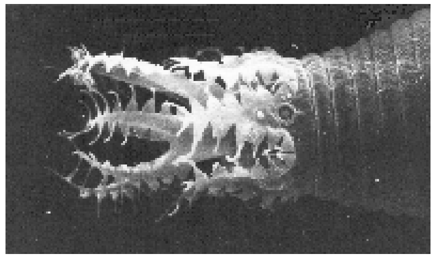

LIFE IN THE SOIL

SOIL BIODIVERSITY: ITS IMPORTANCE TO ECOSYSTEM PROCESSES

Report of a Workshop Held at The Natural History Museum, London, England

August 30-September 1, 1994

Diana W. Freckman, Editor
Natural Resource Ecology Laboratory
College of Natural Resources

Colorado State University
Fort Collins, CO 80523-1499
USA

The funds for the US participants to this workshop and the publication of this report were supported by the National Science Foundation (Grant NSF DEB 94-15311) to D.W. Freckman. UK participation was partially funded by the Natural Environment Research Council. Additional copies of this document may be obtained from the Natural Resource Ecology Laboratory, College of Natural Resources, Colorado State University, Fort Collins, CO 80523, USA. Publication Date, October 1994.

Acknowledgments: We thank Dr. Steve Blackmore and The Natural History Museum for hosting the workshop. Arlene Boaman (Colorado State University) and Nicola Donlon and Suzanne Tate (The Natural History Museum) organized the meeting. In addition to the review by workshop participants, the early drafts of this report benefited from comments by Clifford Gabriel, Peter Raven, Virginia Brown, Ericha Courtright, Mark Easter, Bob Niles, Arlene Boaman and Laura Powers. Kay McElwain provided technical assistance with the electronic manuscript.

Table of Contents

EXECUTIVE SUMMARY

Soils are one of the most poorly researched habitats on earth. The functioning of this thin dark covering on the surface of the earth is vital for the survival of the biosphere in its present form. The impact of burgeoning human populations has destroyed the soil physico-chemical environment and the soil's species through activities such as: inputs of chemicals from the atmosphere, disposal of waste products in soils, ground water contamination, and physical modification or removal of soil by cultivation and erosion. Soil degradation has

also resulted in the mobilization of carbon and nitrogen as greenhouse gases forcing climate change. Information on the effect of these impacts on the loss of soil biodiversity and the loss of key functions [e.g., biogeochemical cycles of carbon (C), nitrogen (N), sulfur (S), potassium (K), phosphorus (P), oxygen (O)] in the biosphere is fragmentary. Ecological principles derived from macroscale above-ground research have been transferred without basis to soil organisms that function at the microscale, providing an incomplete foundation for predicting sustainability. Nevertheless, ecologists have shown the importance of soil biota to ecosystem processes such as nutrient cycling, carbon storage, and maintenance of plant diversity, through studies that combine a number of taxa into functional or trophic groups. Global change research examining the effects of soil warming has revealed the key role of the soil biota in regulating methane (CH_4), nitrous oxide (N_2O), and carbon dioxide (CO_2) losses from soil, which impact processes in aquatic and atmospheric systems. Research has continued to show the value of soil biota to the biological control of human and agricultural pests, in biotechnology, and for remediation of hazardous wastes. Clearly, species of soil biota are tightly linked functionally to above-ground biotic interactions. They perform ecological services that strongly impact the quality of human life and have enormous potential for providing economic benefits, e.g., the isolation and identification of the soil fungus Penicillium that led to a large pharmaceutical industry of antibiotics.

Soil biota remain among the vast unknown life on our planet, a dark frontier, despite their critical importance to understanding ecosystem function. For example, thousands of species of microbes and invertebrates inhabit just a square meter of temperate grassland soil, organisms whose identities and contributions to sustaining our biosphere are largely undiscovered (Figure 1). The elucidation of species diversity of soils in conjunction with sustainability assessments of soil-mediated ecosystem processes must be a high priority in global biodiversity efforts. Yet, although biodiversity efforts at the global level have consistently highlighted the need for studying soil organisms, there are few scientists with soil taxonomic or soil ecological expertise. For example, soil research was a priority recommendation in a 1980 USA National Research Council Report, Research Priorities in Tropical Biology, because of a lack of knowledge linking soils to vegetation diversity in the seasonal and humid tropics. The recommendation emphasized movement of nutrient and trace-element ions through the soil biota as a means of learning about soil species and food webs.

In 1989, the National Science Board of the National Science Foundation (1994) issued a report (Loss of Biological Diversity: a Global Crisis Requiring International Solutions) which targeted soil biodiversity for immediate international collaborative research. More recently, several international efforts have recognized the compelling link between the above- and below-ground biota and proposed characterization of soils (Heal et al., 1993) and soil biota (Groombridge, 1992; Hawksworth and Ritchie, 1993; National Research Council, 1993).

