CONCEPTS, REVIEWS, AND SYNTHESES

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Merging aquatic and terrestrial perspectives of nutrient biogeochemistry

Abstract Although biogeochemistry is an integrative discipline, terrestrial and aquatic subdisciplines have developed somewhat independently of each other. Physical and biological differences between aquatic and terrestrial ecosystems explain this history. In both aquatic and terrestrial biogeochemistry, key questions and concepts arise from a focus on nutrient limitation, ecosystem nutrient retention, and controls of nutrient transformations. Current understanding is captured in conceptual models for different ecosystem types, which share some features and diverge in other ways. Distinctiveness of subdisciplines has been appropriate in some respects and has fostered important advances in theory. On the other hand, lack of integration between aquatic and terrestrial biogeochemistry limits our ability to deal with biogeochemical phenomena across large landscapes in which connections between terrestrial and aquatic elements are important. Separation of the two approaches also has not served attempts to scale up or to estimate fluxes from large areas based on plot measurements. Understanding connectivity between the two system types and scaling up biogeochemical information will rely on coupled hydrologic and ecological models, and may be critical for addressing environmental problems associated with locally, regionally, and globally altered biogeochemical cycles.

Keywords Nutrient cycling · Nutrient limitation · Nutrient retention · Ecosystem comparison · Linkages

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Introduction

A historical separation between the approaches and cultures of the terrestrial and aquatic subdisciplines characterizes the field of biogeochemistry. Today, massive alteration of global biogeochemical cycles by humans has forced a more integrated consideration of biogeochemical fluxes from atmosphere to land to water. However, the legacy of separate approaches hinders attempts to understand biogeochemical phenomena across large landscapes when connections between systems are important. Compelling examples of linkages between terrestrial and aquatic ecosystems are the connection between land-based human activity and the hypoxic dead zones in the Gulf of Mexico (Alexander et al. 2000) and eutrophication of coastal marine ecosystems (National Research Council 2000). Management problems such as eutrophication demand the development of integrated models of biogeochemistry that incorporate both terrestrial and aquatic elements of landscapes. Furthermore, differences in the two approaches have not served attempts to scale up plot measurements to estimate fluxes from large areas. For example, large differences between known inputs and outputs of nitrogen (N), measured for watersheds of many sizes, often are attributed to denitrification (Van Breemen et al. 2002). However, it is not known with certainty where in the landscape the N is lost, and most denitrification studies are restricted to very small scales. Finding the missing N requires consideration of both terrestrial and aquatic perspectives and is both a basic and applied challenge to the science.

Differences in physical and biotic characteristics of aquatic and terrestrial ecosystems may have led to methodological and theoretical divergence between the subdisciplines, but may also provide the basis for understanding the conceptual linkages among them. Key differences between aquatic and terrestrial ecosystems that influence biogeochemistry include the structure of landforms, hydrologic residence time, the nature of nutrient pools, and characteristics of the dominant biota. Several concepts, generalizations, and even paradigms of nutrient biogeochemistry are shared by aquatic and terrestrial researchers and arise from a focus on nutrient limitation, nutrient retention, and nutrient transformations. However, theory may also differ dramatically among different ecosystem types, owing to different approaches, conceptual models, assumptions, and system characteristics. In this paper, we refer to the view of reality that arises from a shared set of concepts, models, assumptions, and approaches in a scientific community as a paradigm, widely held and reasonably well tested statements or abstractions as generalizations, labeled regularities in phenomena as concepts, and systems of concepts that are simplified representations of realities as conceptual models (after Pickett et al. 1994).

We first examine key elements of the structure of aquatic and terrestrial ecosystems that might have led to the differences and disparate approaches of the two subfields. We then compare the two subfields by identifying common questions and selected generalizations of both terrestrial and aquatic biogeochemistry, and finally we consider whether the primary drivers and controls are similar in aquatic and terrestrial ecosystems. We hope to expose similarities and differences in paradigms that have emerged from research on these questions and link these ideas to specific characteristics of the respective systems. Because the research interests of the authors center on cycling of the elements N, carbon (C), and phosphorus (P) through ecosystems, our treatment of biogeochemistry is focused primarily on these essential nutrients and takes an ecosystem perspective. We acknowledge that there are many other approaches to the study of elemental fluxes and transformations that we do not cover here. Yet, by merging perspectives of aquatic and terrestrial biogeochemistry, we hope to suggest fruitful avenues for cross-fertilization between the two fields, and pose questions to drive future integrative work.

Key biophysical characteristics of aquatic and terrestrial ecosystems

Differences in physical and biological characteristics of aquatic and terrestrial ecosystems may account for many of the differences in approach and conceptual models of biogeochemistry. Clearly, the most important distinction between the descriptors aquatic and terrestrial relates to the abundance and action of water. We contend that a few key biogeophysical parameters most strongly translate to differences in biogeochemical cycling across these ecosystems (Table 1). Such biogeophysical differences have also led to use of different research methods and, ultimately, to different paradigms for the different environments.

Structure of landforms

Geomorphology explains the slow physical processes by which landforms are created, forging the template on which faster biogeochemical dynamics occur. The time-scale of the dominant geomorphic processes is different in terrestrial and aquatic systems. In floodplains, rivers, and streams, fluvial processes such as sediment erosion, deposition, and sorting influence biogeochemical processes by causing variation in soil or sediment texture and redox conditions (Pinay et al. 2000; Johnston et al. 2001). Such conditions often vary on shorter timescales concomitant with streamflow variability. On the other hand, processes governing the location of large river networks operate over much longer timescales, and virtually nothing is known of the biogeochemical consequences of stream network structure (Fisher 1997).

Organization and structure of lake districts is governed by slower geomorphic processes, such as those on the timescale of glacial advance and retreat. The position of lakes within a landscape (a relict of glacial retreat) can be an important geomorphic control on lake water chemistry

Table 1. Key physical and biological characteristics of aquatic and terrestrial ecosystems. See text for more detailed description of characteristics

