 1984, Meyer 1988), and hence one would expect that biological activity in the hyporheos would have a profound influence on elemental dynamics in the stream as a whole. Our data in this area are sorely lacking.

The potential importance of anaerobic processes in stream ecosystems is beginning to be recognized on spatial scales ranging from the interior of a decomposing leaf (D. Lawson, Michigan State University, personal communication) to microzones in the sediments (Dahm et al. 1987, Jorgensen and Revsbech 1985) to the bottom sediments of beaver ponds (Naiman et al. 1986). In general, studies of anaerobic processes in streams consider pockets of anaerobic conditions in predominantly aerobic systems, for example denitrification occurring in the epilithic film of a well-oxygenated stream (Triska and Oremland 1981, Ventullo and Rowe 1982). Anaerobic processes could be important in regenerating nutrients and could influence the dynamics of nitrogen, phosphorus, sulfur, carbon, and iron in streams. The importance of anaerobic processes in the overall element economy of a stream will vary with disturbance frequency, extent of debris accumulations, and nature of the benthic substratum. In streams where organic loading is high and sulfate and nitrate concentrations are low, one would expect methanogenesis to be an important carbon
sink. Anaerobic processes occurring in the watershed, particularly in the riparian zone and floodplain, will influence the supply rate of elements to the stream.

Interactions between elements have been demonstrated to influence element concentrations in streams. For example in streams in the Great Smoky Mountains, pH and alkalinity increase downstream owing to tributary inputs, and the concentration of soluble monomeric aluminum decreases. Dilution from tributaries with low aluminum concentration does not account for the entire aluminum decrease, indicating that aluminum is precipitating and/or being adsorbed in the stream channel under the higher pH conditions. The downstream decreases in P and DOC are most likely due to their adsorption to precipitated hydrous aluminum oxides (J. W. Elwood, unpublished data). The consequence is an oligotrophication of downstream reaches. These kinds of elemental interactions are probably important in other streams as well and are worthy of investigation. Aquatic humic substances interact with metals and nutrients, and in streams where they are high in concentration (e.g., blackwater rivers), complexation of humics with metals and nitrogenous compounds can influence the availability of metals and nutrients to the biota (Thurman 1985).

Humic substances may also be important in biotic interactions in streams. The high DOC in blackwater rivers may include a bioactive substance that can influence macroinvertebrate distribution and behavior through its impact on olfaction. Olfaction influences the behavior of the organisms in which it has been studied (e.g., mayflies [Peckarsky 1980], stoneflies [Williams 1986], and other groups). Grazing insects are able to taste and appear to use this cue when feeding (Hart 1981, Kohler 1984); high concentrations of humic substances may alter olfaction and therefore feeding behavior.

**Spiraling concept**

Spiraling (Elwood et al. 1983, Newbold et al. 1981) is a unifying concept that is applicable to studies of elemental dynamics in streams. Spiraling is nutrient cycling combined with downstream transport, i.e., nutrients are displaced downstream as they pass through a cycle. The cycle is both open and closed. It is closed in the sense that a nutrient can pass through the same chemical or trophic level many times during its residence in a stream. It is open in the sense that completion of the cycle does not occur in place, but rather involves some downstream displacement before the cycle is closed. The spiraling concept thus deemphasizes the view of streams as spatially bounded units of the landscape because cycling continues indefinitely as nutrients move along a spatial (i.e., longitudinal) axis.

The spiraling concept offers a useful tool for latitudinal comparisons of elemental dynamics in streams and for assessing the importance of internal recycling vs. lateral and longitudinal linkages. For example, if one were interested in assessing controls on community structure and productivity at a point in a stream, a measure of spiraling length would permit an evaluation of the influence from upstream at that point; a longer spiraling length implies more inputs and hence greater controls from upstream reaches. In this sense, a study of spiraling broadens our focus from a single spot in the stream to reaches and how they are linked. The spiraling concept also offers a mechanism for linking studies of community dynamics and element cycling in streams; for example, measures of nutrient spiraling after experimental manipulations of grazers allow one to assess the impact of grazers on nutrient dynamics (e.g., Mulholland et al. 1983). Measures of spiraling are most interesting for the limiting nutrient in a stream.