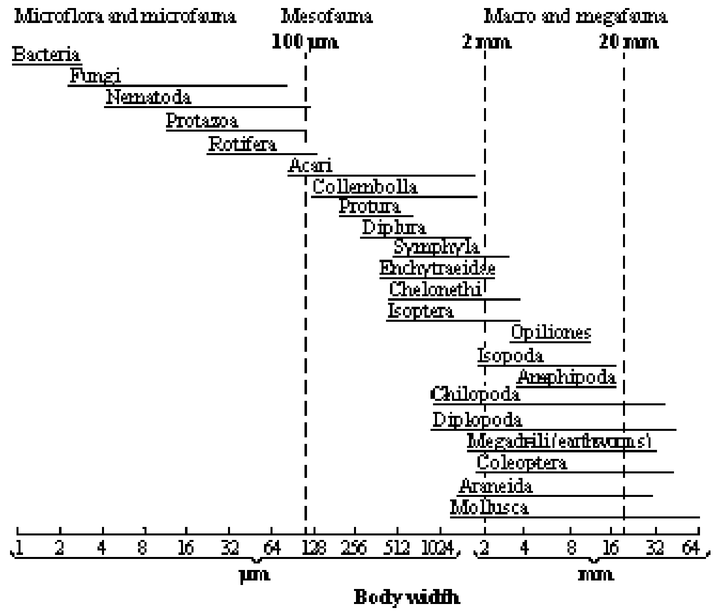

Fig. 1. Size classification of organisms in decomposser food webs by body width.
(after Swift, Heal and Anderson 1979)

Unfortunately, biologists have historically given less urgency for identification of soil organisms and elucidation of their roles in soil ecology when faced with the magnitude of change and loss of above-ground biodiversity. Traditionally, the systematics and ecology of soil species have been the purview of forestry and agricultural research, particularly in the United States. Agricultural management generally has been driven by production and, in many cases, the use of pesticides and fertilizers, which has masked the importance of the soil biota. Consequently, there is an acute lack of baseline data on the critical roles played by soil biota -- and the individual roles of soil taxa -- in maintaining soil structure, soil fertility, and mediating important ecosystem processes such as decomposition. The best known soil species belong to groups such as the ants, symphylans, plant pathogens and termite pest species, along with key beneficial taxa such as nitrogen-fixing bacteria, mycorrhizae and predaceous fungi and earthworms.

At a workshop at the Natural History Museum in London (August 30 to September 1, 1994) jointly funded by the National Science Foundation (US) and the Natural Environmental Research Council (UK), systematists, ecologists and conservationists addressed soil biodiversity as related to ecosystem function. This report summarizes the three days of deliberations. The workshop discussions were based on the initial understanding that (A) soil biota are integral to ecosystem function; (B) baseline data on most soil species, their ecological role, their systematic position, geographic occurrence, and abundance does not exist; and (C) there are insufficient resources and time to inventory all of Earth's biota. Therefore we view as urgent priorities:

1. the need to study soil biodiversity using research projects and designs that relate the systematics of soil taxa to key ecosystem processes, and
2. the need to make these research projects international for compelling reasons:

individual nations lack a critical mass of expertise for identifying the soil biota; communities at present cannot be compared; therefore, ecological comparisons across biotic zones and ecosystem regimes and economies of scale in ecosystem and systematic analyses are a priority.

[Return to the top of the document]

GENERAL RECOMMENDATIONS

Interdisciplinary interactions

- Involve a wide array of scientists including: biologists (microbiologists, molecular biologists, zoologists, ecologists, biochemists, botanists and physiologists), soil chemists, soil physicists, geologists, hydrologists, modelers and information management specialists in research efforts relating soil biodiversity to ecosystem function. Primary beneficiaries of this research effort, and thus, necessary participants, would include funding agencies that support the basic sciences, as well as non-government organizations, and international and national agencies with priorities in global change, land use management, restoration of biodiversity, prevention and mitigation of pollution and creation of a sustainable global environment (for example, in the USA, the United States Department of Agriculture's (USDA) Soil Conservation Service, Experiment Stations, and Forest Service; the Department of Energy; the Environmental Protection Agency; the Department of Interior's National Biological Survey and US Geological Survey).
- Employ the concepts and techniques of molecular biology in soil biodiversity studies. Applications of molecular biology are dependent on genetic analyses of the still to be identified planet's biota that resides largely in the soil and sediments.
- Make efforts to establish the economic importance of soil biota. Provide support for a review and synthesis based on the direct and indirect values of soil species.
- Encourage experts in other scientific disciplines, including engineering, computing science, atmospheric sciences, medicine, chemistry and physics, to develop and transfer techniques for use in taxonomic protocols, information management, and discrimination of life at the microscale in soil.
- Ensure research experiments on plant physiology and plant growth, and on soil processes, are made with knowledge of the soil organisms present. Omission of organisms, e.g., soil fauna, can lead to erroneous results.

Taxonomic efforts

- Provide resources (personnel and funds) for analyses and syntheses of systematic and biogeographical information on soil biota. For example, there is insufficient knowledge to test the correlation between soil and above-ground species diversity and richness, or to determine the range of soil microbes, fungi and invertebrates that exist in habitats. However, there is data on the geographical distribution and balance of different groups of soil biota. In the warmer climes, the decomposition process is related to termite activity, whereas in colder parts of the world, termites are absent, and different groups of organisms are involved with the decomposition process. Biogeographical and systematic knowledge would be beneficial in many ways, e.g., identifying species of economic importance, comparing rates of decomposition, predicting impacts of loss of species.

- Take steps to increase the global pool of taxonomic experts in soil biota. Identify immediately the location and stage of career of existing taxonomists to enable (A) the contribution of those near retirement, particularly through training of graduate students and postdoctorates, and (B) the production of taxonomic products on poorly known soil organisms. Innovative training approaches using parataxonomists and soil ecologists must be considered. Additional sources of funding and university and national agency administrative support may be required to train students internationally, because for many soil taxa only one or two systematists may remain worldwide. Training students in novel methods and identification should be enhanced through Internet accessibility, video links, satellite transmission links, workshops and other means.
- Develop new methods that take advantage of the latest technological breakthroughs for detecting, sampling, collecting, culturing, and identifying microfauna and microorganisms. No single method can extract or discriminate all soil taxa, but common methods may be applicable across diverse groups of invertebrates and microbes. The intent is to inventory a diversity of organisms from different soils as soon as possible. Therefore, organize a workshop to determine, recommend and publicize standardized approaches for sampling, extracting and identifying soil taxa across ecosystem regimes.
- Provide resources for synthesis of a comprehensive manual for soil ecologists and taxonomists, combining a number of recent protocols and handbooks, as well as some of the older protocols. Assure that the manual is available in tropical countries for training purposes.
- Develop ways to incorporate an ecological approach to taxonomy to ensure that the skills of taxonomists will be supported by long term funding. New students as well as current researchers should be provided with the resources to build a new interdisciplinary discipline of taxonomy and ecology, that will enhance the knowledge of species and address the critical problems regarding loss of species.
- Link Research Museums with soil biodiversity research through:

    Curating and maintaining voucher specimens, sequences, culturable microorganisms (which represent less than 10% of the soil microbes), images, tissues and field records

    Research and curatorial appointments for taxonomists studying soil life

Extensive information management and dissemination of soil biota collections and associated data and authority files (i.e., information networks)

Education of the public (informal and K-12) on the importance of the ecological processes that operate in the soil and the need for soil sustainability

Systematic training of taxonomists in soil biodiversity

Information Management

- Incorporate taxonomic and ecological information into data models at the earliest stage of detailed planning for the project.
- Develop an information management protocol for linking ecological processes and biodiversity data (e.g., vouchers, site conditions, gene sequences data) prior to sampling for biodiversity.
- Develop metadata standards for organizing information on ecological processes to facilitate ecosystem descriptions and information management.
- Assemble existing data on soil taxa and ecosystem processes to determine the state of knowledge of the functional roles of species at given sites and to guide future inventory and research efforts.
- Establish an Internet network dedicated to soil biodiversity. Establish electronic keys with images, and a help service on Internet.

[Return to the top of the document]

SPECIFIC RECOMMENDATIONS

1. We recommend the initiation and establishment of a world-wide program consisting of a multi-site network for monitoring and working with global biodiversity of soils. The long term research network will provide, in a focused manner, the connections of soil taxa to sustainability, to economics and valuation of soils, to education, to the biosphere and to theoretical biology. The network will contribute on a global scale to understanding the relationship of the diversity of soil organisms to the diversity of life, to the discovery of ways in which the soil biota are unique, and will tell us about biological phenomena in a general, comparative way.
2. We recommend that the priority investigations of soil global biodiversity in the multi-site network should be experiments designed to connect and inter-relate ecosystem processes to taxonomic studies (soil all taxa biotic inventories). The experiments should provide a common focus for multi-site, integrated, interdisciplinary,

collaborative, and international work.

3. We recommend two experiments that were discussed and outlined at the workshop, carbon flux and decomposition, as examples of initial experiments that would capture the linkage between a soil all taxa biotic inventory and ecosystem processes. We suggest that these two experiments be conducted as a package experiment in as many sites as possible. As an additional experiment, we recommend that all taxa biotic inventories be conducted in soil depth profiles at a few selected sites to relate pedogenesis and the distribution of soil chemical and physical factors to soil taxa.

   We believe these two processes, carbon flux and decomposition, represent excellent models for examining how an ecosystem process determines or is driven by the composition of the soil biota. Specifically, the experiments chosen are model processes for exploring the relationship of soil biodiversity and ecosystem function because: (1) the experiiments are major processes common to all ecosystems; (2) the processes involve a diversity of soil biota, from microbes to earthworms; (3) C and N flux and decomposition are dynamic processes that occur across varying spatial scales and involve different taxa at different periods of time (succession); (4) the study of these processes and their relationship to biotic diversity requires a range of expertise across disciplines and involves many kinds of technology; (5) previous research has established the major features of the processes and their controls; (6) hypotheses on the relationship of the soil biota to ecosystem function remain poorly explored, and are presently limited to a few groups of organisms; and (7) the links between ecosystem vegetation type/diversity and the diversity/type of soil biota are best explored at sites dedicated to long term ecological research, where a good deal of baseline, historical, ecosystem and biotic knowledge has already been achieved.

   Specific criteria for selection of sites should include: well-characterized soil systems typical of the ecosystem and preferably where GIS grids are established; historic data bases on vegetation and previous land management; ongoing and future environmental monitoring; and limited public access to the long term experiments.
4. We recommend the formation of a multi-disciplinary task force to address new approaches for identifying soil biota, using the new technologies. This could be initially be implemented by interchanging suggestions for technology through Internet following advertisements placed in Science, Nature and other journals.

[Return to the top of the document]

THE TIMELINE FOR RESEARCH

Immediate

- Identify a network of well-described sites based on previous history and current long term support for maintenance of environmental data collection (for example, the

United Kingdom Environmental Change Network sites (ECN) and the United States National Science Foundation Long Term Ecological Research sites (LTER).

- Establish a one year project with one person from each proposed experimental site to be responsible for extraction and compilation of existing soil biotic databases and to participate in a cross-site synthesis/comparison. Analyze and interpret existing comprehensive data on soil biodiversity from a limited number of well-described sites. The purpose of this initial study would be to identify trends with which to formulate/develop hypotheses and plan the next stage of biodiversity/ecological research at particular sites. Additional information compiled would be valuable in any inventory work.
- At a workshop, present synthesized cross-site information, identify gaps in knowledge and establish hypotheses. Formulate research plans for investigating the relationship between soil biota inventories and ecosystem processes (e.g., carbon flux and decomposition experiments) at particular sites. Publish results in print and electronic form.
- Establish a small working group to design a generalized study of the relationship between biodiversity and ecosystem processes of carbon flux and decomposition. This should include the scientific rationale, experimental approach(es) and outline of appropriate methods to investigate both biodiversity and the processes selected.

