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COMMENTARY

Biogeochemical Hot Spots and Hot Moments at the Interface of Terrestrial and Aquatic Ecosystems

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ABSTRACT

Rates and reactions of biogeochemical processes vary in space and time to produce both hot spots and hot moments of elemental cycling. We define biogeochemical hot spots as patches that show disproportionately high reaction rates relative to the surrounding matrix, whereas hot moments are defined as short periods of time that exhibit disproportionately high reaction rates relative to longer intervening time periods. As has been appreciated by ecologists for decades, hot spot and hot moment activity is often enhanced at terrestrial-aquatic interfaces. Using examples from the carbon (C) and nitrogen (N) cycles, we show that hot spots occur where hydrological flowpaths converge with substrates or other flowpaths containing complementary or missing reactants. Hot moments occur when episodic hydrological flowpaths reactivate and/or mobilize accumulated reactants. By focusing on the delivery of specific missing reactants via hydrologic flowpaths, we can forge a better mechanistic understanding of the factors that create hot spots and hot moments. Such a mechanistic understanding is necessary so that biogeochemical hot spots can be identified at broader spatiotemporal scales and factored into quantitative models. We specifically recommend that resource managers incorporate both natural and artificially created biogeochemical hot spots into their plans for water quality management. Finally, we emphasize the needs for further research to assess the potential importance of hot spot and hot moment phenomena in the cycling of different bioactive elements, improve our ability to predict their occurrence, assess their importance in landscape biogeochemistry, and evaluate their utility as tools for resource management.

Key words: biogeochemical cycles; carbon; nitrogen; spatial scale; temporal scale; water resources management.

INTRODUCTION

Heterogeneity is an inherent attribute of many natural systems and a subject of considerable interest to many disciplines within the broader field of ecol-

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ogy. In the case of biogeochemistry, fluxes of elements such as carbon (C) and nitrogen (N) and rates of biogeochemical cycling are often spatially and temporally variable. Zones of enhanced fluxes and reaction rates where terrestrial and aquatic ecosystems meet have been recognized, or suspected, for decades. In his classic essay on "The Stream and its Valley," Hynes (1975) questioned the fate of excess N applied to agricultural fields in Britain, after recent investigations had shown that there was no comparable rise in the N concentrations of adjacent river waters (Tomlinson 1970). Although Hynes speculated that biological uptake might explain the apparent N retention, research in subsequent years has clearly implicated denitrification reactions that occur in anoxic microsites of soil columns or spatially restricted anoxic zones beneath riparian environments (Parkin 1987; Sexstone and others 1985; Peterjohn and Correll 1984; Lowrance and others 1984). These isolated zones of enhanced biogeochemical cycling have become popularly known as "hot spots" (Parkin 1987; Hill and others 2000). Biogeochemical activity can also be "hot" in the temporal dimension, producing "hot moments," or periods of time during which rates of biogeochemical processes are enhanced. Examples of hot moments include pulses of dissolved organic C (DOC) leaching from near-stream soils during snowmelt in alpine watersheds (Boyer and others 1997) and pulses of N uptake during rain events in cold desert plant communities (Gebauer and Ehleringer 2000).

The existence and importance of hot spots and hot moments are recognized in the ecological community, but a solid understanding of the underlying mechanisms that produce hot spots is still lacking. The lack of a mechanistic understanding of these phenomena is a significant impediment to the construction of budgets and the modeling of biogeochemical cycles across different spatiotemporal scales. Our inability to predict when and where high process rates will occur in a landscape also impedes the effective management of soil, water, and even air resources. We believe that a full understanding of the controls on biogeochemical hot spots requires a better appreciation of the movement of water along hydrologic flowpaths. Biogeochemical hot spots often occur where hydrological flowpaths intersect, or where flowpaths encounter a substrate containing complementary reactants. Water enhances biogeochemical fluxes in two ways: It transports elements across space, and it provides conditions that enhance biogeochemical cycling rates. Areas in the landscape may be converted to hot spots by the movement of water. Thus, an understanding of the role of hydrologic flowpaths in bringing together reactants is of utmost importance if we want to predict when and where biogeochemical hot spots will occur and how they might change with scale.

It is important to distinguish hot spots from the related concepts of spatial heterogeneity and ecotones, and to distinguish hot moments from the more generic concept of disturbance. A biogeochemical hot spot is a specific form of spatial heterogeneity represented by a patch of higher biogeochemical reaction rates. Biogeochemical hot spots commonly occur at the boundary or ecotone between two features in a landscape. However, not all biogeochemical hot spots are located at ecotones, and certainly not all ecotones are biogeochemical hot spots. Furthermore, although heterogeneities and ecotones are generally identified by some distinct change or difference in structure or abundance, hot spots are representations of process heterogeneity, or abrupt changes in *rates*, not structure. Lastly, a disturbance is "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). Many biogeochemical hot moments do indeed coincide with disturbances, but not all disturbances produce the increased rates of biogeochemical reactions that define hot moments.

In this paper, we briefly explore the conceptual constructs of hot spots and hot moments and present examples of how they influence biogeochemical cycles and processes. We focus on hydrologically coupled terrestrial and aquatic systems and trace the changing nature and importance of hot spots across different scales. Our goal is to develop a framework for the understanding of biogeochemical hot spots as they relate to hydrologic flowpaths. We conclude by discussing the implications of hot spots and hot moments for natural resource management and by offering some recommendations for future research.

What Are Biogeochemical Hot Spots and Hot Moments?

Biogeochemical hot spots are areas (or patches) that show disproportionately high reaction rates relative to the surrounding area (or matrix). Hot moments are short periods of time that show disproportionately high reaction rates relative to longer intervening time periods. Hot spots and moments may occur separately, but they may also overlap when high reaction rates occur for short periods of time in

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specific locations. The concepts can apply to either one or several biogeochemical reactions. However, hot spot reactions are often limited because one reactant is unstable in the dominant biogeochemical environment, or because the reaction only proceeds under particular/specific conditions (for example, anoxia). From a mechanistic standpoint, hot spots are sites where, and hot moments are times when, individual ingredients (reactants) for specific biogeochemical reactions coincide. A continuous source of reactants, often supplied by a hydrologic flowpath, is necessary to maintain high processing rates.

In theory, hot spots and moments may be defined at any spatial (molecular to global) or temporal (millisecond to eon) scale. Here we focus primarily on spatial scales ranging from cm ^{2} to 10^5 km^2 and on temporal scales ranging from minutes to centuries. We also limit our discussion to C and N cycling in terrestrial and freshwater aquatic systems. Next, we present some defining mechanistic characteristics of hydrologically mediated hot spots and hot moments.

