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Biogeochemistry research needs: observations from the ecosystem studies program of The National Science Foundation

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Abstract. This comment presents current and emerging areas of research which the U.S. National Science Foundation believes have special promise for advancing ecosystem science. These areas are: (1) major element cycle interactions; (2) trace element and organic compound controls on ecosystem dynamics; (3) the role of consumers on ecosystem dynamics; (4) ecosystem dynamics in contrasting environments; (5) landscape ecology; and (6) enhancement of theory and methodology. The Ecosystem Studies Program of the National Science Foundation has identified these as areas to be emphasized in its long range planning program (revised March, 1985). Biogeochemical studies are emphasized in many of these research priority areas.

Introduction

The division of Biotic Systems and Resources of the U.S. National Science Foundation (NSF), which contains the Ecosystem Studies Program, funds about 90% of the basic research carried on by U.S. colleges and universities in the disciplines of systematics, population biology, physiological ecology, non-marine general ecology and ecosystem science. The Division funds 55–60% of all basic and applied work in these areas at those U.S. institutions (NSF 84–336). Extensive contact with the academic research community through proposal review, panel meetings, program site reviews, workshops, conferences and rotating program officers allows program officers in the Division to integrate current views within the research community. These integrations are used to update the priorities of the programs.

Areas of emphasis: Ecosystem Studies Program

This comment identifies research areas for emphasis in biogeochemistry and ecosystem science derived from the contact between the Ecosystem Studies Program and the research community. A thorough literature review on each topic is beyond the scope of this paper; however, selected examples will be used to characterize topics. These topics are not independent and each must be considered in the context of the others.

I. *Major element cycle interactions*

Much of the literature of ecosystem science and biogeochemistry deals with cycles of elements, but there is a bias toward separating individual cycles to characterize them. Thus, we have abundant literature on *the* N cycle, *the* P cycle and *the* S cycle. There is little theory or conceptual base for the coupling and interactions of those element cycles. The elements most commonly studied, carbon, nitrogen, phosphorus and sulfur, are linked to each other by biotic and abiotic processes in ecosystems. Primary production links elements by incorporation into tissue, but primary production also is influenced by dynamic and variable interactions of elements subject to both abiotic and biotic control. McGill and Christie (1983) provided a general analysis of major element interactions in soil-plant systems. There, C provides the energy to drive nutrient cycles at the organism level and the skeleton on which to store many elements at the system level. Phosphorus is provided by parent geological material and the supply and rate of cycling of P control the size of the biological and organic components (C skeleton) of the system. Nitrogen and S, primary sources being the atmosphere, link the source of energy (C) with the vehicle controlling its cycling rate (P). McGill and Christie postulate that at the ecosystem level, N and S are functions of the system and respond to fundamental controls (e.g., P supply, climate). They are not of themselves fundamental controls but can alter the environment (e.g., pH) of organisms essential to the system. The stoichiometry of C, N, S and P in soil-plant systems is described as a function of the system, not of one particular group of organisms.

The above general analysis indicates some of the complexity in interactions of different element cycles. Each element has unique chemical characteristics that contribute to variations in such factors as optimal and limiting levels, degree of interaction with other elements, temporal patterns of availability and use and spatial patterns of availability and use. The myriad biological processes which differentially control various element fluxes may be under multiple element limitations. The interactions of elements may be indirect, such as affecting the oxidation-reduction conditions that control the dynamics of other elements. The interactions may be related through different hierarchical levels; one level (e.g., microbial release through mineralization) influencing another level (e.g., ecosystem productivity and element incorporation). Future research must accomodate multiple limiting factors, spatial and temporal scales and multiple hierarchical levels – a difficult task.

II. *Trace element and organic compound controls on ecosystem dynamics*

A. *Trace elements.* Most ecosystem studies emphasize the major elements. However, there are 25–30 elements in organic tissue that may interact in ways that influence macronutrient dynamics. A good example is that of sulfate inhibition of molybdenum (Mo) uptake resulting in nitrogen limitation

(Howarth and Cole, 1985). Molybdenum is a necessary trace element for nitrogen fixation and nitrate reduction. Silvester (1985) reported widespread enhancement of nitrogenase activity in forest floor samples due to Mo additions. Stimulation of nitrogen fixation rates up to six times the control rates was found and even where control rates were high, such as the eastern slopes of the Coast Range in Oregon, Mo addition caused significant enhancement. In Oregon and Washington, the geographic range of Mo stimulation was generally confined to the area between the peaks of the Coast and Cascade Ranges.