Early 1996

- Research Proposals submitted to funding agencies for research to test hypotheses identified from the one-year project.

Long Term Vision

- Identify a global network of sites linked through a set of research platforms with experiments on soil biotic inventories and ecosystem processes (e.g., decomposition and C and N flux).
- Enhance participation (private, agency, university and global collaborators) of this Long Term Network on Soil Biodiversity and Ecosystem Function through both intensive (more detailed analyses) and extensive (minimal research package identified by participants) efforts.
- Provide a synthesis of the contributions and roles of soil taxa at genetic, community and ecosystem levels of organization as results become available, to assure that key species are widely recognized.
- Increase the educational commitment to training students internationally, particularly in the tropics, about the importance of soil, the dark frontier.
- Encourage transfer of knowledge to the public and new generations on the significance of life in the soil.
- Implement management plans that will maintain soil quality and contribute to the sustainability of the planet.

[Return to the top of the document]

THE PROBLEM

Soils are a critical and dynamic center for the majority of ecosystem processes in both natural and managed ecosystems. Nutrient turnover, nutrient uptake by plants, soil fertility, formation of soil organic matter, nitrogen fixation, methane production, CO_2 production, soil development, and production of organic acids that weather rocks, are all dynamic processes contributing to the sustainability of the planet. Soils are the major global storage reservoir for carbon in the form of organic matter (estimates of about 1500 X 10x15 gC are stored in soils). The living microbes, fungi and invertebrates that comprise the soil food web are responsible for changing carbon and nitrogen through several steps of decomposition to forms available for plant growth, while at the same time contributing to the rate of production and consumption of CO_2, methane, and nitrogen. The annual flux of CO_2 that returns to the atmosphere as a result of decomposition and other soil processes amounts to approximately 68 X 10x15 gC/yr (Schlesinger, 1991). Global modifications that alter the balance of the carbon fluxes, such as land use and climate change, also affect the spatial and temporal distribution of ecosystem resources, and impact not only vegetation diversity and landscape vegetation patterns, but the soils and soil biota involved in processes such as decomposition and the rate of release of greenhouse gases.

Soils, like water and air, are natural resources that unify terrestrial ecosystems, and which, like water and air, are being degraded by humans. We have caused soil pollution, ground water contamination and erosion, human impacts resulting in a loss of carbon and nutrients from the soil. These actions are taken without knowing how resilient and stable the soils or the ecosystem processes will be in different environments. Today, scientists realize that soil is not just a "buffer". Instead, the soil, including the transition zone between surface soil and groundwater (Marmonier et. al., 1993; Stanford and Ward, 1992) and between soil and aquatic habitats, and the soil biota within these diverse habitats, are all interlocking components interacting with vegetation and climate and necessary for the functioning of terrestrial ecosystems.

Despite some knowledge of how soil organisms maintain critical processes such as carbon storage and nutrient cycling and influence plant species diversity (Huston, 1993), or how soil organisms participate in forming soil structure, the organisms themselves remain a "black box" in our understanding of how soil systems function. Without accurate knowledge of soil biodiversity, the structure and interactions of the soil organism community, and the relationship of soil biology to ecological processes, management of ecosystems, and the models of ecosystem functioning upon which management is based, will always be less than rigorously understood.

The biodiversity in soils is structured into food chains and webs which are important determinants of ecosystem function (Heal et al., 1994; Hendrix et al, 1986; Moore and de Ruiter, 1991). The soil food webs are also the basis of food supply for food chains above-ground, for example, small mammals. A few experiments have indicated that a loss of biodiversity can diminish the functioning of ecosystem processes (Verhoef and Brussaard, 1990). That anthropogenic activities can decrease soil biodiversity is well-documented, particularly in the fauna of agroecosystems, where the addition of fertilizers increases plant productivity but masks the importance of soil biota in providing available nutrients to plants. Complimentary evidence from experiments has shown that increases in biodiversity can enhance plant growth, nutrient mineralization and resistance to stress (Clarholm, 1989; Couteaux et al., 1991; Elliott et al., 1979; Lavelle et al., 1992). Even after human disturbance, soil biodiversity generally is greater than above-ground diversity. Species composition within soil food webs may change due to this disturbance, making the impact of species loss more difficult to determine.

Few of the soil organisms can be identified to species. Why is there so little information on key soil species and their ecological roles in maintaining the functioning of ecosystems? Why can't all species in a soil habitat be identified? Some of the reasons are: (1) the soil is an opaque medium and the in situ identification of most organisms is impractical; (2) organisms in the soil represent a number of phyla (microbes to earthworms) making interactions and ecological roles difficult to assess; (3) organisms range in size from microscopic to macroscopic, and morphology within a taxon can vary throughout the life cycle; (4) the methods for extracting many microorganisms, fungi and mesofauna from soils have not been determined and techniques for culturing them are not developed, presenting problems for identification and enumeration; (5) lack of emphasis on soil taxa as resources and as critical parts of ecosystem function has contributed to the extinction of systematists who can identify the organisms involved in critical roles in soil; (6) the temporal and spatial scale of their habitat (soil particles to landscape) varies with the organism; and (7) the taxa of soil food webs change with the physico-chemical environment, the quality of organic matter, climate and geography, resulting in few comparisons of the ecological roles of soil taxa in different ecosystems. Currently, due to the difficulties enumerated above, many of the ecological roles of soil biota are attributed to trophic groups, or groups of species with similar morphology, not to species. Consequently, our science has limited ability to apply knowledge for the management of soil biodiversity to promote the sustainability of soil quality. Therefore, for the soil system, it is essential and urgent that we establish the cause and effect relationships between the loss of species and the impact on terrestrial and global ecosystem processes.