Hot Spots Occur Where Hydrological Flow Paths Converge with Other Flow Paths or Substrates Containing Complementary Reactants

High biogeochemical processing rates are often sustained by converging hydrological flowpaths, where each flow carries materials essential to the reaction (Figure 1a). For example, the convergence of shallow and deep ground water flowpaths at stream margins may produce hot spots of denitrification. Hedin and others (1998) described one such hot spot along Smith Creek in southwestern Michigan. In this case, shallow anoxic ground water carrying electron donors (DOC, CH_4, and NH_4^+) converged with upwelling deep ground water carrying electron acceptors (NO_3^- and N_2O), creating a zone of high denitrification less than 1 m wide. The denitrification hot spot remained relatively stable over the 2-year duration of the sampling.

Hyporheic zones, the area of saturated sediments beneath and beside streams and rivers where ground water and surface water mix (Edwards 1998), are also ideal sites for the convergence of chemically distinct flowpaths and the development of hot spots. Harvey and Fuller (1998) described a hot spot of manganese (Mn) oxidation in the Pinal Creek basin of Arizona. In this case, low-pH, metal-rich ground water mixed with higher-pH surface water. The resulting increase in pH of the metal-rich water removed the thermodynamic constraints on Mn oxidation. The reaction was also released

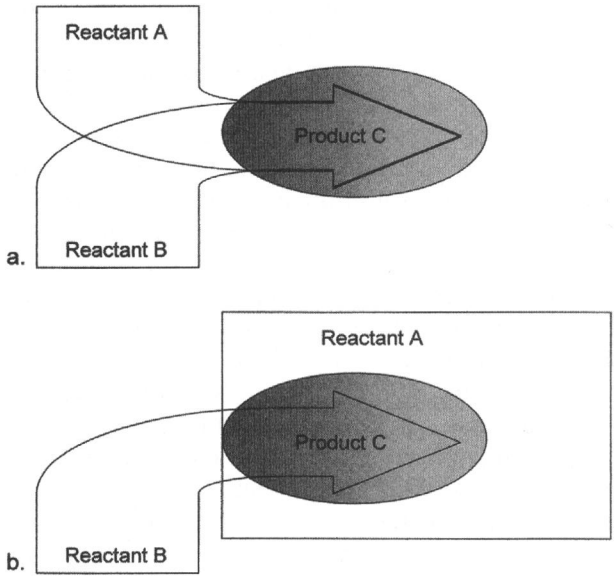

Figure 1. Schematic illustrations of hot spot formation (a) at the convergence of hydrologic flowpaths carrying complementary reactants or (b) where flowpath carries reactant A into a substrate containing reactant B.

from kinetic constraints by the abundance of surface sites with reactive sediment coatings (metal oxides and Mn-oxidizing bacteria). The degree of enhancement of the reaction was not only quantified at the fundamental scales of grains (in lab batch experiments) and in situ hyporheic flowpaths, but also at the stream-reach scale using solute tracers and modeling. The reach-scale investigation showed the larger-scale consequences of biogeochemical reactions that are enhanced in hyporheic zones.

Hot spots may also develop at the confluence of two rivers with contrasting chemistries. Perhaps the most striking example occurs at the confluence of the Negro and Solimões rivers, which drain different subbasins of the Amazon. The Negro River contains virtually no suspended sediments (Richey and others 1986) and relatively high concentrations of DOC (around 9 mg/L) (Richey and others 1990), whereas the Solimões River carries abundant suspended sediment (Richey and others 1986; Guyot and others 1998) but lower concentrations of DOC (around 4 mg/L) (Richey and others 1990). The convergence of these waters produces a hot spot of DOC sorption onto suspended sediment particles (Mounier and others 2002; Gadel and others 2000). Other examples of converging flowpaths that create biogeochemical hot spots may be found in estuaries where fresh and saline waters mix, and in the

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oceans where upwelling or downwelling brings together water of distinct chemistries.

A single hydrologica flowpath may also create a hot spot by transporting limiting reactants to a substrate containing the remaining reactants (Figure 1b). In desert stream sediments, hot spots of denitrification and respiration have been identified in association with plant roots (Schade and others 2001). Where subsurface flowpaths encountered the roots, there were immediate and substantial (from hundreds of micrograms per liter to zero micrograms per liter over centimeters of distance) reductions in nitrate (NO_3^--N) concentration, while oxygen consumption, denitrifying enzyme activity, and bacterial numbers increased. The plant roots provided the reactant (labile organic C from plant roots) missing from the subsurface flowpath.

Along the Boyne River in southern Ontario, ground water transports NO_3^- into organic-rich river channel deposits or peat, producing a hot spot of denitrification that is only a few meters wide (Hill and others 2000). Such streamside denitrification hot spots have become virtually synonymous with riparian zones. The actual hot spot, however, may occupy a relatively small portion of the riparian zone because these hot spots do not owe their existence to the riparian zone, per se, but to the movement of NO_3^- -rich ground water into an organic, reducing substrate. This collection of ingredients, and thus this type of hot spot, occurs not only in riparian zones but also in wetlands (Johnston and others 2001), hyporheic zones (Holmes and others 1996; Triska and others 1989), and individual soil profiles (Parkin 1987).

Hot Moments Occur When Episodic Hydrological Flowpaths Reactivate and/or Mobilize Accumulated Reactants

When hydrologic flowpaths are variable in time, hydrologically mediated hot spots may occur in restricted hot moments. During the intervening dry times, reactants often accumulate. The most striking examples occur in desert settings. During dry periods, biogeochemical processing rates in desert soils are very low, and N and C accumulate from dry deposition or leaf fall. Precipitation stimulates rapid mineralization and plant uptake (Noy-Meir 1973; Gallardo and Schlesinger 1992; Zaady and others 1996a, 1996b) as well as periods of elevated trace gas fluxes (Hartley and Schlesinger 2000). Both plants and microbes are able to exploit the episodic availability of nutrients, but temporal partitioning may prevent competition among different plant species (Gebauer and Ehleringer 2000). The arrival of water in the form of precipitation thus creates a hot moment for N mineralization and other N transformations (Davidson and others 1993). When all but one ingredient of a biogeochemical reaction are present, the system may be said to be *primed*, and only the addition of the final ingredient is required to generate the hot moment. Water is an essential reactant, catalyst, or medium for many reactions; thus, the coming and going of water commonly leads to the activation and deactivation of biogeochemical processes.