Spiraling length can be measured with stable isotopes. For organic carbon, all that is required is a measure of downstream flux and respiration (Newbold et al. 1982a). For other elements, uptake length can be measured with additions of the element of interest, although it is critical that the additions be at concentrations below the half-saturation constant for uptake (Newbold et al. 1982b). In this type of experiment, turnover length would have to be measured by radioactively labelling a compartment and following the loss of radioactivity, but this measure could be done reliably in laboratory channels. It may be possible to use dilution of experimentally added stable isotopes as a measure of regeneration; for example the $^{15}$N/$^{14}$N ratio will change as $^{14}$N is regenerated along a stream reach. This technique has been applied to planktonic communities (Morrissey and Fisher 1988). The measurement of turnover
length would benefit from further methodological development. An important future research direction for the measurement of carbon spiraling in streams will be to differentiate the components of total organic carbon spiraling in a river. Initially that will probably mean considering DOC and POC separately; that is straightforward for the measure of transport, but more problematic for the measure of respiration. The next step will be to improve analytical methods to dissect DOC into its components and to compare spiraling of fractions that differ in their bioavailability. Ideally we wish to measure spiraling length of biologically available DOC fractions, but this is not possible at the moment.

Carbon spiraling length has been measured in a variety of streams (e.g., Edwards and Meyer 1987a, Minshall et al. 1983, Newbold et al. 1982a), but spiraling length for a nutrient has only been measured for phosphorus in Walker Branch, Tennessee (Mulholland et al. 1985b, Newbold et al. 1981, 1983) and in experimental laboratory channels (Mulholland et al. 1983, 1985a). It needs to be done for other elements in other types of streams. In Walker Branch, spiraling length varied from 10 to 160 m, largely due to differences in standing stock of organic matter (Mulholland et al. 1985b). Other factors that will influence spiraling length are hydrologic regime, grazer activity, temperature, and algal activity. In large rivers the spiraling concept may be most usefully applied by dissecting the system and examining the role of the various components in controlling spiraling length.

One of the critical questions to which the spiraling concept can be applied is the extent to which the biotic community retards downstream transport of elements, i.e., the relative importance of biotic retention vs. abiotic transport. Evidence from Walker Branch shows that the biotic community associated with leaf detritus is responsible for most of the uptake of phosphorus (Mulholland et al. 1985b); macroinvertebrates do not account for much of the spiraling length of P because a relatively small fraction of the total spiraling flux of P passes through the invertebrate community (Newbold et al. 1983). Invertebrates, however, may alter the spiraling indirectly through activities such as grazing. An application of the spiraling concept that should provide insight into mechanisms controlling nutrient dynamics in streams is the impact of consumer (either fish or invertebrate) density or species diversity on spiraling length. These studies of the impact of structure on function would be of broad ecological interest.

**Stream processes regulated by nutrient supply and availability**

The discussion to this point has considered controls on nutrient supply and availability in streams; we now change our perspective and consider what processes are controlled by nutrient supply and availability.

**Productivity and decomposition**

In well-lit streams, primary productivity is often stimulated by additions of nitrogen or phosphorus (e.g., Grimm and Fisher 1986), although fewer data are available for tropical streams (e.g., Pringle et al. 1986). It is likely that the extent and nature of nutrient limitation will vary as much within as between latitudes. The subject of nutrient limitation of primary productivity in streams has been extensively reviewed (e.g., Bott 1983). An important area for further research is the interaction between nutrient limitation and grazing pressure as controls on algal productivity. A fruitful experimental approach would be to combine nutrient levels and grazing levels to assess their relative importance. These ideas are developed below in the section on whole system manipulations.

Concentrations of micro-nutrients (Patrick 1978), macro-nutrients (Pringle and Bowers 1984), and grazing (Gregory 1983, Patrick 1970) can also affect algal species composition. A useful extension of this information will be to consider how changes in algal community structure influence rates of nutrient recycling in the stream. For example, a shift to more palatable species may accelerate nutrient regeneration through grazing.