The greatest barriers to research in soil biology are methodological. Sampling and identification methods are taxon-specific, and many techniques are in their developmental infancy. There is no single extraction or collection method that will quantitatively extract or collect all soil organisms, or even one phylum. The scientist chooses a sampling and extraction method based on the experimental question, the soil habitat, and the scientific knowledge of method limitations. The status of techniques for the identification of taxa has advanced in the past 5-10 years with molecular methods, but still, there is no single method for identification of the members of a phylum.

The present taxonomic knowledge of soil biota has been recently summarized (Groombridge, 1992; Hawksworth and Ritchie, 1993; O'Donnell et al., 1994; Systematics Agenda 2000, 1994). In general, our knowledge of species distribution, abundance, population structures, and ecological roles and requirements are poorly known or understood. The status of identification and ecological roles of the soil biota, by size, could be assessed as follows:

1. Larger soil fauna (invertebrates) -- these can be collected quantitatively and qualitatively from soils, many may be identified to species and their ecological roles are known in general. These roles include: (a) Direct processors of organic matter (e.g., snails, earthworms, enchytraeid worms, woodlice, millipedes, silverfish, bristletails, termites), (b) Predaceous regulators (e.g., spiders, centipedes, true bugs, carabid beetles, ants), (c) Secondary consumers (e.g., springtails, mites, other beetles), (d) Creators of soil structure (earthworms, millipedes, termites, and many members of other categories). Taxa that cannot currently be reliably identified include: enchytraeid worms, many mites, larval beetles and flies, parasitic wasps and bark lice. Knowledge of these soil organisms varies dramatically with locale. Only a few locations have well described invertebrates.
2. Micro- and Mesofauna (invertebrates) -- assays vary in the ability to quantitatively and qualitatively extract these organisms from the soil. Knowledge of the ecological functions of this group is generally lacking. Many are predators, consumers of bacteria and fungi, and are involved in regulating the rate of decomposition. Springtails (Collembola) and other insects appear to have a reasonable base of taxonomic specialists although in some taxa, only one or two such individuals may exist. However, reliable identifications may be impossible or difficult to obtain for many groups of protozoa, rotifers, tardigrades, nematodes and mites. There are few molecular methods available for these diverse taxa, and their ecological roles are based primarily on trophic group estimates of their ecological function in ecosystem processes.
3. Microbes -- advancements over the past 10 years have been substantial and additional methods are available for the assessment of bacterial and fungal biodiversity. However, each method suffers from technical or interpretative limitations, and no single method provides an unequivocal estimate of bacterial or fungal diversity. Species that can be identified by culture techniques or visual techniques are not necessarily important in situ. There are "indirect methods" that can be used to correlate diversity with processes between sites, and once their relationship to a process is shown, "direct" and new methods could be used to determine species diversity. Some of the methods for bacterial diversity presently include chemosystematic-based determinations of taxon-specific cellular constituents (fatty acids, sterols, secondary compounds, proteins, etc.), nucleic acid based approaches [whole community nucleic-acid hybridization, community DNA reassociation

kinetics, and cloning and sequencing of polymerase chain reaction (PCR)-amplified 16sRNA gene sequences from community DNA samples] and nucleic-acid function-based methods such as hybridization of probes to genes (potential function) or mRNA (expressed function) unique to particular enzymatic activities. Traditional morphological methods combined with molecular identifications provide important tools for the assessment of fungal diversity. As with bacteria, assays of fungal chemical diversity (e.g., enzymatic and chemosystematically important cellular constituents) and new technology can contribute to identification.

Integrated projects to assess soil biodiversity have been suggested at many scientific levels, but efforts have been generally targeted to conservation efforts of disappearing habitats. The following is not a comprehensive list, but illustrates the breadth and global consensus for increasing the priorities for research in soil system function and soil biodiversity.

In 1980, a National Research Council Report (Research Priorities in Tropical Biology) noted, "A comprehensive understanding of ecosystems must ultimately depend on basic knowledge of the organisms that make up these systems." The report stressed the need for resources to advance knowledge on soil biota. A National Science Foundation LTER-sponsored Workshop on Systematics and Ecology of Soil Organisms outlined the need for joint research efforts on soil biota (Corvallis, OR, 1985). The Hungarian Society for Soil Science dedicated a conference to Soil Biology and the Conservation of the Biosphere (Szegi, 1984). In 1989, the National Science Board of the National Science Foundation (Loss of Biological Diversity: A Global Crisis Requiring International Solutions) emphasized soil biodiversity as an immediate focus for international collaborative research. A National Research Council Report (1993) noted that "Our lack of knowledge of microorganisms and invertebrates, which are estimated to make up as much as 88% of all species, seriously hampers our ability to understand and manage ecosystems." USA federal research efforts such as the National Biological Survey (NBS), the Long Term Ecological Research (LTER), the Environmental Protection Agency's EMAP, the USDA's Soil Conservation Service, the USDA Forest Service, the USDA Experiment Stations and the US Geological Survey, have been suggested as means to increase research and understanding of soil biodiversity. More recent international workshops (International Conference on Soil Resilience and Sustainable Land Use, October 1992, Hungary; Soil Biodiversity, Soil Ecology Society Meetings, April 1993, Michigan, USA; Beyond the Biomass, Compositional and Functional Analysis of Soil Microbial Communities, March, 1993, Wye, England; Scientific Committee on Problems of the Environment, Program on the Ecosystem Function of Biodiversity, March, 1994, California, USA) have concluded that priority efforts of soil research should be to understand the functional roles of the diverse but poorly understood below-ground organisms. These reports have recognized the connection of the below-ground biota to sustaining the function of our biosphere and to solving the ecological problems related to soil systems (Groombridge, 1992; Hawksworth and Ritchie, 1993; National Research Council, 1993).