	Terrestrial	Wetland	Stream	Lake
Structural features				
1. Landforms				
(a) Time scale and types of dominant geomorphic processes	Long-term	Medium, fluvial, glacial	Short-term, fluvial	Medium, glacial
(b) Key structural elements	Vegetation, litter, soil	Vegetation, litter, soil, water, detritus	Water, streambed and sediments	Epilimnion, hypolimnion, sediment
2. Hydrology				
(a) Water residence time	Short-medium (except GW)	Medium	Short	Long
(b) Water volume	Low	Medium	Medium	High
(c) Prevalence of anoxia	Rare; microsites only	Abundant	Restricted to subsurface	Restricted to sediments or hypolimnion
3. Nutrient pools				
(a) Reactive sites	Mineral aggregates, organic horizons, rhizosphere	Organic horizons, sediment-water interface	Sediment-water interface	Suspended particles, sediment-water interface
(b) Ratio dissolved/particulate nutrient pools	Minute	Small	Large	Large
(c) Major sites of nutrient storage	Soils, vegetation	Detritus, soils, vegetation	Detritus, sediments	Sediments, fish
(d) Detrital C:N ratio	Higher	Higher	Lower	Lower
4. Biota				
(a) Lifespan of primary producers	Long	Long	Short	Short
(b) C:N, C:P ratio of primary producers	High	Medium	Low	Low
(c) N-fixers	Symbiotic with long-lived organisms	Symbiotic with long-lived organisms, some free-living	Free-living	Free-living
(d) Ratio consumers:producers	Lower	Lower	Higher	Higher
Element fluxes				
5. External fluxes				
(a) Importance of atmospheric inputs	High (except when fertilized, or low in the landscape)	Medium	Low	Medium
(b) Direction of internal fluxes	Bidirectional vertical	Multidirectional	Unidirectional horizontal	Bidirectional vertical
(c) Primary form of internal transfers	Aboveground - particulate; Belowground - particulate (roots) and dissolved	Aboveground - particulate; Belowground - particulate (roots) and dissolved	Dissolved	Particulate
(d) Internal cycling relative to input or output	Retentive	Intermediate	Leaky	Retentive

in some lake districts (Soranno et al. 1999; Kratz and Frost 2000; Webster et al. 2000), where atmospheric inputs dominate for lakes high in the landscape and groundwater inputs are more important for lakes lower in the landscape.

In terrestrial systems, coarse-textured, glacial outwash surfaces are more permeable to water than are fine-textured, glacio-lacustrine plains and this may influence water availability to vegetation. Age and other character-istics of geomorphic surfaces in terrestrial ecosystems may govern plant community structure (McAuliffe 1994; Hook and Burke 2000), thereby having an influence on biogeochemical patterns. In general, the geomorphic processes that dominate in terrestrial systems (such as glacial retreat and weathering) operate over a slower temporal domain than the dynamic action of fluvial processes related to streamflow variability in running water systems.

Hydrologic residence time

A fundamental difference between aquatic and terrestrial ecosystems is the prevalence of anoxic conditions, which is a function of both water residence time and biological oxygen demand. In aquatic systems, short hydrologic residence times can result in replenishment of reservoirs with oxygen-rich water, while longer residence times can allow for depletion of oxygen by bacterial respiration. The geomorphic template also interacts with hydrologic residence time, influencing patterns of anoxia according to differential permeability of underlying substrates. The capacity for oxygen transport through soil pore spaces and the degree of soil saturation (i.e., the proportion of pore spaces occupied by water) determine whether reducing or oxidizing conditions exist in terrestrial soils, thereby dictating the location of biogeochemically reactive inter-face zones. Thus, water controls many of the fundamental physical differences between terrestrial and aquatic ecosystems by influencing the oxidizing or reducing conditions of reactive sites.

Hydrologic residence time, in concert with sediment reaction capacity, determines the extent to which biogeo-chemical reactions modify the chemistry of flowing water. For example, if nitrate-laden (NO_3^-) groundwater passes slowly through sediment with low denitrification capacity, NO_3^- losses from denitrification may still be large owing to the long residence time. On the other hand, if water flux is very high, denitrification-caused losses will be low unless the flowpath intercepts a region of unusually high reaction capacity. The essential point is that residence time and flowpath must both be considered; even if the former is long, as it may be in terrestrial ecosystems except during intense rainstorms, this does not by itself dictate large effects of reactions on water chemistry unless flowpaths bring critical reactants together (McClain et al. 2003).

Nature of nutrient pools and other structural components

Several key structural components differ between aquatic and terrestrial systems. The ratio of elements in dissolved or particulate forms, the major sites for nutrient storage, and the stoichiometry (elemental ratios) of detrital pools are some of the most notable. In stream ecosystems, for example, dissolved forms of C predominate over fine and coarse particulate forms, including living biomass (Schles-inger and Melack 1981; McDowell and Asbury 1994). Vastly more elemental storage occurs in terrestrial vege-tation than in the biota of lakes or streams, where the largest nutrient pools are usually the sediments (interest-ingly, organisms at high trophic levels store large amounts of nutrients in lakes, Kitchell et al. 1979). Lower decomposition rates under anaerobic conditions (Rich 1979) may result in a large pool of detrital C in many wetlands.

The nature of reactive sites and dominance of partic-ulate and dissolved forms of nutrients affect the way measurements and fluxes are determined. Changes in pool sizes are used ubiquitously to estimate fluxes because it is difficult to measure fluxes directly. The dominance of dissolved organic C (DOC) in aquatic ecosystems relative to all particulate forms may account for the earlier attention paid to DOC in these systems (e.g., Kaplan and Bott 1982) than in terrestrial ecosystems (for a review of DOC in terrestrial systems, see Neff and Asner 2001).

Biotic characteristics

Differences in the lifespan of primary producers in aquatic and terrestrial ecosystems imply differences in the rate of community response to perturbations of nutrient cycles. Rapid shifts in species composition of algal communities are common in aquatic systems (Stevenson 1997; Cottingham 1999; Biggs and Smith 2002); however, community shifts in terrestrial plants occur more gradually over successional trajectories [e.g., colonization of lava fields, abandoned agricultural areas, or retreating glaciers (Crocker and Dickson 1957; Dodd et al. 1995; Kitayama et al. 1995)]. Stoichiometry of primary producers also differs between terrestrial and aquatic ecosystems; mean C:N ratios are at least three times higher in terrestrial autotrophs than in lake seston (Elser et al. 2000). More biomass is allocated to producers relative to consumers in terrestrial and wetland systems as compared to streams and lakes.

External fluxes

The relative importance of atmospheric and weathering inputs to elemental budgets varies among aquatic and terrestrial systems. Weathering represents a major input to certain terrestrial element budgets (especially those of the cations and P), but makes relatively minor contributions to

aquatic budgets. In unfertilized upland terrestrial ecosystems, atmospheric deposition dominates N inputs, and direct atmospheric inputs are also important for wetlands and lakes. However, some terrestrial ecosystems are fertilized (agroecosystems in particular), which overwhelms atmospheric N input on a local basis, and rivals it on a global basis. No such intentional fertilization occurs in most aquatic ecosystems.