Many factors influence the rate at which leaf litter decomposes in streams, including nutrient concentration in the water (reviewed by Webster and Benfield in 1986). Some studies have shown nitrogen to be the critical element, some phosphorus, and some have provided no evidence for nutrient limitation (Webster and Benfield 1986). If the autotrophic community of a stream is nutrient limited, it does not neces-
sarily follow that the decomposer community will be. For example, in the Kuparuk River, Alaska, phosphorus additions stimulate primary productivity, but not Carex decay (Peterson et al. 1985). What is needed at this point is a clear assessment of the conditions under which nutrients will be limiting, and what factors influence which will be the limiting nutrient. Both microbial oxidation and mass loss due to biotic and abiotic fragmentation occur during leaf decay. In addition to watershed influences on stream chemistry, the relative importance of these two processes (among both leaf species and streams) will probably influence the degree to which decay is nutrient-limited; where microbial processes are more important, the potential for nutrient limitation should be greater.

In studies of leaf decomposition it is critical that we move beyond simply assessing mass loss and attempt to separate losses due to microbial processes, invertebrate activity, and physical fragmentation. How does the fractional loss from microbial respiration vary with leaf species (e.g., greater for "fast" species?) and what are the implications of this for the stream ecosystem? For example, if fragmentation is the primary mechanism of mass loss, some of the FPOM and associated nutrients remain in the stream; however if microbial respiration is dominant, the carbon is lost and nutrients are regenerated and made immediately available.

Throughout most of this discussion, we have indicated that we anticipate variation within latitudes to be as great as variation between latitudes. Leaf decomposition may be an exception to this. We doubt that there will be a clear latitudinal gradient in the degree to which nutrients limit decomposition, but consistent differences in other controls on leaf decay rate are expected. Although a range of temperature conditions exist in tropical streams (Covich 1988—see this issue), there are more warmwater environments in lower latitudes, and elevated temperature clearly increases decay rate (Webster and Benfield 1986). The timing of leaf input is also different—pulsed in higher latitudes and more continuous in lower latitudes. Clear differences in chemical composition of leaves along a latitudinal gradient could also influence decay rate. There are well-documented differences in decay rate of different leaf species (Webster and Benfield 1986). To the extent that allelochemicals in tropical leaves are antifungal and antibacterial, they will retard decay rate unless the stream microflora have evolved a resistance to these compounds. Allelochemicals that protect the plant from terrestrial herbivores may also influence their palatability to shredders and hence their decay rate. Potential trace metal influences need to be considered in evaluating latitudinal gradients in leaf decay. Although some tropical plants appear to be enriched in aluminum (Sanhueza et al. 1988), some temperate riparian species (e.g., Rhododendron) are also aluminum accumulators; the relevant question is the relative abundance of aluminum (or a similar substance) accumulators along a latitudinal gradient. Temperate leaves placed in tropical streams decompose more rapidly than in a temperate stream (J. Stout, Michigan State University, personal communication). More work with reciprocal transplants would be helpful in clarifying the various factors (e.g., environmental conditions, leaf species, adaptations of stream microflora) leading to temperate vs. tropical differences in leaf decay rate.

Little is understood about the relative importance of bacteria and fungi in leaf decomposition along a latitudinal gradient in streams or about the extent to which nutrient regime controls their relative importance. There will clearly be changes in fungal species composition in response to changing temperatures (Suberkropp 1984), but the influence of such changes on leaf decay rate needs to be examined.

Detrital decay rate is greatly influenced by the size of the decomposing organic matter. Fungi will be more abundant on large particles, and their role in decomposition relative to bacteria will vary accordingly. Hence the relative significance of nutrient limitation may also vary with particle size. This idea can be extended along the entire size spectrum: wood, whole leaves, fine particulate organic matter (FPOM), dissolved organic matter (DOM). Measures of decay rates of coarse particulate organic matter in streams abound in the literature (Webster and Benfield 1986); we know much less about the decay (i.e., conversion to CO$_2$) of FPOM or DOM in streams. The extent to which nutrient supply rates influence rates of degradation of DOM and FPOM in streams is an important area for future research because DOM frequently provides a major fraction of allochthonous organic matter inputs (e.g., Fisher and Likens
1988] ELEMENTAL DYNAMICS IN STREAMS 423

and FPOM is frequently the dominant component of organic matter standing stock in streams (e.g., Minshall et al. 1983).