Hot moments linked to major disturbances (for example, hurricanes, landslides, fires) are well understood from the ecological standpoint. We would again, however, like to focus attention on the "missing reactant" concept for hot moment creation, as in the case of snowmelt creating a hot moment of DOC leaching in high-elevation or high-latitude watersheds. In Deer Creek, Colorado, DOC concentrations increased rapidly (from 1 to more than 4 mg/L) immediately following the initiation of snowmelt in late April, remained high over a period of approximately 1 month, and then decreased quickly as runoff peaked in early June (Boyer and others 2000). The effect was to flush the system of DOC accumulated under the snowpack. In fact, 82% of the annual mass flux of DOC from the stream occurred during a period representing less than 30% of the year (Boyer and others 2000). DOC flushing is the visible consequence of this hot moment, but the relevant processes in the C cycle were dissolution coupled with transport. Both the dissolution and the transport processes had been inactive because of a lack of liquid water. Hot moments of DOC flushing during snowmelt have been described by several other authors as well (Lewis and Grant 1979; Denning and others 1991; McKnight and Bencala 1990; Boyer and others 1997). Hot spots and hot moments often overlap. For example, the flushing of DOC from the riparian zone of lakes and rivers during a fall storm encompasses the ideas of both a hot spot (within the riparian zone) and a hot moment (during the storm event). However, not all hot spots occur within a hot moment, and not all hot moments are concentrated within a hot spot.

Although we focus our discussion wholly on hydrologically mediated hot spots and hot moments, hot spots and hot moments can also be nonhydrologic in nature (Table 1). A broader definition of biogeochemical hot spots and hot moments might include animal- or disturbance-mediated places and events. For example, grazing lawns produced by ungulates are also biogeochemical hot spots, and a broader view of hot moments could include events such as fire. In grazing lawns, the deposition of

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Table 1. Examples of Biogeochemical Hot Spots that Develop as a Result of Biological, Anthropogenic, or Physical Controls that are Nonhydrologic in Nature

Hot Phenomenon	Definition or Description of Hot Spot	Reference
Atmospheric deposition of N and pollutants	Landscape features that scavenge N and pollutants from the atmosphere	Weathers and others 2000, 2001
Heavy metal accumulation in aquatic animals	Localized aquatic environments in South Africa	Biney and others 1994
Aerosol metals (Ni, Zn, Cr) source	Local urban areas	Chester and others 2000
Air pollution (ozone concentration)	High-elevation catchment near Seattle, WA, USA	Peterson and others 1999
Groundwater contamination by DBCP	Localized groundwater plumes	Loague and Abrams 1999
N cycling	Grazing lawns produced by ungulates	McNaughton 1984
Increasing loads of N and acid deposition	Regions prone to depletion of soil buffering capacity	Busch and others 2001
Mobilization of nutrients	Creation of soil nutrient hot spots by microarthropods	Heneghan and Bolger 1998
Rates of bacterial production	Soils from the nests of snowy petrels	Harris and Tibbles 1997
N mineralization	Nematodes and protozoa on discrete organic substrates, including the rhizosphere	Griffiths 1994
Primary production	Gazelle movements tracking hot spots of primary production	Leimgruber and others 2001
N mobilization and distribution to downwind areas	Addition of anthropogenic N by food production in Asia (fertilizer and cultivation of legumes and rice)	Galloway 2000

N, nitrogen; Ni, nickel; Zn, zinc; Cr, chromium; DBCP,

urine and feces by ungulates helps maintain high productivity in the grasses, thus encouraging greater use of the site by grazers. Thus, such areas become hot spots of high rates of nutrient cycling (McNaughton 1984). Fire represents a hot moment (literally) in the lifetime of a forest community, where the heat of the fire and supply of oxygen from the atmosphere rapidly oxidize C and N to CO_2 and NO_x. As with the previously mentioned hot spots, an increased rate of elemental cycling occurs, and transport (whether in hydrological, biological, or gaseous flows) is a key component in the creation of the hot spot or hot moment. However, in contrast to the hydrologically controlled hot spots discussed earlier, the relevant transport vectors are not water.

How Do Hot Spots and Hot Moments Vary across Scales?

Hot spots can be delineated at spatial scales ranging from molecular to global, and hot moments can be delineated at time scales ranging from instants to millennia. As with all other forms of heterogeneity, the identification of hot spots and moments depends on the system of interest of the scale chosen for a study. As the extent under consideration increases, new, "hotter" hot spots may be encountered in the surrounding area. With increases in grain, hot spots might also disappear as they fall below the resolution of the study. Next, we describe how hot spots change with scale for the process of denitrification. For each example, we describe why the hot spot exists at that scale.

Denitrification is the conversion of NO_3^- to gaseous N (N_2O or N_2). It is performed by particular groups of ubiquitous heterotrophic bacteria that have the ability to use NO_3^- as an electron acceptor during anaerobic respiration. The factors controlling denitrification rates are C and NO_3^- supply and anoxia (Knowles 1981). Appropriate conditions for the formation of denitrification hot spots are found at oxic-anoxic interfaces crossed by a continual water flow. Oxic conditions are needed for NO_3^- production by nitrification, denitrification requires anoxic conditions, and water serves as the transport medium. The underlying physiological basis for denitrification remains the same irrespective of the scale of analysis. However, because direct measurement of denitrification is impossible at larger scales,