Accounting for atmospheric inputs is methodologically problematic in stream reaches because they constitute a greater proportion of total inputs as the reach length increases. For example, on an areal basis, a 20-m reach of stream has identical atmospheric inputs as a 10-m reach of stream, but has half the inputs from upstream. Thus, stream segment budgets are sensitive to the size of segment chosen, and cannot be compared among stream reaches of different size (Fisher 1977; Cummins et al. 1983). This problem is applicable only to stream segments, not to entire stream networks or watersheds. It presents challenges for up-scaling nutrient budgets, and has fostered the development of nutrient cycling metrics that are independent of reach length, such as spiraling length (Newbold et al. 1981). While there is no comparable effect of increasing ecosystem area for upland terrestrial ecosystems, lowland or riparian ecosystems can receive a significant portion of their inputs from upland areas by surface runoff, subsurface flow, and erosion, so they are subject to the same considerations (Table 1).

Internal fluxes

Major fluxes of water and elements within terrestrial and lake systems are bidirectionally vertical. In terrestrial ecosystems, these fluxes take the form of bidirectional atmosphere–vegetation and atmosphere–soil exchanges. In lakes, the dominant vertical flux is sedimentation, as mineral and organic particles and phytoplankton transport nutrients from the well-oxygenated water column to the sediments as they settle. The role of water in advective nutrient transport is of minor concern in terrestrial ecosystems, because the supply of nutrients provided by internal cycling usually exceeds that delivered from lateral sources (e.g., vadose zone transport). Downward fluxes of solutes (i.e., leaching below the rooting zone) are considered in studies of terrestrial ecosystems, but intact terrestrial ecosystems are generally highly retentive of nutrients due to efficient biotic uptake (Aber et al. 1989, 1993; Nadelhoffer et al. 1999b; Binkley 2001) and soil sorption mechanisms (Wood et al. 1984; Nadelhoffer et al. 1999a). Forest modeling has focused primarily on atmospheric inputs, but lateral delivery of water by downslope movement is given more consideration in arid areas where water is limiting and in lowland and riparian areas that receive high inputs from uplands.

Fluxes in stream ecosystems are primarily horizontal and unidirectional across the earths surface (i.e., downstream), although vertical exchanges with the hyporheic zone and lateral exchanges with riparian groundwater are also known to influence biogeochemical processes. Stream nutrient models use the spiraling concept (Webster and Patten 1979) that emphasizes unidirectional flow. Fluxes in wetland ecosystems are multidirectional because of the multiplicity of element input sources and fates, making it difficult to quantify mass balances in wetlands. The form of material transfers (particulate vs. dissolved) above- and below-ground also varies among the different types of ecosystems (Table 1).

Because of focus on these differences, much has been learned about controls on biogeochemical processes in the two ecosystem types and the field as a whole has matured. The similarities and differences among the biophysical components of these systems and the methods used to sample them have resulted in divergent approaches, and, in turn, some biogeochemical generalizations and conceptual models have diverged. Here, we explore those differences, as well as the surviving (or emerging) similarities, in the context of three broad topics: nutrient limitation, nutrient retention, and nutrient transformation.

Concepts and paradigms of terrestrial and aquatic biogeochemistry

Historically, nutrient biogeochemistry has been driven by three fundamental questions: (1) what nutrients limit the rate of primary productivity and ecosystem processes?; (2) to what extent do ecosystems retain nutrients, and what governs the efficiency of retention?; and (3) what factors control the rates of microbial and abiotic transformations of nutrients? Research on all three broad questions has progressed in parallel, but without much communication, in both terrestrial and aquatic ecosystems. We propose that the important structural, biotic, and process differences in these systems explained above (see Table 1) underlie differences in the theory developed and approaches taken by aquatic and terrestrial biogeochemists.

Nutrient limitation

A common motivation for biogeochemical studies in both aquatic and terrestrial ecosystems is to understand what limits primary productivity and energy flow to higher trophic levels. A nutrient is considered to be limiting to primary productivity when its addition results in increased rates of primary production. In both aquatic and terrestrial ecosystems, attention has focused almost exclusively on the macronutrients N and P, and a fundamental paradigm is that only a single factor can limit primary production (i.e., Liebigs Law of the Minimum). However, some clear differences in emphasis have emerged. For example, research has been driven by the goal of reducing aquatic productivity (Likens et al. 1971; Edmondson and Lehman 1981; Carpenter et al. 1998) and enhancing terrestrial productivity (Liebig 1855; Dyck 1994; Evans 1996), with a few notable exceptions [such as aquaculture and fertilization of salmon streams to enhance fish production

(Stockner and Shortreed 1978; Johnston et al. 1990; Alongi et al. 2000)].

Is N or P the limiting nutrient?

The generalization that N limits terrestrial ecosystems and P limits aquatic ones is entrenched in the ecological literature (Schindler 1977; Peterson et al. 1993; Molles 2001; Vitousek et al. 2002b) and reflected in policy, but the generalization fails in many regions. In fact, N often limits primary production in streams and even some lakes, particularly in western North America (Grimm and Fisher 1986; Elser et al. 1990), and P, not N, is the limiting nutrient in many tropical forests (Harrington et al. 2001; Herbert and Fownes 1995). Yet, the expectation of P limitation in lakes as compared to forests is logical if one considers that lakes have lower internal inputs from weathering, and their primary producers have access to P only when it is released from sediments or enters via streamflow. In contrast, forest trees have access to P as it weathers from parent material and enters large and slow-turnover soil pools, and as it leaches through soils from decomposing organic matter.

On the other hand, broad acceptance of the generalization that N limits terrestrial and P limits aquatic ecosystem production in the 1960s and 1970s reflects a geographical bias: most of the aquatic research had been done in regions (e.g., eastern USA) with low-P parent geology (Likens et al. 1971; Likens 1972; Schindler 1977) and relatively high N loading from agriculture (Whitford and Schumacher 1961, 1964; Patrick 1966). Furthermore, few terrestrial biogeochemistry studies exist even today from drier ecosystems of the western USA, where water rather than nutrient availability likely controls ecosystem productivity (Gower et al. 1992; Hart et al. 1992; Kaye and Hart 1998). Nutrient limitation in tropical forest ecosystems with highly leached soils or ancient, highly weathered bedrock was unexplored until a recent infusion of new research in this ecosystem type (e.g., Asner et al. 1999, 2000, 2001; Martinelli et al. 1999; Matson et al. 1999). Because most soils exhibit high storage capacity for N and P, new P inputs from weathering, and relatively long turnover times, P limitation of terrestrial ecosystems is thought to occur only over geologic time (Walker and Syers 1976). Thus, it was the extension of nutrient limitation studies to aquatic ecosystems in geologically youthful landscapes and terrestrial ecosystems along a chronosequence of geologic age (McGill and Cole 1981; Vitousek et al. 1993; Crews et al. 1995) that moved these early generalizations from mere classification to more mechanistic explanation.