Whole system manipulations in studies of nutrient limitation

There is potential for important research in examining the interaction between nutrient limitation and other community processes in streams. Bioassay techniques for determining nutrient limitation vary considerably, and innovative approaches are needed. Whole system experimental manipulations offer a useful experimental approach that is particularly appropriate for testing one’s conceptual understanding of mechanisms controlling structure and function of stream communities. The whole stream experimental approach allows one to quickly demonstrate which components of the entire system are most responsive to the manipulated factor. Subsequent follow-up experiments can focus on the mechanisms of response and the controls. Without the whole system perspective, considerable effort could be misdirected to examine interactions that are of lesser importance in the stream. Experimental manipulations of major components of the community are necessary before we begin analyzing the influence of finer-scale changes in community structure. However, we must exercise caution in drawing inferences from whole stream manipulations that go beyond the boundaries of what the system experiences naturally. The value of whole stream manipulations is evident when one considers questions like the importance of cascading trophic effects (Carpenter et al. 1985) in streams.

Considerable evidence exists that cascading trophic effects are important in streams. Studies have demonstrated that invertebrate predators can control prey populations (reviewed by Peckarsky in 1982, 1984), and that grazers exert a strong influence on algal community composition, biomass, and productivity (reviewed in Gregory 1983). There is, however, little evidence that fish control invertebrate community composition or standing stock (reviewed by Allan in 1983).

Studies of cascading trophic effects in streams need to be extended along the entire food web, from consumers to nutrients. In streams where this has been done, whole system experimental manipulations provided insight. Phosphorus additions to a tundra river lead to increased primary productivity, increased biomass of Brachycentrus and Baeotis, decreased biomass of Simulium, and increased fish production (Peterson et al. 1985), clearly demonstrating the influence of nutrient limitation at several trophic levels. Phosphorus enrichment of a southern Appalachian stream increased leaf decomposition rate, standing stock of blue-green algae, and grazer density; because of increased grazing pressure an initial increase in total algal abundance was not sustained (Elwood et al. 1981). In an Oklahoma stream, experimental manipulation demonstrated that piscivorous fish decreased the abundance of dominant herbivorous fishes, and their decline resulted in increased epilithon standing stocks and lower nutrient concentrations—a clear demonstration of cascading trophic effects (Power et al. 1985). In a southern Appalachian stream, removal of macroinvertebrates decreased leaf processing rates, greatly reduced seston output, and lead to increases in meiofaunal standing stock (Wallace et al. 1982).

The possibilities are numerous for significant research in examining the interaction between food web components extending from nutrients to fish. For example, does nutrient level affect the influence that predators have on stream community structure through controls on population levels of grazers? Conversely, do predators, through their impact on primary consumers, alter nutrient dynamics in the same way that they can alter rates of litter decomposition (Oberndorfer et al. 1984)? This kind of research has provided insight into regulation of lentic community structure (e.g., Neill 1981, Neill and Peacock 1979), and should prove equally useful for studies of stream communities.

Action plan

In this paper we have identified areas where we think there are critical gaps in our understanding of elemental dynamics in streams. In this section we suggest possibilities for new types of research programs in stream ecology that if implemented would promote the type of research that would fill these critical gaps.
Development of methods

Although progress in stream ecology is not necessarily limited by available methods, application of methods from other fields to problems in stream ecology should lead to new insights. One mechanism to foster this would be sponsoring workshops aimed at cross-disciplinary application of methods to a question in stream ecology. Follow-up funds would be necessary to try out the concepts developed at the workshop. In many cases instruments and procedures have been designed for clean, pure samples at high population densities (e.g., bioengineering techniques developed for cell cultures). A stream ecologist wishing to apply these techniques faces problems of interference from dissolved and particulate substances and of low numbers of organisms. This is just one of many instances where a cross-disciplinary discussion of methods would seem a useful first step. Some of the problems discussed in this paper that would benefit from a workshop on methods include biologically meaningful fractionation of organics, spiraling measures, and assessment of elemental dynamics within biofilms and exchanges between biofilms and the water column. As an example, a workshop addressing the question “How do we assess nutrient availability in biofilms in streams?” would be of interest because biofilms appear to be one of the critical interfaces controlling elemental dynamics in streams. Disciplines that should be represented at such a workshop on methods include analytical chemistry, hydraulic engineering, biomedical engineering, biophysics, chemical engineering, and image analysis.