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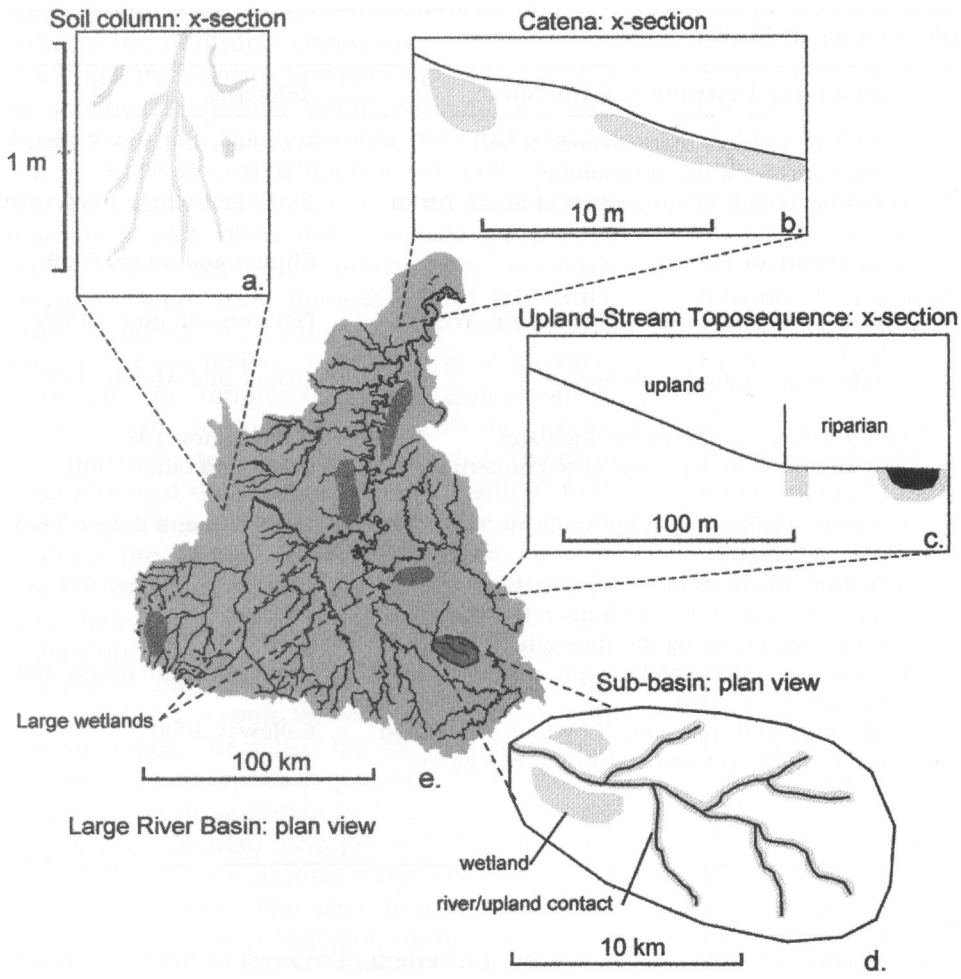

Figure 2. Hot spot of denitrification occur at multiple spatial scales. (a) Hot spots in a meter of soil may occur along root channels where moisture and organic matter content are high. (b) Topographic depressions that accumulate organic matter and retain moisture may be hot spots within a catena. (c) Along a toposequence from upland to river, the soil-stream interface may represent a hot spot where high-nitrate groundwater intercepts organic-rich soils. (d) At the scale of sub-basins, the occurrence of hot spots may be dictated by the spatial configuration of upland-wetland or upland-river contact zones. (e) The percentage of land occupied by wetland's determines denitrification hot spots at the scale of large river basins.

different metrics are used to assess denitrification hot spots across spatial scales ranging from soil profiles to larger basins.

At the scale of a soil profile (1–10 m), denitrification hot spots occur around patches of labile organic matter, for example, plant detritus or manure (Parkin 1987; Christensen and others 1990; Murray and others 1995; Petersen and others 1996); at the anaerobic center of large soil aggregates (Sexstone and others 1985; Seech and Beauchamp 1988; Højberg and others 1994); or in earthworm casts (Svensson and others 1986; Parkin and Berry 1994). Reactants are transported into these hot spots by percolating soil water or ground water (Figure 2a). Note that in the unsaturated zone, hydrological flowpaths will be intermittent, with strong seasonal variations. Thus, denitrification hot spots within unsaturated soil profiles will be active during hot moments.

At the catena scale (10–100 m), the distribution of anoxic zones is controlled by differences in soil texture and natural drainage that affect the duration and timing of soil saturation and the accumulation of organic matter (Pinay and others 2000; Groffman and Tiedje 1989; Pennock and others 1992; Groffman and others 1993; van Kessel and others 1993; Farrell and others 1996; Walley and others 1996). These factors also indirectly influence carbon and NO_3^- availability through their influence on plant community type and microbial activity (Beauchamp and others 1989; Svensson and others 1991).

At the scale of the upland to stream toposequence (circa 100–1000 m), the interface between the upland and riparian zones is typically a hot spot for denitrification. Denitrification is triggered by allochthonous NO_3^- input from uplands along ground water flowpaths (Figure 2c). In most cases, the hot spots for denitrification are at most a few meters wide at the upland margin of these features (Groffman and others 1992; Pinay and others 1993), although they can occur at the riverbed-wetland interface (Johnston and others 2001) or within the wetland or riparian zone, depending on

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the location of ground water flowpaths (Hill and others 2000) and seasonal variations (T. P. Burt and others unpublished). At the same scale, hot spots of denitrification have been identified within rivers in association with hyporheic zones. Instream denitrification is most prevalent at downwelling sites, that is, locations of surface water infiltration into hyporheic zones, where anoxic, organic c–rich subsurface zones receive downwelling NO_3^- from surface water (Triska and others 1984; Holmes and others 1996).

At the scale of 10–100 km, the width of the riparian zone is no longer resolvable and must be replaced by the length of contact between upland and wetland, where NO_3^- from upland sources is delivered to anoxic sites (Figure 2d). At very large scales (100 km and above), the amount of N lost due to denitrification is related to the percentage of land covered by wetlands (Jones and others 1976) (Figure 2e). Due to their anaerobic soils and large C supply, wetlands are hot spots of denitrification (Johnston 1991).

The use of metrics derived at one particular scale to evaluate the denitrification rates at broader or finer scales is typically unsuccessful, despite the fact that denitrification hot spots occur at multiple scales. For instance, at the 100–1000-m scale, riparian zones have been identified as important sites for the removal of upland-derived NO_3^- fluxes via denitrification (Peterjohn and Correll 1984; see Haycock and others 1997 for a review). Attempts to scale up this result by relating the presence of riparian wetlands to NO_3^- elimination via denitrification at the scale of 10–100-km^2 catchments have been largely unsuccessful (Burt and others 1988; Osborne and Wiley 1988; Tufford and others 1998). At this scale, the arrangement of the wetlands relative to the flowpaths is the most critical metric (Basnyat and others 1999; Creed and Band 1998; Johnston and others 1990); it is not captured by total amount of riparian wetland present, but rather is best characterized by length of contact between upland and wetland. For the same reason, attempts to scale down the inverse relationship between percentage of wetland in larger catchments (100 km^2 and above) to NO_3^- fluxes at the outlet of smaller catchments have also failed.