The analysis can become very complex if an evaluation is made of factors influencing the interactions among trace elements which ultimately determine the influence of an element such as Mo on macronutrient availability (i.e. controls of controls of nutrient dynamics). Figure 1 was developed from a number of studies that identified from one to several of the relationships between trace metal anions, macronutrients and environmental parameters.

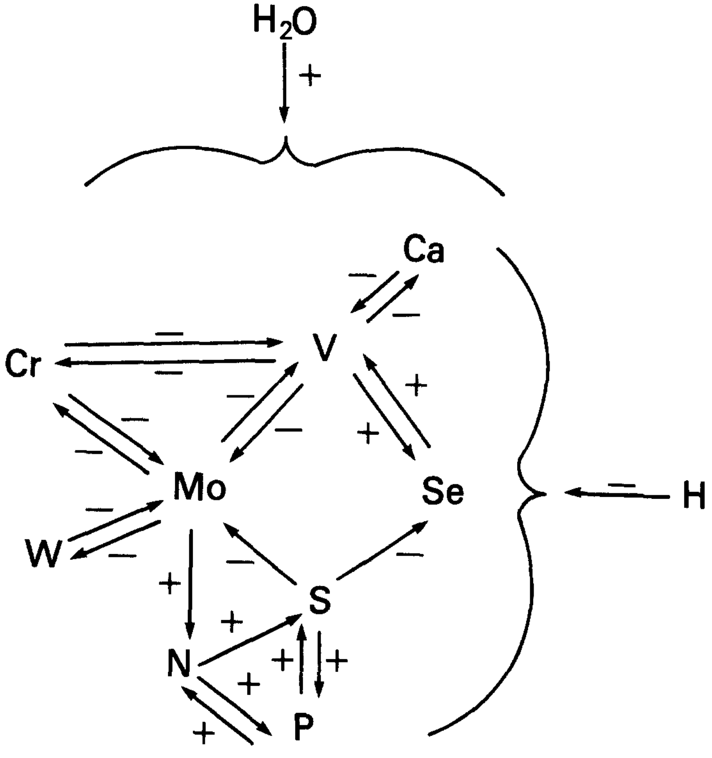

Figure 1. Conceptual relationship among various trace elements, macronutrients and environmental influences (H_2O, H^+). Positive (+) and negative (—) signs associated with arrows refer to documented synergistic and antagonistic interactions, respectively.

Let me emphasize that this figure was synthesized from the literature; no single study has come close to evaluating all the interactions shown. The point is that many factors in addition to sulfate can interact antagonistically with a required microelement such as Mo. Molybdenum is only one example. Interesting hypotheses also could be developed for other element-micronutrient interactions based simply on chemical properties and affinities.

Important interactions also occur in the control of toxic and inhibitory trace elements by macronutrients. Rorison (1985) provides examples of how nitrate enhances aluminum uptake and toxicity in plants. This may figure importantly in why plant species occurring on acidic or calcareous soils differ in their response to sources of nitrogen (ammonium vs. nitrate).

B. *Organics*. Ecosystem studies rarely include detailed analyses of organic chemicals and so are generally unable to evaluate their importance. Organic analyses which are made often are general (e.g., lignin, total phenols) and although correlated with some ecosystem processes, do not have the detail to identify true cause. For example, nitrogen cycling rates are known to be affected by the influence of plant organics on decomposition, mineralization and inhibition of nitrification (Swift et al., 1979; McClaugherty et al., 1980; Lodhi and Killingbeck, 1980). However, it is not known if N availability causes those organics (secondary plant chemicals) to be produced or if other environmental conditions influence the organics that determine N cycling rates. Some laboratory studies have demonstrated that nutrient deficiencies alter plant secondary chemistry while others indicate nutrient variation is unrelated to plant secondary chemistry (Waring et al., 1985).

Over the past several years, particularly since 1975, considerable theoretical development and experimental work has been carried out in an effort to determine the roles of the secondary metabolites or natural plant products in biological systems. At one end of the spectrum these compounds have been described as waste products serving no function in the plant (Robinson, 1974). At the other end of the spectrum, the compounds are described as important in maintaining the nutrient capital of the ecosystem by reducing nutrient availability and minimizing rates of loss (Rice and Pancholy, 1974). There are large differences in predictions of the types and quantities of compounds present in plants, depending on whether the studies are aimed at plant adaptation, plant-herbivore interaction, plant-pathogen interactions or decomposition-mineral cycling. This confusion arises, in part, from the qualitative chemical approach of some studies versus the narrow, specific and quantitative nature of other studies. Also contributing are inadequate methodology, confusion over how ‘stress’ is defined and the reliance on correlative data (see Martin and Martin 1982 for a review). It would seem that the key to understanding the role of secondary metabolites on biogeochemistry would be for nutrient cycling studies to develop more detail on the organic chemistry involved in the living plant, its litter, and the soil and for investigators of plant-animal studies to broaden their studies to include more aspects of the ecosystem.