When net primary production is nutrient-limited, rapid shifts in species composition can occur with changing nutrient levels in many aquatic ecosystems, but such structural changes are rarely seen in terrestrial ecosystems. This difference is a direct consequence of the shorter life spans of organisms in aquatic ecosystems. For example, at low N availability in lakes, free-living, N-fixing cyano-bacteria relieve N limitation and maintain productivity

proportional to P load (Vitousek and Howarth 1991). No corresponding shift occurs in terrestrial communities in the face of N limitation; species replacements do not result in selection for N-fixing organisms. Community shifts do occur, however, over successional trajectories such as the colonization of fresh lava fields or retreating glaciers (Crocker and Dickson 1957; Kitayama et al. 1995), and in grassland systems responding to N inputs (Wedin and Tilman 1993; Steinauer and Collins 1995; Wilson and Tilman 2002).

Thus, factors that dictate whether N or P limits production are linked not to whether a system is aquatic or terrestrial, but rather to characteristics like the nature of external nutrient fluxes, underlying geological substrate, and biotic characteristics. While some of these factors rightly can be assumed to differ between aquatic and terrestrial environments (e.g., access of primary producers to sediment- or soil-associated nutrients, life spans of primary producers and hence response times of communities), others are more correctly assigned to geographical or bioclimatic causes, such as substrate age or extent of soil leaching. An integrative question worthy of pursuit is whether streams, lakes, wetlands, and terrestrial ecosystems in the full range of Earths climatic regions and biomes exhibit local convergence in the identity of the limiting element, especially over geologic time.

What is the role of consumers in nutrient cycling and nutrient limitation?

Biomass allocation among trophic levels differs dramatically between terrestrial and aquatic ecosystems (Table 1). This difference may have led researchers to either emphasize or ignore the role of consumers in biogeochemistry. In terrestrial systems, the role of herbivory (primary consumers) has been examined extensively through studies of the impact of grazing on N availability (McNaughton et al. 2002; Pastor et al. 1993, 1998; Frank et al. 2000), as well as the changes in N availability in prairie dog colonies (Holland and Detling 1990). In aquatic systems, beavers influence the distribution, standing stocks, and availability of chemical elements by hydrologically induced alteration of biogeochemical pathways, and by shifting element storage from forest vegetation to sediments and soils (Naiman et al. 1994). But, unlike in aquatic systems, the role of secondary consumers in influencing nutrient cycling (via trophic cascades) has largely been ignored in terrestrial systems. For example, there are few experimental manipulations of predators in terrestrial systems to look at the strengths of trophic cascades. A recent meta-analysis of such experiments found 84 studies in aquatic systems but only 18 terrestrial examples (Shurin et al. 2002).

Greater storage of nutrients in consumer biomass is characteristic of lakes (Kitchell et al. 1979), and consumers can play a significant role in nutrient cycling in some streams (Grimm 1988a, 1988b). A large body of literature on top down controls and trophic cascades

reveals that food web structure can dictate basic ecosystem function in aquatic environments (Carpenter and Kitchell 1993). Riverine trophic cascades also exist but were recognized much later (Crowl et al. 1983; Power et al. 1992; Flecker and Townsend 1994; Forrester et al. 1999; Pringle et al. 1999). In contrast, food web influences on terrestrial biogeochemical cycles have only recently begun to receive attention (Beare et al. 1995; Elser et al. 2000; Wall et al. 2001). Though some have argued that consumer effects on ecosystem processes are less likely in terrestrial ecosystems (Strong 1992) and though this would be consistent with predictions based on differences in nutrient storage characteristics of terrestrial and aquatic ecosystems (Table 1), the verdict is as yet uncertain. Recently, Shurin et al. (2002) conducted a meta-analysis of published studies on trophic cascades and concluded that indeed, trophic cascades are strongest in aquatic ecosystems. They argued that many of the terrestrial-aquatic differences identified in Table 1 (e.g., key structural elements, nutritional value of primary producers, biomass ratios of consumers: producers), rather than more complex terrestrial food webs (Strong 1992), probably explained this pattern. However, in their analysis, Shurin et al. (2002) also compared five aquatic habitats with only one, lumped terrestrial category. Future research may reveal that, as with aquatic habitats, there is as much diversity among terrestrial ecosystems as between those on land and those in water.

Food web manipulations in lakes and streams can result in strong shifts in biogeochemical properties, such as limiting nutrients (Elser et al. 1988; Schindler and Eby 1997). New theories of consumer-driven nutrient cycling are emerging that are based on stoichiometry of consumers relative to their food in aquatic (largely pelagic) ecosystems (see Elser and Urabe 1999; Sterner and Elser 2002). These ideas have been less rigorously evaluated in terrestrial ecosystems, though a recent summary by Elser et al. (2000) indicates that variation and herbivore–producer imbalances in stoichiometry are at least as great in terrestrial as in freshwater ecosystems. Whether stoichiometric theory provides a general framework for integrating nutrient cycling and energy flow concepts across multiple ecosystem types awaits extension to a wider array of ecosystem types and ecosystem processes.

Nutrient retention

Biogeochemists working in both aquatic and terrestrial ecosystems want to understand how ecosystems process nutrient inputs. Nutrient retention of whole watersheds has been measured by comparing precipitation inputs to streamflow outputs, assuming predominance of atmospheric inputs and streamflow outputs from forests (Table 1). The advent of whole watershed studies led to a profusion of research on terrestrial nutrient retention; scientists could ask how forested watersheds respond to disturbance (Likens et al. 1970), how retention varies with successional age (Odum 1969), whether retention is

greater or less for limiting nutrients (Vitousek and Reiners 1975; Gorham et al. 1979), and how ecosystems handle elevated nutrient loading (Aber et al. 1998). These questions were also asked in aquatic ecosystems (McColl 1974; Edmondson and Lehman 1981; Newbold et al. 1981; Grimm and Fisher 1986; Grimm 1987; Schindler et al. 1987), but using different methods and with different emphases. For example, following on the adage the solution to pollution is dilution, early research on stream nutrient retention aimed to quantify the removal of high nutrient concentrations from the water (McColl 1974); later, metrics of retention unique to streams were developed (Newbold et al. 1981).