Management Implications of Hot Spots and Hot Moments

The spatial and temporal variability in biogeochemical processing attributed to hot spots and hot moments has important implications for natural resource management. In this paper, we have focused on N and organic C, which are important in such resource management problems as eutrophication, toxic algal blooms, hypoxia, heavy metal transport, soil impoverishment, and greenhouse gas fluxes to the atmosphere. To limit the extent and intensity of these problems, managers need to pay attention to the role of hot spots and hot moments as both sources and sinks of the forms of N and organic C that can cause the problems. However, the choice of management strategy depends on whether the hot spots and hot moments are "natural" or "created." In the case of wetlands, natural hot spots may need to be delimited and managed, whereas the creation of artificial hot spots may be desirable, as with artificial wetlands constructed for use in water purification. Hot moments may also be created, as has been done for thousands of years in slash-and-burn agriculture, but natural hot moments can only be anticipated.

The underlying principles of biogeochemical hot spots are already well integrated into the field of wastewater engineering. Bioreactors and other water treatment technologies are used to create artificial hot spots where reactants are combined under ideal thermodynamic conditions. Other created hot spots include constructed wetlands, planted riparian buffer strips, stormwater retention ponds, contour terraces, and hedgerows. In such areas, biogeochemical processes may be artificially stimulated, or physical traps may decrease the flux of elements fixed to sediment particles. Managers should incorporate naturally occurring hot spots into their management schemes, while taking care not to compromise the other ecosystem services provided by such hot spots.

Managers may view biogeochemical hot spots as tools in water quality management, but they should pay particular attention to the hydrologic mechanisms involved in hot spot creation, as well as the scale-dependent nature of hot spots. For example, riparian zones and wetlands are already well appreciated for their role as sinks for sediments and nutrients. In the case of denitrification hot spots, managers should devote attention to the delineation and use of zones *within* riparian zones and wetlands where water, reduced C, and NO_3^- co-occur (Clément and others 2002). On a basin or landscape scale, efforts to protect or create riparian zones should focus on areas immediately down-gradient of and thus hydrologically connected to, NO_3^- source areas (for example, fertilized fields or feed lots). Although a general policy that emphasizes the protection and restoration of riparian zones is laudable, managers should recognize that certain riparian

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zones may be more important due to their position (and hydrologic connectivity) in the basin.

Priorities for Research into Biogeochemical Hot Spots and Hot Moments

Across the international scientific and management communities, there is a growing sense of urgency about the need to improve our understanding of life-sustaining biogeochemical cycles and the human activities that affect them. In a recent report entitled "Grand Challenges in Environmental Sciences," the National Research Council stressed the need to develop methods for predicting the impacts of perturbations at local, regional, and global scales and to find ways to restore these cycles to more natural states (NRC 2001). The development of a more systematic and quantitative understanding of hot spot and hot moment processes is essential to these goals.

We have identified four priorities for future research; (a) to investigate the nature and occurrence of natural hot spots and hot moments in the cycles of a larger number of elements and at different scales; (b) to hone our ability to predict the spatial distribution of hot spots and the temporal distribution of hot moments based on underlying hydrologic, geomorphic, or edaphic patterns in space and time; (c) to use the methods of landscape ecology to evaluate the roles of hot spots and moments in landscape biogeochemistry; and (d) to evaluate the utility of natural and created hot spots and hot moments as resource management tools.

Fundamental to this research is the assessment of the potential importance of hot spot and hot moment phenomena in the cycling of different bioactive elements. Studies of C and N cycling at various scales have clearly pointed to the importance of hot spots and hot moments. Each of these elements has important components of its larger cycle that take place only under atypical conditions—namely, anoxia. It follows that these reactions would occur only in limited spaces and over short time periods. It is thus important to this research to determine where within the cycles of other elements similarly specialized reactions occur and what particular conditions (for example, anoxia, high temperatures, wetting-drying cycles, and so on) are required. Furthermore, the interaction of biogeochemical cycles of different elements is fundamental to hot spot and hot moment concepts because the missing reactants are often those associated with a different element (for example, limitation of N_2 fixation by metal enzyme cofactors whose availability may be strongly linked to redox). Thus, knowing whether hot spots or hot moments converge for different elements may be essential for predicting maximum process rates (or conversely, limitation).

One especially challenging research priority concerns the need to assess the role of hot spot processes in large-scale systems. This determination is particularly critical at ecosystem, landscape, and regional scales, where whole-system estimates of biogeochemical processes are often based on the extrapolation of plot-based measurements to larger scales. For example, soil–atmosphere trace gas fluxes are often measured in small (for example, 0.25-m^2) chambers and extrapolated to ecosystem (for example, 100-m^2) or even larger areas. Whole-system estimates based on such extrapolations are susceptible to significant error if the chamber-based sampling design misses hot spots or the frequency of sampling misses hot moments. One way to minimize these errors is to verify extrapolation-based estimates with some type of whole-system measurements. For example, chamber-based estimates of trace gas fluxes from ecosystems can be verified using micrometeorological methods that measure fluxes over larger scales. Divergence between the methods can point to the presence of hot spots or hot moments in the landscape. It is interesting to note that the observation in the 1970s of low NO_3^- concentrations in streams draining watersheds dominated by agricultural land use was a factor that ultimately led to the discovery of riparian zones as hot spots for the denitrification of NO_3^- at the watershed scale. Thus, it is important to compare of the methods used at mutiple scales where hot spots and hot moments may be relevant.

The emergence of new tools and large collaborative programs also promises to improve the ability of ecosystem scientists to deal with biogeochemical heterogeneity and hot spots across multiple scales. Large collaborative projects such as BOREAS (Boreal Ecosystem–Atmosphere Study) and NOWES (Northern Wetlands Study) and instruments such as MODIS (the moderate resolution imaging spectroradiometer) have helped to foster integrative science, calibrate data collected at different scales, and develop and refine new techniques (for example the remote sensing of vegetation and eddy correlation measurements) (Hall 2001; Glooschenko and others 1994; Hook and others 2001). Techniques for remotely measured parameters—such as canopy light interception, for example—are improving our ability to infer ecosystem behavior at broad scales (Schimel and others 1991), while remote sensing of surface fluxes and vegetation is resolving ever finer

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scales. Advances made in remote sensing techniques at finer scales will become increasingly useful to ecosystem ecologists as they attempt to scale up. The eventual amalgamation of data from the plot-level studies routinely performed by ecologists with the broader-scale measurement techniques of geographers and global ecologists will be fundamental in solving problems of scaling up and scaling down whole-system budgets.