Any discussion of inorganic and organic factors soon leads to an appreciation of the complexity of ecosystems and our current limitations to understand the controls of phenomena such as nutrient cycling. For example, we accept too easily a conclusion that, because an element such as nitrogen cycles slowly or is present in low quantities, the system is 'nitrogen limited'. This apparent deficiency of available nitrogen has been assumed to be a factor controlling the productivity of the ecosystem. Whether the apparent nitrogen limitation is truly limiting the system or is only a *symptom* of other limiting factors has not received critical attention. The examples presented expose the weakness of interpretations based on single factors investigated in isolation.

III. *Role of consumers on ecosystem dynamics*

There are many examples of how animals alter the movement of materials in ecosystems far beyond the degree of influence that their small mass, nutrient and energy demands would indicate. One of the best documented examples is the processing of litter material by invertebrates that allows fungal and bacterial decomposition to proceed twice as fast (Swift et al., 1979). Clarholm (1981) demonstrated that soil invertebrates significantly increased nutrient availability to plants by consuming fungi and bacteria. Examples of the effects of herbivory on the plant community are both positive and negative (Mattson and Addy, 1975). The processing of plant material, living or dead, can influence a number of ecosystem processes through complex feedback mechanisms.

The role of consumers in creating disturbance (i.e., spatial and temporal variation) as well as influencing community response to those changes (e.g., seed dispersal, pollination, selective herbivory) represents a powerful regulating factor that has to be included in ecosystem science. It will be a fundamental aspect of studies at the mosaic and landscape scale. Whether these phenomena are identified as disturbance or normal and predictable ecosystem pattern is related to the scale at which the environment is viewed.

The vast majority of ecosystem studies focus on the aboveground component (the easy part). The belowground and the role of its consumers are poorly understood, as is the interaction between above- and belowground consumers. Ingham and Detling (1984) demonstrated that grassland areas with high herbivory from prairie dogs and bison also had high herbivory rates for root-feeding nematodes. Plants subject to these consumers had higher nutrient levels than ungrazed control plants. It is not known to what degree aboveground consumers influence consumers belowground or vice versa. Some of our inability to predict and understand responses of aboveground consumers may be because of unknown variations, patterns, etc., in the belowground counterpart.

Although consumers can cause very large effects in relation to their own material needs, there is probably a range of effects. At the upper end of that range lie the 'keystone' species, whose effects may be orders of magnitude larger than expected. Disturbance of these species may significantly disrupt many ecosystem processes or even the structure of entire landscapes. One of the classic 'keystone' species is the beaver (*Castor canadensis*) whose wood-cutting and dam-building activities markedly affect headwater regions, as much as 30–50% of the total length of second to fourth order streams (Naiman and Melillo, 1984). Compared to stream riffle areas, beaver activities alter nutrient cycling, decomposition, light characteristics, stream primary production and inputs of precipitation, throughfall and allochthonous material. Concomitant with these changes, the extent of wetland surface area increases, influencing the nature and intensity of interactions between the stream channel, biological components of the ecosystem and the surrounding forest. Historically, small streams in North America had different features than the streams studied today. The significant ability of beaver to cause storage of sediment and nutrients and to increase stream habitat diversity, frequency of disturbance and in-stream material processing has profound implications for current stream ecology concepts (Naiman and Melillo, 1984).

Another 'keystone' species may be the termite of arid zones, whose activities result in litter decomposition rates greatly exceeding expectations based on climatic data (Whitford et al., 1982). Other examples are bison, caribou, salmon, carp, alligators and the hippopotamus. Species such as these need major study, not only in terms of how their activities affect ecosystems, but also to identify system attributes and constraints that result in the presence of 'keystone' species. Do all ecosystems have them? Why or why not?

IV. *Landscape ecology*

Today, it is well accepted that most studied systems are not homogeneous or in an equilibrium condition. Those assumptions were commonplace in earlier studies, primarily for convenience. Further advances in our understanding of ecosystems now precludes the use of those assumptions. Landscape ecology is the current disciplinary area whose focus is understanding spatially and temporally homogeneous *and* heterogeneous geomorphic and living systems. Specifically, landscape ecology considers the development and dynamics of spatial heterogeneity, spatial and temporal interactions among and exchanges across heterogenous landscapes, influences of spatial heterogeneity on biotic and abiotic processes and management of spatial heterogeneity (Risser et. al., 1984).