At the most fundamental level, ecosystem retention is expressed as input less output, with the difference accumulating within nutrient pools of the system (Fig. 1A). Among ecosystem types, differences in the ratio of dissolved to particulate pools, major sites of nutrient storage, the magnitude and direction of internal fluxes (Table 1), as well as methodological difficulties in separating different storage pools led to divergent conceptual models of input and output (e.g., Fig. 1B–D). Nevertheless, a simple paradigm provided a point of
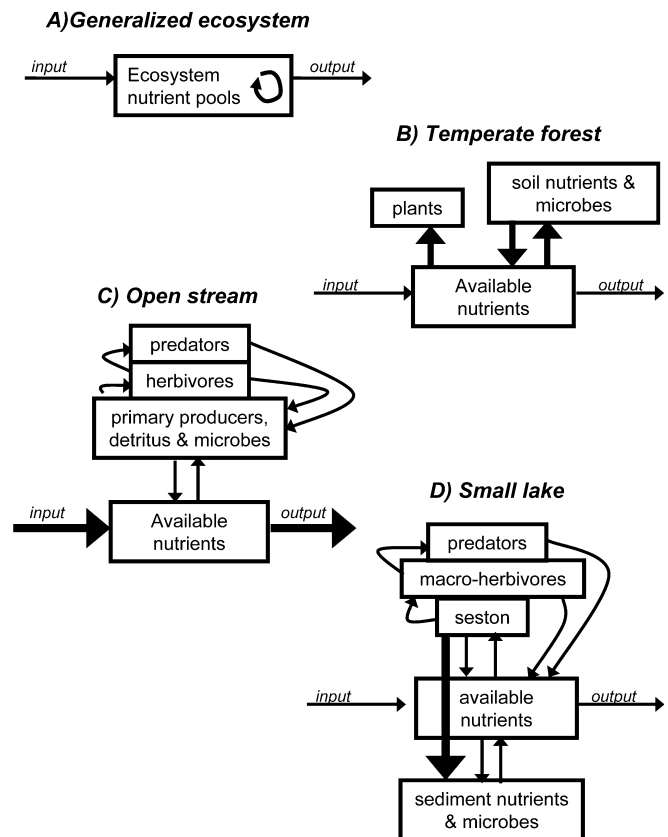
Fig. 1 Comparison of conceptual nutrient cycling models for **A** a generalized ecosystem, **B** a temperate forest (adapted from Vitousek et al.1998), **C** an open (*unshaded*) stream, and **D** a small lake. Size of *arrows* reflects relative magnitude of fluxes. Although all compartments shown are present in all ecosystem types, only the minimum set required for realistic depiction (based on literature reports of nutrient cycling) of the ecosystem is shown

departure for research in all systems, based on the principle of mass balance: at steady state (constant nutrient storage, or no net nutrient accrual), nutrient inputs equal outputs. Typically, nutrient storage within biomass dominates system storage (Vitousek and Reiners 1975). The simplicity of this paradigm of course yields many exceptions, with reasons for lack of conformity varying among ecosystem types. For terrestrial systems, especially forests, early emphasis on plant uptake proved inadequate, since microbial mechanisms of retention can be important (Vitousek and Matson 1984; Stark and Hart 1999). In most streams and rivers, steady state is the exception rather than the rule because of frequent disturbance. Even if biomass is constant, for example in productive desert streams late in succession, solute uptake can exceed release at steady state because it is balanced by transport losses in particulate form (Grimm 1987; Vitousek et al. 1998). Yet, in most streams, nutrient inputs via hydrologic vectors are often very close to hydrologic outputs. Lakes, on the other hand, can accumulate nutrients at steady state (if we consider just the nutrients stored in the plankton) because of sedimentation.

The contrasting emphases among ecosystem types can be traced to differences in methods of measuring retention and of defining the boundaries of the system under consideration. Watersheds contain both aquatic and terrestrial elements, yet the precipitation input-stream-flow-output measure invites attribution of retention to forest uptake alone (e.g., Vitousek and Reiners 1975). Stream nutrient models use the spiraling concept (Webster and Patten 1979) that emphasizes unidirectional flow, but terrestrial ecologists hardly consider material movement at all (except as streamflow or leaching losses). Because of these differences in emphasis and means of measuring input and output, much more attention is paid in streams to retentive capacity conferred by hydrologic properties, whereas in terrestrial ecosystems biotic mechanisms of uptake and retention by plants and soil organic matter are the focus.

Even the term retention itself is used differently between researchers in the two areas: aquatic (or at least stream) ecologists define retention as the difference between hydrologic input and output (e.g., Stream Solute Workshop 1990; Fisher et al. 1998; Peterson et al. 2001), so that gaseous losses would count as mechanisms of retention. When terrestrial ecologists speak of retention, they are usually referring to the difference between total inputs (largely precipitation and weathering) and total outputs (including hydrologic and gaseous losses), and this is the definition that most easily transfers from common usage of the word. We suggest, for the sake of improving communication, that the latter definition be adopted by all biogeochemists, or at least that authors carefully define their terms. The stream ecologists definition of retention might be replaced with the term removal, in reference to loss of nutrients from transport by whatever mechanism.

Considered independently, terrestrial and aquatic ecosystems differ in their capacity to retain nutrient inputs owing to characteristics of their biota and their nutrient pools, and because of differences in internal fluxes and residence time (Table 1). Ecosystem structure in terrestrial ecosystems such as forests is well buffered against a sudden influx of material, since the primary producers (trees) are long-lived and thus have slow community response times. Furthermore, soils in terrestrial ecosystems buffer against biogeochemical changes in a way that has no analogue in aquatic systems. Soils contain both large stores of various nutrient elements, as well as efficient mechanisms of nutrient retention and recycling. Phosphorus, for example, is tightly retained in northern hardwood soils due to plant and microbial uptake and abiotic adsorption (Wood et al. 1984). Nitrogen flux is also strongly controlled by soils and, in many terrestrial ecosystems, soil is the major sink for N inputs whether of anthropogenic (Baker et al. 2001) or natural origin (Barrett and Burke 2002).

As a proportion of standing stocks, N fluxes from forests are minute, typically well below 1% (e.g., Likens and Bormann 1995; Chestnut et al. 1999). Data for streams and rivers are sparser, but on a channel-area basis, N fluxes are equal to or considerably larger than standing stocks (e.g., Triska et al. 1984; Grimm 1987; Merriam et al. 2002) Thus, biotic control over nutrient pools and exports (Bormann and Likens 1979) appears greater in forests than in streams. Plot-scale studies of forest nutrient dynamics have been successful in characterizing stand to landscape nutrient dynamics (Williard et al. 1997; Brooks et al. 1999), but reach-scale stream nutrient retention has seldom been extrapolated to entire stream networks. Whether cross-system comparisons are appropriate or even possible at plot, reach/stand, or stream network/ watershed scales is unclear.