Our ability to predict the location of hot spots, or the time of occurrence of a hot moment, might be improved by expanding our understanding of the spatial and temporal hydrologic, geomorphic, and edaphic templates that underlie larger landscapes. Thus, there is a need for research—and tools—mapping spatiotemporal patterns of physical conditions to optimum hot spot or hot moment conditions. As an example, we know from hydrologic research that there are preferential flowpaths that potentially support large fluxes of water from landscapes to water bodies. If missing reactants are carried via such routes to "primed" streamside locations, hot spots are likely to develop there. Yet we lack precise tools to predict the spatial location of these flowpaths and thus to accurately map hot spots to the landscape features that might control their distribution.

Existing concepts and models of ecosystem biogeochemistry are most applicable to homogeneous systems that have only minimal exchanges with other ecosystems (Schimel and others 1991). Landscape ecological approaches can be used to determine such fundamental methodological issues as when it is necessary to consider the spatial arrangement of landscape elements. For example, landscape indicators of cover (such as percentage of agricultural land use or wetlands in a watershed) have been used to predict a variety of water chemistry parameters (N, Phosphorus [P], DOC) (Gergel and others 2002). Interesting questions arise when proportional metrics fail: When is a spatially explicit approach necessary to understand watershed function? Does the utility of a spatially explicit approach vary by the percent of watershed disturbed, or by watershed size, or by elemental flux? Landscape ecology, a discipline inherently focused on the role of spatial heterogeneity, is informed by the use of the spatial tools for example, remote sensing, GIS, and spatial modeling—that initially helped to spawn it. Many of the tools of landscape ecology could be used to develop a deeper conceptual spatial framework for the understanding of biogeochemical fluxes.

For natural resource managers to be able to utilize hot spot and hot moment phenomena as tools in management programs, the research community must address more pragmatic questions. To achieve management goals, solid information is required on the specific capabilities of hot spots and hot moments. Which hot processes are most effective against which kinds of pollution? Where exactly in the system (that is, in which landscape features) are these pollution-reduction processes most efficient? What is the throughput of polluted water in these features (for example, riparian zones or wetlands)? What are the concentrations and flow thresholds at which the efficiency of these processes drop off or do other services become compromised? How do efficiencies and thresholds vary with season and time? The answers to these and similarly detailed questions will enable planners and engineers to integrate hot spots and hot moments into system designs. For natural and constructed riparian zones and wetlands, some progress has been made toward generating this sort of engineering-relevant information so that N and P runoff can be reduced (for example, see Mander and others 1997; Uusi-Kamppa and others 2000).

There are also issues that must be addressed regarding the economic tradeoffs entailed by conserving landscape features for water quality management instead of developing them for other purposes. Finally, an effort must be made to investigate the impact of anthropogenic disturbances on hot spot and hot moment processes. The unprecedented number of forest fires in recent years has served as a dramatic illustration of how forest management practices can exacerbate the hot moment phenomenon of fire. The deforestation of riparian zones and the drainage of wetlands are other widespread anthropogenic disturbances that invariably affect hot spot functions. How are other hot spot and hot moment phenomena being affected by the human alteration of relevant landscape features, and what are the ramifications for the utility of these processes in natural resources management? These are the types of questions that should drive research priorities and shape the research agenda in the coming decade.

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REFERENCES

Attrill MJ, Ramsay PM, Thomas RM, Trett MW. 1996. An estuarine biodiversity hot-spot. J Mar Biol Assoc UK 76:161–75.

Balmford A, Deutsch JC, Nefdt RJC, Clutton-Brock T. 1993. Testing hotspot models of elk evolution. Behav Ecol Sociobiol 33:57–65.

Basnyat P, Teeter LD, Flynn KM, Lockaby BG. 1999. Relationships between landscape characteristics and nonpoint source pollution inputs to coastal estuaries. Environ Manag 23:539–49.

Beauchamp EG, Trevors JT, Paul JW. 1989. Carbon sources for bacterial denitrification. Adv Soil Sci 10:113–42.

Biney C, Amuzu AT, Calamari D, Kaba N, Mbome IL, Naeve H, Ochumbaz, Osibanjo O, Radegonde V, Saad MAH. 1994. Review of heavy metals in the African aquatic environment. Ecotoxicol Environ Safety 28:134–59.

Boyer EW, Hornberger GM, Bencala KE, McKnight DM. 2000. Effects of asynchronous snowmelt on flushing of dissolved organic carbon. Hydrol Proc 14:3291–308.

Boyer EW, Hornberger GM, Bencala KE, McKnight DM. 1997. Response characteristics of DOC flushing in an alpine catchment. Hydrol Proc 11:1635–47.

Braccia A, Batzer DP. 2001. Invertebrates associated with woody debris in a southeastern U.S. forested floodplain wetland. Wetlands 21:18–31.

Burt TP, Pinay G, Matheson FE, Haycock NE, Butturini A, Clément JC, Danielescu S, Dowrick DJ, Hefting MM, Hilbricht-Ilkowska A, and others. Water table fluctuation in the riparian zone: comparative results from a pan-European experiment. J Hydrol. Forthcoming.

Burt TP, Arkell BP, Trudgill ST, Walling DE. 1988. Stream nitrate levels in a small catchment in south west England over a period of 15 years (1970–1985). Hydrol Proc 2:267–84.

Bury RB, Pearl CA. 1999. Klamath-Siskiyou herpetofauna. Nat Areas J 19:341–50.

Busch G, Lammel G, Beese FO, Feichter J, Dentener FJ, Roelofs GJ. 2001. Forest ecosystems and the changing patterns of nitrogen input and acid deposition today and in the future based on a scenario. Environ Sci Poll Res 8(2):95–102.

Chester DK, Degg M, Duncan AM, Guest JE. 2000. The increasing exposure of cities to the effects of volcanic eruptions. Global Environ Change B 2:89–103.

Christensen S, Simkins S, Tiedje JM. 1990. Spatial variation in denitrification. Soil Sci Soc Ame J 54:1608–13.

Clément JC, Pinay G, Marmonier P. 2002. Seasonal dynamics of denitrification along topohydrosequences in three different riparian wetlands. J Environ Qual 31:1025–37.

Cowling RM, MacDonald IAW, Simmons MT. 1996. The Cape Peninsula, South Africa. Biodivers Conserv 5:527–50.

Creed IF, Band LE. 1998. Export of nitrogen from catchments within a temperate forest. Water Resources Res 34:3105–20.

Davidson EA, Matson PA, Vitousek PM, Riley R, Dunkin K, Garcia-Mendez G, Maass JM. 1993. Processes regulating soil emissions of nitric oxide and nitrous oxide in a seasonally dry tropical forest. Ecology 74:130–9.