Biological centers program

At least four possibilities for stream ecology centers are worthy of further discussion among stream ecologists. The centers we propose are for the most part facilities for field research. Although these centers may be quite different from those conceived in other disciplines (e.g., centers built around a supercomputer or sophisticated network of telescopes), it is appropriate in a science dedicated to understanding the natural environment.

Any of the centers would be open to the entire community of stream researchers. A useful analogy might be the fleet of ships maintained by the National Science Foundation and available for oceanographic research. Just as an oceanographer requests ship-time, a stream ecologist could request “stream-time.” Although a core staff would be necessary to maintain the monitoring base or the major long-term manipulations at the centers (like the crew on a ship), the management of these facilities should maximize the research done by scientists who are not employees of the center.

A key to the success of such a venture would be the position of research coordinator. This person will need to coordinate work of individual investigators and promote cooperative research between individuals working on different aspects of stream ecology. If full use is to be made of the available experimental treatments, the coordinator should insist that investigators put their major effort into defining the impact of the experimental treatment on the aspect of the system that interests them, be it nutrient uptake kinetics, fish species diversity, or something else. Investigators wouldn’t necessarily have to work together as long as they focus on the experiment and work at the right spatial and temporal scale. Investigators would need to communicate their results quickly to the coordinator to facilitate synthesis and planning of future experiments.

We propose here four potential stream ecology centers, listed in order of increasing potential contribution to the field:

1. Artificial Channel Reality Check (ACRC).—There are problems for which manipulation of natural streams will be either unfeasible or unethical (e.g., toxicant release). Artificial streams offer an alternative approach to examining lotic ecosystems. Artificial stream studies have made significant contributions to the field of stream ecology (e.g., McIntire 1973), but their costs are such that individual investigators or institutions may not be able to afford ones that truly mimic a natural channel. An artificial streams center could provide such a facility. One goal of this center would be to develop artificial channels that can be controlled and manipulated and that mimic natural channels in characteristics such as hydraulics, geomorphology, water quality, temperature, light quantity and quality, and characteristics of the biological community. Hence a “reality check” would be one mission of this type of center: How do we design artificial channels that truly mimic nat-
ural streams? To what extent is exact duplication of the taxonomic composition of natural channels necessary? Other relevant questions include: At what scale are artificial streams appropriate? For example, they could be quite useful for examining phenomena in biofilms, but not useful for examining watershed-level phenomena. When evaluating one parameter, are other factors kept constant or allowed to vary? An artificial stream center might also be an appropriate place to do pilot studies on methods development. The authors do not agree on the usefulness of artificial channels. Some consider them a distraction that siphons off resources and talent; others find them to be one of several useful approaches to studying streams.

(2) Individual Collaboration on Streams and Rivers (ICSR).—This alternative could be thought of as enrichment of the status quo. Rather than developing new stream research centers, another alternative would be to encourage new grant applications for collaborative research on streams. Teams of researchers could tackle a problem on a diversity of levels encompassing physiological, population, community, and ecosystem ecology. If expertise from each of these subdisciplines were directed at a common whole stream experiment (e.g., controls on and effects of nutrient supply and availability in a stream), leaps in understanding should be possible. The River Continuum Study is an example of how this type of cooperative study can make significant contributions to the field, although not all subdisciplines were involved in this project and it was descriptive rather than experimental.