[Return to the top of the document]

CRITICAL AREAS OF RESEARCH

We have concluded from discussions at the workshop that the best way to identify and develop an understanding of how the diverse soil taxa operate in ecosystems is to coordinate studies of inventories of soil taxa and selected ecosystem processes. We propose these studies occur across a network of intensive and extensive sites that are presently funded as long term research sites in different ecosystems and countries. It is necessary to focus initially on comparative studies on these few sites and processes because of the considerable expenditures required and the limited number of scientists that could reasonably become involved. We suggest that this research needs to link scientists internationally in many disciplines and agencies, since a critical mass of expertise for identifying all the soil biota does not appear to exist in any one nation.

EXPERIMENTS

The two ecosystem process experiments prioritized for detailed biotic inventories are addressed here as separate experiments, but are, in fact, best executed as linked so that maximum detailed results can be obtained for minimal costs. They address key issues that were discussed during the workshop, and have as strengths the incorporation of many of the recommendations of both systematists and ecologists.

We have concluded that two processes, carbon and nitrogen flux and decomposition, represent excellent models and experiments for examining how ecosystem processes determine and are related to the composition of the soil biota. Carbon flux would represent an experiment of a whole process (C transformation in soils) that could be conducted with the decomposition experiment at a few intensive sites. Decomposition is an important component of the carbon transformation in soils, and would be an experiment that could be conducted both with C flux at the intensive sites and singly at a wide range of extensive sites.

Carbon flux is the measure of the exchange of carbon as gaseous CO_2 between ecosystems and the atmosphere, and the balance between photosynthesis by vegetation, and respiration by animals, plants and microbes. All the major "greenhouse gases" (CH_4, N_2O, CO_2) are to a large extent produced and/or absorbed by the soil, depending on the environmental conditions. More importantly, their production (CH_4, N_2O) or absorption (CO_2 via plants or algae) in soil is biologically mediated by the soil biota. Similarly, nitrogen can be measured as it changes forms during nitrogen cycling and is released to the atmosphere. Carbon flux would represent an experiment of a whole process that could be conducted with the decomposition experiment at a few intensive sites.

Decomposition is viewed as an integrative process involving all taxa, and inevitably involving nutrient cycles (C, N, S, P, etc.). The organisms responsible for decomposition of litter in soils respire CO_2, and thus play an important part in the global carbon balance. The process of organic matter decomposition [the cascade from plant litter to resistant soil organic matter (SOM)] is dependent on three factors as noted in the OPQ triangle (Swift, Heal and Anderson, 1979): Organisms (O), Physico-chemical environment (P), and the chemical composition or Quality of the organic matter (Q). It is well recognized that the variation in Q determines the rate of decomposition and the composition of the biota. When the quality of the litter has a low C/N, fast decomposition of litter is mediated by fast growing organisms (r-selection). When litter has a high C/N quality, K-selection of organisms occurs and the decomposition is slow. Therefore, the biodiversity of soil organisms is determined by the quality of organic matter input to soil, and that in turn is dependent on the composition of the vegetation. Thus there is a link between the diversity (and type) of vegetation and the diversity (and type) of decomposers through litter quality.

These processes were selected as models for which experiments can be designed to explore the relationship of soil biodiversity (a soil all taxa biotic inventory) and ecosystem function for reasons addressed in the Executive Summary. In addition, (1) hypotheses on the relationship of the soil biota to ecosystem function remain to be explored, and are presently limited to particular groups of organisms; (2) the link of ecosystem vegetation type and diversity to the diversity and type of soil biota provides relevance and logic to an inventory on sites of long term ecosystem research; (3) decomposition and carbon flux experiments could be coupled to trace gas emissions and global climate change experiments on many sites; and (4) the historical database which exists for decomposition and carbon flux, and the well developed methods for analysis of these processes would form a firm foundation for the application and testing of new technologies as well as for interpretation of these processes on soil biodiversity.

These experiments have similar requirements:

- Implementation at sites with well-described soil systems, preferably where GIS grids are established; sites should have historic data bases on previous land management, ongoing and future environmental monitoring, limited public access to the long term experiments (site security), and preferably, data of existing soil biota.
- Involvement of biologists (microbiologists, molecular biologists, zoologists, systematists, ecologists, botanists and physiologists), soil chemists, soil physicists, geologists, hydrologists, modelers and information management specialists, would enhance planning. Cross-training to increase participants' knowledge base of methodological procedures and priorities would be promoted.
- Inclusion of taxonomists and biologists for continued and lasting connectivity between the taxonomic and process components of the experiments.
- Detailed inventory of soil biological diversity at sites varying in climatic and plant species diversity (e.g., varying organic matter (Q)uality and (P)hysico-chemical environment).
- Quantitative assessment of the role of neglected taxa and encouragement of increased

attention to the systematics of these groups.

- Deposition and preservation of voucher specimens and/or other biological materials (e.g., DNA samples). This will require that the culture collection centers and the museums are involved at an early stage and necessary preservation protocols are followed or developed.
- Long term data collection, modeling.
- Training of students in ecology and taxonomy, and the development of scientists that can study the biology of soil species, freely crossing the boundaries of these two disciplines.
- Development and application of new taxonomic and ecological techniques.
- Experimental designs that incorporate appropriate statistical comparisons within and between sites of varying organic matter quality.