The need for a general theory of ecosystem nutrient retention is heightened by recognition that human activities have accelerated nutrient cycling and enhanced nutrient inputs (Galloway et al. 1995; Vitousek et al. 1997). Assessing nutrient retention in both terrestrial and aquatic ecosystems must be made in a context-dependent manner, as patterns of nutrient retention and loss may vary depending on overall nutrient status, successional stage, and biogeophysical setting. Nitrogen budgets at low deposition rates often show missing sources rather than sinks (Hedin et al. 1995; Chestnut et al. 1999), but in experimentally manipulated or heavily polluted terrestrial environments where N deposition is large (and uncertainties in inputs, such as N fixation, are thus proportionally smaller), retention of N almost always occurs (Aber et al. 1998). Typically, N retention is over 50%, and most is retained in poorly described soil organic matter pools by biotic or abiotic mechanisms (Nadelhoffer et al. 1999a, 1999b; Binkley 2001; Dail et al. 2001; Barrett and Burke 2002). However, forests can become leaky when their capacity for storage of N is exceeded (so-called N saturation), leading to increased loading to streams (Emmett et al. 1993). Lakes have more rapid community response times, but the dilution of input materials by the water matrix means that input loading must be high in

order to elicit a within-lake concentration change. Dilution may enable rivers and streams to handle pulsed, one-time inputs, but these systems are likely to respond rapidly and dramatically to chronic changes in external nutrient supply. The short residence time in streams and rivers means that on an areal basis, NO_3^- only infrequently shows significant retention in a stream reach, both when levels are increased many-fold over background (e.g., McColl 1974; Richey et al. 1985; Munn and Meyer 1990) and when NO_3^- is present at low, ambient conditions (Peterson et al. 2001). In the context of a whole drainage basin, however, stream N retention and transformation may be significant (Alexander et al. 2000; Peterson et al. 2001; Seitzinger et al. 2002). The disparity between these scales is unresolved, but resolution may lie in the consideration of small streams in their landscape context.

Although generalizations about individual ecosystem types can be made, they contribute little to a theory of nutrient retention because real landscapes are heterogeneous mixtures of aquatic and terrestrial elements. In mixed-use landscapes, nutrient inputs are often much greater than outputs. For example, the P budget for an agricultural landscape in Wisconsin exhibits only minor exports to the recipient aquatic system (Lake Mendota); instead, massive amounts of P accumulate in slow-turnover soil pools (Bennett et al. 1999). At the very large scale of the eastern U.S. seaboard, N inputs greatly exceed exports in river water (Boyer et al. 2002), yet the main sites of N retention are unidentified. The same imbalance can be seen at a wide variety of scales; the important point is that any explanation must consider the contribution to retention of both terrestrial and aquatic elements and the interfaces between them. Indeed, a landscape view of river corridors predicts that retention will vary predictably with distance from the stream (the central element of the corridor), and that retention will be enhanced by connections among the different elements of the corridor [i.e., at interfaces or hot spots; (Fisher et al. 1998)]. Riparian zones themselves are just such hot spots of nutrient retention at larger scales (Tabacchi et al. 1998; Gold et al. 2001; McClain et al. 2003); these are ecosystems whose biogeochemical function cannot be conveniently described with either terrestrial or aquatic paradigms.

Nutrient transformations

A complete understanding of input–output relationships must open the black box of the ecosystem, focusing on specific processes that account for retention or loss of material inputs. Interest in the underlying mechanisms causing input–output discrepancies led to work on specific transformations, from which a host of questions and generalizations have emerged (Fig. 2). Here, we focus on several key questions that have received attention in both aquatic and terrestrial studies.
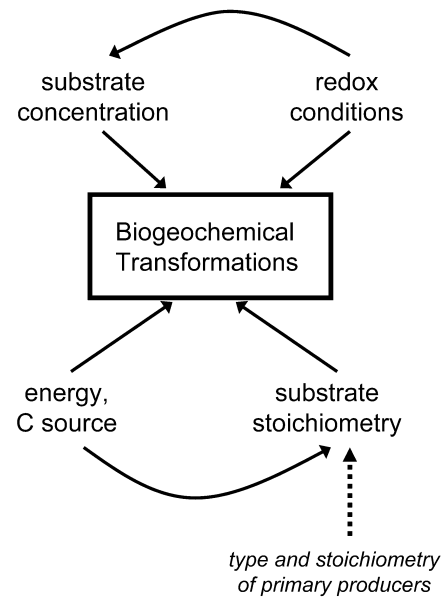
Fig. 2 Four key controls on rates of microbially mediated biogeochemical transformations in both aquatic and terrestrial ecosystems. Substrate elemental stoichiometry is strongly determined by the stoichiometry of the dominant primary producers

What factors control rates of decomposition?

Aquatic and terrestrial biogeochemists share the view that the C:N ratio of decomposing material influences rates of decomposition in forests and streams. In a stream or on the forest floor, decomposition of high-C, low-N terrestrial leaf litter is slower than that of litter with a lower initial C:N ratio. Over the course of decomposition the ratio converges on a lower, more uniform value (Webster and Benfield 1986; Aber and Melillo 1991; Irons et al. 1994). This similarity persists even though other factors regulating litter decomposition differ dramatically. In stream ecosystems, for example, physical breakdown of large leaves occurs relatively rapidly due to water currents and the action of shredding invertebrates, whereas microbial attack is the primary pathway during the early stages of decomposition in terrestrial ecosystems (Webster and Benfield 1986). In terrestrial ecosystems, root production represents a high percentage of detritus production, yet we know little about the factors regulating root decomposition (Silver and Miya 2001).

There has been little explicit comparison of decomposition rates in aquatic and terrestrial systems (Wagener et al. 1998), yet one might predict that rates would co-vary between terrestrial catchments and their streams across biomes if C:N of leaf litter is indeed a primary control. A more general concept is that elemental content of detritus coupled with redox dictates rates of detrital decomposition. The elemental stoichiometry of the detrital pool in any ecosystem is a reflection of nutrient ratios of all of the major biotic compartments as influenced by the turnover rates of those compartments. Thus, in comparing decomposition rates among temperate forests, small streams draining them, and peatlands and large lakes within the

same catchment, we would predict fastest detrital decomposition in the lakes (low C:N:P owing to its planktonic origin), slower in forests and streams (high C:N:P in leaf litter), and slowest decomposition in peatlands (higher C:N:P and restricted decomposition due to anoxia). In contrast, larger streams or those in regions where aquatic primary productivity is high (e.g., deserts and grasslands) may exhibit more rapid decomposition because detrital pools are dominated by periphyton (lower C:N:P).

What element limits heterotrophic microbial processes?