Included in the heterogeneity of landscapes is the combination of aquatic and terrestrial habitats. The modern concept of stream systems (i.e., 'continuum', 'nutrient spiralling'), at least in their earliest versions, had little consideration of the landscape matrix in which streams lie. Future studies must consider aquatic habitats as elements of a complex landscape (Callahan, 1985).

The major aspect of the landscape concept relates to how different characteristics of the spatial elements (e.g., patches) within a landscape influence movements of materials and energy. The individual patches, stands, or communities are not independent and simply summing results of studies of each element will not lead to an understanding of the landscape. The classic paper of Watt (1947) argued that an understanding of the community required an understanding of the relationship of the various phases to each other. The interactions among the phases are complex and there is little in the way of theory or concept development to help us understand them. The rates of exchange among landscape components may be enhanced or inhibited by biotic and abiotic vectors. The degree of difference between landscape components may interact strongly with how the biotic and abiotic vectors influence exchanges.

The juxtaposition of components within the landscape also may affect the influence of vector exchange. Consider the following simple example: two landscapes, each of which has three types of patches which differ in some functional or material processing characteristic; rapid, medium, slow. Equal numbers of each patch type occur in both landscapes; however, 'rapid' patches are in contact only with 'slow' patches in one landscape and 'rapid' patches are in contact only with 'medium' patches in the other. 'Medium' patches would be in contact with 'slow' patches in both cases. How different would the dynamics of each of these hypothetical landscapes be? Simple diffusion theory would suggest more rapid rates of exchange in the landscape with 'rapid-slow' contact (steeper gradient); however, another concept suggests the greater the differences in reaction rates, the less likely strong interactions will occur between them (O'Neill et al., 1986). Perhaps both of these patterns of interaction can occur in each of the landscape designs but for different materials or nutrients. How significant are biological vectors in preventing passive diffusion patterns from occurring? Do these biological 'gradient-reversal' vectors result in sharply delineated patches (i.e., sharp boundaries)? Are the boundaries dynamic, or in some type of quasi-equilibrium? How are boundaries recognized and by what biological entities? These simple questions only scratch the surface of the biological complexity and dynamics of landscape structure and function.

Another major facet of studying at landscape levels is the recognition of scale. The need for this recognition has been common to every conference and workshop I have attended during the past year. Ecological dynamics occur over a broad spectrum of space-time scales and defining and isolating the relevant scale of dynamics is a critical step in setting up any problem.

Arguments over endogenous versus exogenous disturbance are problems of scale. An exogenous, uncontrolled disturbance, by definition, comes from *outside* the spatial scale of the study system. Increasing the spatial scale of the study can suddenly result in the same perturbation being incorporated into the dynamics of the system. O'Neill et al. (1986) provide a good example in the case of fire in several systems. Vegetation survival is not threatened by fire if the landscape system is large relative to the area burned. In fact, vegetation may be dependent upon fire. Temporal scale also can be a factor. By increasing the frequency of the fires and decreasing fire intensity, the spatial needed to incorporate the fire (i.e., fire becomes a system attribute) becomes smaller. An interesting current controversy is whether the plant community is under selection pressure to increase fire frequency. A related question asked by Risser et al. (1984) is, 'How does landscape heterogeneity affect the spread of disturbance?' Spatial variability that enhances or inhibits perturbation intensity, frequency and extent could be one of the most important features for understanding landscape dynamics. It is becoming clear that we must view the world at the spatiotemporal scale at which it responds rather than the space and time frame in which we operate' (O'Neill et al., 1986).

V. *Ecosystem dynamics in contrasting environments*

The vast majority of our ecological literature concerns temperate latitude ecosystems. Ecological 'surprises' tend to occur when concepts from these systems are applied to or tested in the environments of other latitudes. For example, Whitford et al. (1982) found plant decomposition rates in the desert environment of southern New Mexico twice as rapid as would be predicted by climatic (Actual Evapotranspiration) based models developed in more mesic environments (Meentenmeyer, 1978). The adaptations of desert invertebrate detritivores resulted in a higher rate of activity than was allowed for in the mesic-environment model.

We need more study of ecosystem dynamics in boreal environments, wet tropics, tropical savannas, deserts and mediterranean climates. These environments represent large portions of the terrestrial biosphere; however, their ecosystem attributes are often estimated with relatively few studies or predictions from other environments. These biomes must be studied if we are to identify the 'general properties of ecosystems' called for in the Cary Conference on the Status and Future of Ecosystem Science (28 April, 1985). Research in these environments may be more expensive and logistics difficult, but they are critical to our ability to validate ecosystem concepts and develop a global perspective.