[Return to the top of the document]

EXPERIMENTAL STRATEGIES

The Integrated Biodiversity and Function Experiments

1. The soil biodiversity and decomposition experiment

The experiment was selected by workshop participants as one of the priorities because it is a major process occurring in all ecosystems involving a wide range of taxa. Besides ecosystem processes, this experiment could be particularly useful in identifying indicator groups involved in sustainability or for monitoring environmental perturbation, since the key species would be associated with the main functions of the decomposition process. We suggest that a model for this experiment should be the successful and ongoing US LTER Long-term Intersite Decomposition Experiment Team (LIDET) that compares decomposition rates and the changing chemical status of the same quantities and types of organic matter at many ecosystems of differing climates. A comparable experiment was undertaken in a transect across a number of European countries in the Decomposition (DECO) project, and across Canada with the Canadian Intersite Decomposition Experiment (CIDET). However, the succession of soil taxa involved in decomposition were not measured as part of LIDET, DECO or CIDET. Our experimental strategy would be to incorporate a new decomposition experiment in climatically different ecosystems to allow temporal and spatial monitoring of soil biota as decomposition of selected standard organic matter substrates proceeds. A coordinated effort in identifying the succession of organisms as the residues decompose will relate the taxa to the decomposition process.

The major questions addressed by this experiment are: (1) How does quality of organic matter influence soil biodiversity in different climatic regimes? (2) How are soil taxa linked to decomposition processes and the physico-chemical environment spatially and temporally? (3) To what extent does the structure of the soil community influence decomposition processes and are similar functions performed by different taxa in different environments?

We suggest that a few initial sites be selected for intensive analysis of the soil biota. Sites with a base of, and present taxonomic experience and knowledge of soil organisms would be good initial sites for an intensive study, but must also have ongoing environmental monitoring, soil characterization and other criteria listed previously. The ECN and LTER sites are suggested as fulfilling these criteria. The experimental framework would be established by scientists following analyses of databases on decomposition and soil taxa at selected sites (see Timeline). Similar protocols and procedures would necessarily be used at each of the sites. The types of measurements, the standardized organic materials to be distributed for the decomposition experiment, the time frame for sampling and the methods for inventorying the organisms and decomposition process, will need to be agreed upon by participants before setting up the intensive site experiments. The standard quantities of organic matter will be placed in litter bags, which are sealed mesh screen envelopes (Anderson and Ingram, 1993). The mesh size selected for the different bags will exclude organisms of different sizes; thus, all soil biota could be included, or just the smaller invertebrates and microbes. We propose that an all taxa biotic inventory of soil biota (ATBI) should occur as related to mass loss of the standard organic resources distributed at each of the sites. Organisms that cannot be identified quickly will be catalogued and preserved according to the process agreed upon by the participants in the experiment.

2. The soil biodiversity and carbon and nitrogen flux experiment

The main approaches of these experiments will be to manipulate the biodiversity and observe the effect on C and N fluxes, manipulate the C and N fluxes and observe the effects on biodiversity, and disrupt the system and observe the consequences on both biodiversity and C and N fluxes.

The major questions addressed by this experiment are: (1) How does soil biodiversity affect the carbon and nitrogen pools and fluxes? Related to this is, how do the magnitudes of carbon and nitrogen flux through the soil sub-system and how does organic matter quality (Q) affect the diversity and structure of soil organisms? (2) Is spatial distribution of the soil taxa dependent on the quality and quantity of carbon and nitrogen inputs in addition to their placement?, and (3) What is the relationship between biodiversity and resilience in soils? Does biodiversity change as soil systems recover from disturbance? What are meaningful measures of resilience?

We suggest that the measurement of carbon and nitrogen fluxes through the soil biota should be followed using stable isotopes (Table 1). For this approach to work, experimental sites must be selected where plant communities are dominated by either C3 or C4 species, such as exist in temperate grassland ecosystems. We suggest that both disturbed (agroecosystems) and natural sites (containing multiple species) be compared at each location. For example, use of ecosystems in the US and the UK would allow us to test the generality of the observed phenomena.

We do not intend to dictate a specific experimental design without more discussion and analysis of the one year synthesis at a future workshop as noted in the suggested timeline. At present, we propose an outlined experiment that, in our collective discussion of experimental options, appeared to address the workshop priorities. We have concluded that treatments should incorporate a realistic series of manipulations so that we may observe the impact of disturbance on soil biotic structure and function, and on changes in carbon and nitrogen fluxes and movement. Manipulations could include: (1) application of one or more biocides, which would remove or reduce selected taxa. Candidate biocides are insecticides, nematicides, fungicides, antibiotics and other metabolic inhibitors that have some degree of taxonomic specificity. Although there are limitations to this technique, it has been used successfully to determine changes in soil foodwebs and ecosystem properties. This treatment could also be used to investigate the resilience of the soil system if the treatments were applied over the long term; (2) removal of grass litter (following mowing) from one set of plots and its addition to others; and (3) application of a pollutant (e.g., a heavy metal, which we do not condone but use as an example of the type of manipulation) which would affect most taxa. An intensive study of litter decomposition would be possible within this overall experimental design, concentrating on food webs, the particular role of different groups of microorganisms and the differential spatial distribution of fungi compared to bacteria. Plant sequestration of carbon is almost universally aided by mycorrhizal fungi, a group that needs substantial attention by systematists and biologists.