A fruitful area for future research in both aquatic and terrestrial ecosystems is examination of nutrient limitation to heterotrophic production. As discussed above, there is a rich literature describing nutrient limitation of primary productivity in aquatic and terrestrial environments, but there is a distinct lack of information in both environments regarding nutrient limitation of heterotrophic production. The idea that heterotrophic microbial processes are limited by C availability is widely accepted in both aquatic and terrestrial ecosystems, but limitation by other elements has been inferred from changes in decomposition rate and microbial biomass with nutrient addition or under variable nutrient environments (Howarth and Fisher 1976; Fog 1988; Gallardo and Schlesinger 1994; Suberkropp and Chauvet 1995; Hart and Stark 1997; Tank and Webster 1998; Hobbie and Vitousek 2000). Nutrients other than C are likely to be limiting in situations where detrital organic matter is nutrient-poor (Fig. 2), which likely occurs more often in terrestrial than in aquatic ecosystems (except in small forest streams, where detrital organic matter originates in the forest rather than the stream; Table 1). Moreover, there is increasing evidence that not only the amount of C but also its quality may limit decomposition rate, both in aquatic (Leff and Meyer 1991; Jones1995; Koetsier et al. 1997; Strauss and Lamberti 2002) and terrestrial (Hart et al. 1994a; Hart 1999; Hobbie and Vitousek 2000) ecosystems.

Anaerobic respiratory pathways (denitrification, sulfate reduction, methanogenesis) clearly are restricted to anoxic zones in all ecosystem types. Anoxic zones are most prevalent in aquatic environments where, owing to the lower solubility of oxygen in water, regions with high microbial activity or low hydrologic turnover rates can quickly become oxygen depleted. However, the availability of an electron acceptor (e.g., NO_3^- or sulfate) and sufficient C to support microbial metabolism also are requisite conditions for these processes to occur. Often, maximum rates of denitrification are observed where subsurface flowpaths carrying NO_3^- intercept C-rich, anoxic sites such as those surrounding the rooting zone of plants (Jacinthe et al. 1998; Schade et al. 2001); indeed, it is just this convergence of conditions at a localized site, usually an interface between two different habitats, that creates a biogeochemical hot spot (McClain et al. 2003), a CTZ (critical transition zone; Bardgett et al. 2001; Wall et

al. 2001), a control point (Hedin et al. 1998), or TEAPs (terminal electron accepting processes; Lovley et al. 1994; Morrice et al. 2000). These ideas can be summarized as an emerging paradigm of biogeochemistry: Microbially mediated nutrient transformations that are governed by redox achieve maximal rates at aquatic-terrestrial interfaces (hot spots).

What controls the supply of NO3− via nitrification?

For some biogeochemical processes, such as nitrification, a lack of information may preclude comparison of terrestrial and aquatic ecosystems. In terrestrial environments, nitrification leads to greater mobility (and hence export) of N and greater N availability to some primary producers. This is because movement of the nitrification reactant [the cation, ammonium (NH_4^+)] is impeded by the negative charges that dominate the surfaces of soil particles, whereas movement of product (the anion, NO_3^-) is not. Controls on nitrification in temperate forests have been studied extensively using a variety of experimental techniques and intellectual approaches (Binkley and Hart 1989; Hart et al. 1994b; Gundersen et al. 1998a). These studies show that NH_4^+ availability drives the rate of nitrification, since chemoautotrophic nitrifiers are poor competitors for NH_4^+ compared with plants and heterotrophs under conditions of N shortage. Although there is a large body of literature on nitrification in running waters and wetlands receiving sewage inputs (e.g., Cooper 1984; Hemond and Fechner-Levy 1999), until recently there was relatively little information on factors controlling rates of nitrification in the small streams that drain temperate forests or other biomes where NH_4^+ concentrations are low. Recent use of isotopic tracers in whole-stream experiments (e.g., the Lotic Intersite Nitrogen eXperiment, or LINX) shows that in situ rates of nitrification are surprisingly high, with from 10% to 50% of tracer $^{15}NH_4^+$ addition converted to $^{15}NO_3^-$ (Mulholland et al. 2000; Hamilton et al. 2001; Bernhardt et al. 2002; Dodds et al. 2002; Merriam et al. 2002).

Mechanistic controls on nitrification are reasonably well understood for terrestrial ecosystems, but not for aquatic ecosystems. The C:N ratio of the forest floor has been proposed as an indicator of rates of net nitrification and susceptibility to NO_3^- leaching (Gundersen et al. 1998 b). Differences in topography and associated spatial heterogeneity of oxic/anoxic interfaces control the spatial arrangement of NH_4^+ and NO_3^- hot spots in wetland soils (Clement et al. 2002; Pinay et al. 1989; Hedin et al. 1998). There is no analogous model for factors controlling nitrification in streams, although recent work in the hyporheic zone suggests that spatial heterogeneity in mineralization rate along flowpaths controls nitrification via supply of NH_4^+ (Jones et al.; 1995), and other mechanistic studies have shown microbial competition for NH_4^+ between heterotrophs and autotrophs (Strauss and Lamberti 2000). Cross-system comparison of controls on nitrification would go a long way towards developing a

general understanding of this important process (McDowell et al., in preparation).

Vitousek et al. (2002a) recently compared ecological controls of dinitrogen fixation across a wide variety of ecosystem types (temperate and tropical forests, grasslands, deserts, lakes, estuaries, and streams) and N_2-fixing systems (free-living autotrophic, symbiotic, and heterotrophic). They asked: what explains the wide disparity in the success of N_2 fixers in different environments. Although N_2 fixation may represent a major N input to some ecosystems, N_2 fixers do not dominate all ecosystems where N limits primary productivity, as might be expected. Vitousek et al. (2002a) argue that trace element or P limitation and grazing pressure specific to N_2 fixers (or their hosts) emerge as important ecological controls on the process in most of these cases. Grimm and Petrone (1997) reported ranges of whole-ecosystem, annual N_2 fixation rates in a variety of ecosystems. The reported range for terrestrial systems is similar to the range for wetlands, lakes, and streams. While not exhaustive, these ranges confirm that differences among terrestrial and aquatic systems, per se, are not likely to account for natural variability in the process. Rather, if Vitousek et al. (2002a) are correct, understanding how ecological controls vary across ecosystem types, and within ecosystems in space and time, is likely to be most fruitful.

Are abiotic mechanisms important in nutrient retention?

Ecologists focus much of their attention on biotic mechanisms of nutrient retention, although many elements show reduced exports due to abiotic processes such as adsorption or formation of metal or organic complexes. More attention has been paid to abiotic retention mechanisms in terrestrial ecosystems (especially soils; e.g., Kalbitz et al. 2000; Qualls 2000; Dail et al. 2001; Barrett and Burke 2002) than in aquatic ecosystems, and in streams than in lakes (e.g., Meyer and Likens 1979; Klotz 1988; Haggard et al. 2001). This is a logical consequence of the way materials move through these different systems. Soils act as an adsorption column, with dissolved materials coming in frequent contact with adsorption sites on solid phases. In streams and large rivers, the bulk of dissolved solute is transported in the water column, flowing over rather than through sediments (e.g., Wagener et al. 1998). However, in contrast to the highly isolated water column of lakes, exposure of transported materials to adsorption surfaces does occur during surface-groundwater exchanges through the beds of streams or along lateral flowpaths in the hyporheic zone of river corridors (Harvey and Fuller 1998; Kay et al. 2001). In essence, abiotic transformations are restricted to sites usually associated with soil or sediment, or with high light intensity where photobleaching and degradation of organic matter can occur (Osburn et al. 2001). Organisms can migrate to a nutrient source, grow more rapidly, or induce enzymes in response to the increased availability of a limiting nutrient. Hence, biotic mechanisms of retention are more plastic than abiotic ones, and are effective in both aquatic and terrestrial ecosystems. Where both abiotic and biotic retention occur, their interaction often results in enhancement of biotic uptake, as biota employ mechanisms to access abiotically sequestered nutrients.