VI. *Enhancement of theory and methodology*

The areas discussed above are especially limited by a lack of theory and development of concepts. Ecosystem science is very complex and includes many scientific disciplines. Each of these individual disciplines has a well developed conceptual base; however, applying them to the ecosystem scale has not always proved successful. Attempts to extend population dynamics theory or island biogeography theory to the ecosystem and landscape scale are common examples (O'Neill et al., 1986). Increased recognition of the importance of spatial and temporal scale appears to be a promising avenue for developing a conceptual base and we need to encourage this development. We also need to interact with and take advantage of disciplines that work at regional and global scales, such as atmospheric chemistry and oceanographic sciences. These disciplines are attempting to model global dynamics, but realize the significance of smaller scale biological processes. These disciplines are having as much difficulty coming down in scale as ecologists are having going up in scale. It would seem to be a potentially valuable interaction.

Another major limitation for ecosystem science is inadequate methodology. We are very technique-limited when compared with, for example, the physical-chemical sciences where equipment building is part of problem-solving research, or the medical disciplines where the market encourages private industry to fund a massive research and development program. We need to enhance the development of analytical methods and equipment for our needs. The methodological areas are limited because they are very difficult and expensive. There also is little scholarly reward for a 'biologist' to do this rather applied research. The funding agencies also are less prone to support projects that develop techniques versus more 'exciting' science. Solving our technique limitations will require that the scientific community involved in the peer review process acknowledges the value of individuals solving these problems. This may allow increased funding for that type of project. We need to encourage interaction with scientists in other disciplines where equipment and method development are important to the progress of their science. Interdisciplinary research of this nature represents the most rapid way to ameliorate these limitations.

We also need additional statistical methodology and analysis techniques. In my opinion, we rely too heavily on measures of central tendency (e.g., arithmetic average) and statisitical methods that use replication to simply *accommodate* temporal and spatial variation. Too often researchers represent a process or an ecosystem with a single number to make comparison easy or to lable a box or arrow in a model. The real information in a process or ecosystem comes from its variable nature, its ability to respond to the environment. Our statistical techniques and analyses need to accurately represent that variation and utilize it in evaluating ecosystem concepts.

Areas of emphasis: Division of Biotic Systems and Resources

Other programs within the Division of Biotic Systems and Resources also fund significant numbers of research proposals dealing with biogeochemistry. The Division develops long range planning information in which it recognizes existing and emerging areas capable of providing significant advances in all of the ecological disciplines. Table 1 represents the areas that are relevant to biogeochemistry research. The list is not based on priorities but is arranged along

Table 1. Existing and emerging research areas capable of providing significant advances in biogeochemistry research. These were selected from areas identified in the Division of Biotic Systems and Resources Basic Planning Information (revised April, 1985)

1) Microbial Ecology
    a. Microbial control of decomposition and release of major biogenic elements in soil and sediment (E, ES)*
    b. Functional diversity and succession of soil microbes of the rhizosphere (E)
    c. Functional significance of symbiotic microbial communities of the rhizosphere (E, ES)
    d. Mutual interactions of soil microorganisms with green plants (symbiosis, disease) and soil invertebrate predators (E)
    e. Susceptibility of microbial communities to invasion by alien organisms, natural or genetically engineered (PBPE, E)
2) Physiological mechanisms of plant adaptation to nutrient scarcity (PBPE, E)
3) Plant/animal interactions; molecular basis and community influences (E, ES)
4) Disturbance and recovery effects on ecological dynamics and community patterning (E, ES)
5) Research on long-term ecological phenomena (E, ES)
6) Landscape ecology – functional amalgamation of ecosystem units into larger landscape entities, the next step toward global biology (ES)
7) Global biogeochemistry (ES)

*PBPE – Population Biology and Physiological Ecology program
E – Ecology Program
ES – Ecosystem Studies Program

a continuum of increasing scale of approach (spatial and organizational). The topic titles are self-evident and the programs with major responsibility are designated.

The long range plans within the programs of the Division of Biotic Systems and Resources are intended to provide a degree of focus within each program that is consistent with the views of the community about the research directions that are capable of providing significant advances. The individual programs are in a unique position to develop this concensus because of the extensive contact with the research community. Publications such as this are intended to focus and feed back that information. In this way we hope to encourage more research in the areas that have a high probability of advancing our science.

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