(3) Experimental Streams and Rivers Area (ESRA).—The Experimental Lakes Area in Ontario has made a significant contribution to lotic ecology through its effective use of whole ecosystem experiments. A center that has under its control several manipulatable lotic ecosystems, and a strong research coordinator who is able to attract wide participation in the experiments from scientists around the world, could make significant contributions to the field of stream ecology. The center should have a strong support staff and a budget to maintain the facility and keep the experiments running. As discussed above, the scientific research should not be done by center staff, but rather by scientists from the community at large. The center should have at its disposal the funds to support salaries of visiting investigators for periods up to a year. This would offer scientists from both research and teaching institutions a place and financial support to study the effect of the experimental manipulation (e.g., nutrient enrichment or predator removal) on the processes or organisms that interest them. There are several keys to the success of a project like this: the research coordinator, accessibility to the scientific community, adequate maintenance and repair program, and a strong technical support staff. A major drawback to this kind of a center is that resources would be concentrated at a site in a single geographic region and hence conclusions might not be applicable in a wide range of streams.

(4) Benchmark Streams and Rivers (BSR).—An alternative to developing a single experimental streams area would be to develop a network of streams and rivers in a range of latitudes and hydrologic regimes that would be amenable to manipulation. If we were able to do whole stream nutrient enrichment experiments in a representative range of lotic ecosystems we would make significant progress in understanding the scientific questions posed in this paper. The needs for a series of benchmark streams would be similar to those described above: a strong research coordinator, accessibility to the scientific community, adequate maintenance and repair program, and a strong technical support staff. The U.S. Geological Survey has established a Hydrologic Benchmark Network that includes 57 streams across the U.S. in different physiographic regions with relatively protected watersheds and different hydrologic (and hence disturbance) regimes (Cobb and Bieseecker 1971; M. E. Gurtz, U.S. Geological Survey, personal communication; Resh et al. 1988—see this issue). These offer a wide range of streams to choose from in the U.S., although it would be necessary to extend this network to arctic and tropical regions not currently part of the Hydrologic Benchmark Network. Several excellent research stations that already exist in these regions would be appropriate for the international cooperative research envisioned here. First through fifth- or sixth-order streams should be included in this network, i.e., work should not be done exclusively in first- and second-order streams. The major focus of a network of experimental stream centers would be on comparative stream ecology over gradients of latitude, stream size, and disturbance regime. The
research coordinators would need to ensure that the experiments were of the appropriate nature and scale to provide comparable results.

**Summary: future research directions**

We have argued that controls on elemental supply and availability in streams include both landscape-level and within-stream processes that operate on a range of temporal and spatial scales. The temporal scales about which we know the least lie at both extremes: long-term (decade to century) processes and short-term events such as storms. One fruitful direction for further research is examining the impact of short-term events like storms on element availability to the biological community, and how that impact compares with other physical and biological processes regulating elemental dynamics. A key question in future studies of elemental dynamics in streams is the relative availability of the various forms of an element to the biological community. We need to move beyond combining many forms of an element into a single operationally-defined fraction (e.g., DOC), which is a composite of forms varying greatly in their availability to the biota; instead we should concentrate on individual compounds or groups of compounds.

It is critical that future stream research address the question of the relative importance of longitudinal linkages (upstream-downstream), lateral linkages (riparian, floodplain), and within-stream recycling as regulators of element supply to the biota. To what extent and on what temporal and spatial scales is the biological requirement for various elements met by internal recycling vs. lateral or longitudinal sources?

Our understanding of the controls on elemental supply and availability will be enhanced by studies in several key areas. The concept of nutrient spiraling has facilitated study of elemental dynamics in streams and could fruitfully be applied to a greater variety of streams to further our understanding of linkages between structure and function in stream communities. The extent to which the microbial food loop is an important regenerator of nutrients is unknown for stream ecosystems. Several poorly understood ecotones in streams are sites in which critical processes occur that may control elemental supply and availability to the biota. These include biofilms, the hyporheic zone, floodplains, and zones of transition between anaerobic and aerobic conditions. The extent to which elemental bioavailability in streams is influenced by interactions among elements is also not well understood.

Availability of elements has been demonstrated to regulate decomposition and primary productivity in some streams. The impact of this on higher trophic levels is less clearly understood. A better understanding of the interactions between elements and key ecological processes in streams could be achieved by the use of whole system manipulations supplemented with intensive studies of key processes and parameters. A network of experimental streams over a wide range of latitudes and disturbance regimes would allow researchers to address these critical questions in stream ecology.

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