Denning AS, Baron J, Mast MA, Arthur M. 1991. Hydrologic pathways and chemical composition of runoff during snowmelt in Loch Vale watershed, Rocky Mountain National Park, Colorado USA. Water Air Soil Pollu 59:107–23.

Dobson AP, Rodriguez JP, Roberts WM, Wilcove DS. 1997. Geographic distribution of endangered species in the United States. Science 275:550–53.

Edwards RT. 1998. The hyporheic zone. In: Naiman RJ, Bilby RE, editors. River ecology and management. New York: Springer-Verlag. p 399–429.

Farrell RE, Sandercock PJ, Pennock DJ, Vankessel C. 1996. Landscape-scale variations in leached nitrate. Soil Sci Soc Am J 60:1410–15.

Flather CH, Knowles MS, Kendal IA. 1998. Threatened and endangered species geography. BioScience 48:365–76.

Gadel F, Serve L, Benedetti M, Da Cunha LC, Blazi JL. 2000. Biogeochemical characteristics of organic matter in the particulate and colloidal fractions downstream of the Rio Negro and Solimões rivers confluence. Agronomie 20:477–90.

Gallardo A, Schlesinger WH. 1992. Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. Biogeochemistry 18:1–17.

Galloway JN. 2000. Nitrogen mobilization in Asia. Nutri Cycl Agroecosyst 57(1):1–12.

Gebauer RLE, Ehleringer JR. 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81:1415–24.

Gergel SE, Turner MG, Miller JR, Stanley EH, Melack JM. 2002. Landscape indicators of human impacts to riverine systems. Aquati Sci 64:118–128.

Glooschenko WA, Roulet NT, Barrie LA, Schiff HI, Mcadie HG. 1994. The Northern Wetlands Study (Nowes) - An Overview. J Geophys Res-Atmos 99 (D1):1423–1428.

Griffin PC. 1999. Endangered species diversity 'hot spots' in Russia and centers of endemism. Biodivers Conserv 8:497–511.

Griffiths BS. 1994. Microbial-feeding nematodes and protozoa in soil—their effects on microbial activity and nitrogen mineralization in decomposition hotspots and the rhizosphere. Plant Soil 164(1):25–33.

Groffman PM, Gold AJ, Simmons RC. 1992. Nitrate dynamics in riparian forests. J Environ Qual 21:666–71.

Groffman PM, Rice CW, Tiedje JM. 1993. Denitrification in a tallgrass prairie landscape. Ecology 74:855–62.

Groffman PM, Tiedje JM. 1989. Denitrification in north temperate forest soils. Soil Biol Biochem 21:613–20.

Guyot JL, Callède J, Molinier M, Guimarães V, Oliviera E. 1998. La variabilité des débits des principaux fleuves du bassin amazonien. Bull Inst Fr Etudes Andines 27:779–88.

Hall FG. 2001. Introduction to special section: BOREAS III. J Geophys Res-Atmos 106 (D24):33511–33516.

Hapke B, Dimucci D, Nelson R, Smythe W. 1996. The cause of the hot spot in vegetation canopies and soils. Remote Sens Environ 58:63–8.

Harris JM, Tibbles BJ. 1997. Factors affecting bacterial productivity in soils on isolated inland nunataks in continental Antarctica. Microb Ecol 33(2):106–23.

Hartley AE, Schlesinger WH. 2000. Environmental controls on nitric oxide emission from northern Chihuahuan Desert soils. Biogeochemistry 50:279–300.

Harvey JW, Fuller CC. 1998. Effect of enhanced manganese oxidation in the hyporheic zone on basin-scale geochemical mass balance. Water Resources Res 34:623–36.

Haycock NE, Burt TP, Goulding KWT, Pinay G. 1997. Buffer zones. Hertfordshire (UK): Quest Environmental.

Hedin LO, Von Fischer JC, Ostrom NE, Kennedy BP, Brown MG,

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Robertson GP. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. Ecology 79:684–703.

Heneghan L, Bolger T. 1998. Soil microarthropod contribution to forest ecosystem processes. Plant Soil 205(2):113–24.

Hill AR, Devito KJ, Campagnolo S, Sanmugadas K. 2000. Subsurface denitrification in a forest riparian zone. Biogeochemistry 51:193–223.

Højberg O, Revsbech NP, Tiedje JM. 1994. Denitrification in soil aggregates analyzed with microsensors for nitrous oxide and oxygen. Soil Sci Soc Am J 58:1691–98.

Holmes RM, Jeremy J, Jones B, Fisher SG, Grimm NB. 1996. Denitrification in a nitrogen-limited stream ecosystem. Biogeochemistry 33:125–46.

Hook SJ, Meyers JEJ, Thome KJ, Fitzgerald M, Kahle AB. 2001. The MODIS/ASTER airborne simulator (MASTER) - a new instrument for earth science studies. Remote Sens Environ 76:93–102.

Hynes HBN. 1975. The stream and its valley. Verh Int Verein Limnol 19:1–15.

Johnston CA, Detenbeck NE, Niemi GJ. 1990. The cumulative effect of wetlands on stream water quality and quantity. Biogeochemistry 10:105–41.

Johnston CA. 1991. Sediment and nutrient retention by freshwater wetlands. Crit Rev Environ Control 21:491–565.

Johnston CA, Bridgham SD, Schubauer-Berigan JP. 2001. Nutrient dynamics in relation to geomorphology of riverine wetlands. Soil Sci Soc Am J 65:557–77.

Jones JR, Bokofka BP, Bachmann RW. 1976. Factors affecting nutrient loads in some Iowa streams. Water Res 10:117–22.

Knowles R. 1981. Denitrification. In: Paul EA, Ladd JN, editors. Soil biochemistry; vol 5. New York: Marcel Dekker.

Leimgruber P, McShea WJ, Brookes CJ, Bolor-Erdene L, Wemmer C, Larson C. 2001. Spatial patterns in relative primary productivity and gazelle migration in the eastern steppes of Mongolia. Biol Conserv 102(2):205–12.

Lewis WM Jr, Grant MC. 1979. Relationships between flushing and yield of dissolved substances from a mountain watershed. Soil Sci 128:353–63.

Loague K, Abrams RH. 1999. DBCP contaminated groundwater. hot spots and nonpoint sources. J Environ Qual 28:429–46.

Lombard AT, Cowling RM, Pressey RL, Mustart PJ. 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas plain, South Africa. Conserv Biol 11:1101–16.

Lowrance R, Todd R, Fail J Jr, Hendrickson O Jr, Leonard R. 1984. Riparian forests as nutrient filters in agricultural watersheds. BioScience 34:374–7.