Toward an integration of perspectives

In our analysis of biogeochemical questions and generalizations, we referred to the distinctive features of aquatic and terrestrial ecosystems that have led to different generalizations, methods, or approaches in these two types of systems. Features such as landforms, hydrology, nutrient pools, lifespan of dominant biota, as well as the direction and magnitude of fluxes (Table 1) underlie many of the differences we found. For example, differences in biomass apportionment among trophic levels may underlie differences in the role of consumers in nutrient cycles. Also, a relatively short water residence time and large nutrient pools in vegetation and soils contribute to the explanation for why biotic retention is more important than hydrologic retention in terrestrial ecosystems. In other cases, similarities in theory persist despite the fundamentally different features of terrestrial and aquatic systems. For example, whether N or P is the primary limiting nutrient is related not to structural features but rather to potential nutrient sources and substrate age. Further, factors explaining variation in nutrient mineralization rate are related to characteristics of decomposing substrates such as their elemental stoichiometry rather than to broad features of the ecosystems listed in Table 1.

Common generalizations and questions among aquatic and terrestrial ecosystems were most evident for the category of nutrient transformations and less evident for whole-system attributes such as nutrient retention. One reason for this discrepancy may be that understanding specific nutrient transformations requires knowledge of fine-scale mechanisms based on fundamental first principles, which are similar across different ecosystem types. For example, the debate about whether N is the limiting nutrient in terrestrial ecosystems and P limits aquatic productivity dissolves when a more explanatory, mechanistic model incorporating information about nutrient sources (and their variation with substrate age) is applied. Finer-scale processes that are more amenable to mechanistic explanation may be more transferable across ecosystems. In contrast, generalizations about nutrient retention capacity of ecosystems (e.g., streams are unretentive and forests are retentive) are merely categorical and do not yield theory that is transferable across ecosystems. We suggest that more mechanistic explanations are likely to hold across a wide array of ecosystem types. Therefore, understanding the spatial and temporal constraints that dictate where and when such biogeochemical processes can occur will permit greater predictability at the whole-ecosystem level.

Further challenges

Our contention is that progress in understanding complex relationships and feedbacks between landscapes and surface waters has been limited by the lack of integration of aquatic and terrestrial perspectives. A paucity of synthetic modeling and measurement techniques may have contributed to this deficiency (Hutjes et al. 1998; Tenhunen and Kabat 1999). Recent progress in the development of new measurement and modeling tools, and theoretical advances arising from interdisciplinary interaction, promise greater progress in developing an integrated understanding of biogeochemistry that is applicable to complex landscapes.

Integrated models of biogeochemical fluxes that incorporate both terrestrial and aquatic elements of landscapes are needed for consideration of any scale larger than the traditional unit of empirical study for ecologists (e.g., a stream reach, the epilimnion of a lake, a forest stand, a grassland plot). Amid concern over acid rain, hydrologists developed some of the earliest spatially explicit, watershed-level models coupling flow and reactive solutes to better understand controls on acid neutralizing capacity (e.g., Chen et al. 1982). In parallel, terrestrial ecologists were developing plant–soil models to describe biogeochemical dynamics in forests (see Perruchoud and Fischlin 1995 for a review and comparison). Recently, models of in-stream biogeochemical dynamics have been developed (Wollheim et al. 1999; Peterson et al.2001) and, in some cases, linked to hydrologic models (Morrice et al. 1997); however, seldom have stream-reach models been coupled with watershed models (but see Wade et al. 2001).

Newer models couple hydrological, biological, and geochemical processes and controls. For example, the regional hydro-ecologic simulation system (RHESSys) combines mechanistic representations of biogeochemical and hydrological processes to predict storage and losses of nutrients (e.g., Tague and Band 1998; Band et al. 2001, 2002). The merging of concepts, and then models, from hydrology and ecology may have been inevitable, and efforts seeking to couple models of water and material transport to models of ecosystem function have become a mainstream research interest (Rodriguez-Iturbe 2000).

Advances in remote sensing also will be extremely important for merging aquatic and terrestrial biogeochemistry. Instruments such as MODIS (Moderate Resolution Imaging Spectroradiometer) have allowed calibration of data collected at different scales and prompted new techniques for remote sensing of vegetation (Hook et al. 2001). Remote sensing capabilities in aquatic systems are also growing rapidly; water surface elevation, flood stage, temperature, Secchi depth, turbidity, suspended particulate inorganic material, sediment and algal chlorophyll concentrations all can be determined remotely (Alsdorf et al. 2000; Torgersen et al. 2001; Ammenberg et al. 2002; Koponen et al. 2002; Mertes 2002). Linking data from plot-level studies with remotely acquired data that cover broad spatial scales will be fundamental to analyzing hydrologic and biogeochemical changes in terrestrial and aquatic ecosystems simultaneously.

Recently, there have been many changes in the social structure of science in the United States that we believe have fostered collaborations among terrestrial and aquatic biogeochemists. Data are increasingly shared among researchers across disciplines (e.g., via the Long-Term Ecological Research networks database that is free to the public); national science agencies are promoting interdisciplinary collaborations between hydrologists and ecologists (e.g., the National Science Foundations crosscutting activities in Biocomplexity, and their focus on water, energy, and biota within the Hydrologic Sciences Program); and scientific societies are engaging larger numbers of disciplines, for example, the newly-formed Biogeosciences sections of the American Geophysical Union (AGU) and the Ecological Society of America. Such activities, along with synthesis activities sponsored by NCEAS (National Center for Ecological Analysis and Synthesis), AGU (e.g., a recent Chapman conference on ecohydrology), the National Research Council (e.g., 1999 ecohydrology workshop), and CUAHSI (Consortium of Universities for the Advancement of Hydrologic Sciences) will foster significant and productive exchanges of ideas among disciplines. Through merging perspectives, modeling and measurement techniques, biogeochemical research communities can begin to develop integrated theories that encompass both aquatic and terrestrial components of heterogeneous landscapes.

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