McKnight DM, Bencala KE. 1990. The chemistry of iron, aluminum, and dissolved organic material in three acidic, metal-enriched, mountain streams, as controlled by watershed and in-stream processes. Water Resources Res 26:3087–100.

McNaughton SJ. 1984. Grazing lawns. Am Nat 124:863–86.

Mander U, Kuusemets V, Lohmus K, Mauring T. 1997. Efficiency and dimensioning of riparian buffer zones in agricultural catchments. Ecol Eng 8:299–324.

Mounier S, Benedetti M, Benaim JY, Boulegue J. 2002. Organic matter size and dynamics in the Amazon river. In: McClain ME, editor. The ecohydrology of South American Rivers and wetlands.: Special publication no. 6. International Association of Hydrological Sciences.

Murray RE, Feig YS, Tiedje JM. 1995. Spatial heterogeneity in the distribution of denitrifying bacteria associated with denitrification activity zones. Appl Environ Microbiol 61:2791–3.

Noy-Meir I. 1973. Desert ecosystems. Annu Rev Ecol Syst 4:25–51.

[NRC] National Research Council. 2001. Grand challenges in environmental sciences. Washington (DC): National Academy Press.

Osborne LL, Wiley MJ. 1988. Empirical relationships between land use/cover and stream water quality in an agricultural watershed. J Environ Manag 26:9–27.

Parkin TB. 1987. Soil microsites as a source of denitrification variability. Soil Sci Soci Am J 51:1194–9.

Parkin TB, Berry EC. 1994. Nitrogen transformations associated with earthworm casts. Soil Biol Biochem 26:1233–8.

Pennock DJ, van Kessel C, Farrell RE, Sutherland RA. 1992. Landscape-scale variations in denitrification. Soil Sci Soc Am J 56:770–6.

Peterjohn WT, Correll DL. 1984. Nutrient dynamics in an agricultural watershed. Ecology 65:1466–75.

Petersen SO, Nielsen T, Frostegard A, Olesen T. 1996. O_2uptake, C metabolism and denitrification associated with manure hotspots. Soil Biol Biochem 28:341–9.

Peterson DL, Bowers D, Brace S. 1999. Tropospheric ozone in the Nisqually River drainage, Mount Rainier National Park. Northwest Sci 73:241–54.

Pickett STA, White PS. 1985. The ecology of natural disturbance and patch dynamics. New York: Academic Press.

Pinay G, Black VJ, Planty-Tabacchi AM, Gumiero B, Décamps H. 2000. Geomorphic control of denitrification in large river floodplain soils. Biogeochemistry 30:9–29.

Pinay G, Roques L, Fabre A. 1993. Spatial and temporal patterns of denitrification in riparian forest. J Appl Ecol 30:581–91.

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystones. BioScience 46:609–20.

Richey JE, Hedges JI, Devol AH, Quay PD, Victoria RL, Martinelli LA, Forsberg BR. 1990. Biogeochemistry of carbon in the Amazon River. Limnol Oceanogr 35:352–71.

Richey JE, Meade RH, Salati E, Devol AH, Nordin CF Jr, dos Santos U. 1986. Water discharge and suspended sediment concentrations in the Amazon River: 1982–1984. Water Resources Res 22:756–64.

Schade JD, Fisher SG, Grimm NB, Seddon JA. 2001. The influence of a riparian shrub on nitrogen cycling in a Sonoran Desert stream. Ecology 82:3363–76.

Schimel DS, Kittel TGF, Parton WJ. 1991. Terrestrial biogeochemical cycles - Global interactions with the atmosphere and hydrology. Tellus A 43:188–203.

Seech AG, Beauchamp EG. 1988. Denitrification in soil aggregates of different sizes. Soil Sci Soc Am J 52:1616–21.

Sexstone AJ, Revsbech NP, Parkin TB, Tiedje JM. 1985. Direct measurement of oxygen profiles and denitrification rates in soil aggregates. Soil Sci Soc Am J 49:645–51.

Sutherland RA, Vankessel C, Farrell RE, Pennock DJ. 1992. Landscape-scale variations in plant and soil nitrogen-15 natural abundance. Soil Sci Soc Am J 57:169–78.

Svensson BH, Bostrom U, Klemedtsson L. 1986. Potential for higher rates of denitrification in earthworm casts than in the surrounding soil. Biol Fertil Soils 2:147–9.

Svensson BH, Klemedtsson L, Simkins S, Paustian K, Rosswall T.

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1991. Soil denitrification in three cropping systems characterized by differences in nitrogen and carbon supply. Plant Soil 138:257–71.

Tomlinson TE. 1970. Trends in nitrate concentrations in English rivers in relation to fertilizer use. Water Treat Exam 19:277–93.

Triska FJ, Kennedy VC, Avanzino RJ, Zellweger GW, Bencala KE. 1989. Retention and transport of nutrients in a third-order stream in northwest California. Ecology 70:1894–905.

Triska FJ, Sedell JR, Cromack K, Gregory SV, McCorison FM. 1984. Nitrogen budget for a small coniferous forest stream. Ecol Monogr 54:119–40.

Tufford DL, McKellar HNM, Hussey JR. 1998. In-stream nonpoint source nutrient prediction with land-use proximity and seasonality. J Environ Qual 27:100–11.

Uusi-Kamppa J, Braskerud B, Jansson H, Syversen N, Uusitalo R. 2000. Buffer zones and constructed wetlands as filters for agricultural phosphorus. J Environ Qual 29:151–8.

van Kessel C, Pennock DJ, Farrell RE. 1993. Seasonal variations in denitrification and nitrous oxide evolution at the landscape scale. Soil Sci Soc Am J 57:988–95.

Walley FL, Vankessel C, Pennock DJ. 1996. Landscape-scale variability of N mineralization in forest soils. Soil Biol Biochem 28:409–17.

Weathers KC, Cadenasso ML, Pickett STA. 2001. Forest edges as nutrient and pollutant concentrators. Conserv Biol 15:1506–14.

Weathers KC, Lovett GM, Likens GE, Lathrop R. 2000. The effect of landscape features on deposition to Hunter Mountain, Catskill Mountains, New York. Ecol Appl 10:528–40.

Zaady E, Groffman PM, Shachak M. 1996a. Litter as a regulator of nitrogen and carbon dynamics in macrophytic patches in Negev desert soils. Soil Biol Biochem 28:39–46.

Zaady E, Groffman PM, Shachak M. 1996b. Release and consumption of nitrogen from snail feces in Negev desert soils. Biol Fertil Soils 23:399–405.

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