Experiments will necessarily be designed for long term use to effectively measure changes in carbon and nitrogen fluxes and detect changes in soil biodiversity. We suggest that these studies be set up sequentially, with the first phase lasting approximately two years so that we may obtain an inventory of organisms and to establish their patterns of distribution and movement within the soil. The second phase would establish manipulation treatments for three to four years, with half the biocide plots released from treatment after 1 year and allowed to recover. The third part of the experiment would last two years or more, allowing all plots to recover so that we may measure resilience by following the change in biodiversity and concomitant dynamics of C and N fluxes. During this final phase, biodiversity will again be assessed to determine if species loss is related to key ecosystem processes. If appropriate, additional funding could be sought to extend this recovery period.

As with the decomposition experiment, similar protocols must be used at the intensive sites within each country for the C and N flux experiment. We anticipate that novel and improved methods that combine enumeration with chemical and isotopic analysis will be required for some groups of organisms so that we may observe the interrelationship between population dynamics and flux of C and N. Table 1 shows 1) the taxa to be identified for both the C-N flux and decomposition experiments, 2) the techniques available for their characterization, and 3) the level of information on carbon flux within each group:

Table 1. Techniques for the carbon flux experiment that presently could be used for soil biota.

Taxon	Systematic characterization	Carbon flux measurement
Bacteria	Molecular	Possibly GC-MS (need *ca.* 11 g of soil)
Fungi	Morphological/molecular	GC-MS (sterols) resolution uncertain
Protozoa	Morphological	No known method
Nematodes	Morphological/molecular	GC-MS
Arthropods	Morphological/molecular	GC-MS
Annelids	Morphological	GC-MS
Molluscs	Morphological	GC-MS
Plant roots	Morphological	GC-MS

Movement of tracers through the components of the ecosystem (including the soil taxa) would be followed after the application of a single, strong pulse of isotopically distinct CO_2 by fumigation using FACE technology and of 15N (topical application as NO3). A source of CO_2, that offers the maximum contrast with the isotope signal of the existing vegetation and organic matter should be selected. The isotope should be assayed as it occurs within individual taxa. Isotope loss by respiration and leaching should also be measured. The resolution to which individual taxa can be used for stable isotope measurements of carbon flux has yet to be determined. It will certainly be feasible for more abundant and important taxa, and even where individual taxa cannot be assayed separately, it will be possible to relate ecological processes to the overall diversity of the soil trophic network. Measurement of carbon flux within microbial taxa may require the development of novel techniques. For example, gas chromatography-mass spectrometry can be used to identify the isotopic content of species-specific molecules. The stable isotope method is precise, accurate and safe, but ultimately limits the scale of the experiment to the maximum area for which it is practical to fumigate with CO_2. Grasslands are preferred to forest, since the isotope will enter process pathways quickly, and since fumigation is feasible with current technology.

We conclude that this experiment is important because it provides a comparison across and within ecosystems for:

1. Measurement of the link between carbon and nitrogen flux and gross diversity.
2. Determination of the significance of diversity within functional and taxonomic groups in maintaining and regulating C and N fluxes.
3. Measurement of the links between diversity and resilience and of the importance of spatial distribution in determining function.

[Return to the top of the document]

THE TIMELINE FOR RESEARCH

Immediate

- Identify a network of well-described sites based on previous history and current long term support for maintenance of environmental data collection (for example, the United Kingdom Environmental Change Network sites (ECN) and the United States National Science Foundation Long Term Ecological Research sites (LTER).
- Establish a one year project with one person from each proposed experimental site to be responsible for extraction and compilation of existing soil biotic databases and to participate in a cross-site synthesis/comparison. Analyze and interpret existing comprehensive data on soil biodiversity from a limited number of well-described sites. The purpose of this initial study would be to identify trends with which to formulate/develop hypotheses and plan the next stage of biodiversity/ecological research at particular sites. Additional information compiled would be valuable in any inventory work.
- At a workshop, present synthesized cross-site information, identify gaps in knowledge and establish hypotheses. Formulate research plans for investigating the relationship between soil biota inventories and ecosystem processes (e.g., carbon flux and decomposition experiments) at particular sites. Publish results in print and electronic form.
- Establish a small working group to design a generalized study of the relationship between biodiversity and ecosystem processes of carbon flux and decomposition. This should include the scientific rationale, experimental approach(es) and outline of appropriate methods to investigate both biodiversity and the processes selected.

Early 1996

- Research Proposals submitted to funding agencies for research to test hypotheses identified from the one-year project.

Long Term Vision

- Identify a global network of sites linked through a set of research platforms with experiments on soil biotic inventories and ecosystem processes (e.g., decomposition and C and N flux).
- Enhance participation (private, agency, university and global collaborators) of this Long Term Network on Soil Biodiversity and Ecosystem Function through both intensive (more detailed analyses) and extensive (minimal research package identified by participants) efforts.
- Provide a synthesis of the contributions and roles of soil taxa at genetic, community

and ecosystem levels of organization as results become available, to assure that key species are widely recognized.
- Increase the educational commitment to training students internationally, particularly in the tropics, about the importance of soil, the dark frontier.
- Encourage transfer of knowledge to the public and new generations on the significance of life in the soil.
- Implement management plans that will maintain soil quality and contribute to the sustainability of the planet.

[Return to the top of the document]

LITERATURE CITED

Anderson, J. M. and J. S. I. Ingram. 1993. Tropical Soil Biology and Fertility: A Handbook of Methods. Second edition. CAB International, Wallingford, UK.

Clarholm, M. 1989. Effects of Plant-Bacterial-Amoebal Interactions on Plant Uptake of Nitrogen under Field Conditions. Biology and Fertility of Soils 8:373-378.

Couteaux, M. M., M. Mousseau, M.-L. Celerier, and P. Bottner. 1991. Increased Atmospheric CO_2 and Litter Quality: Decomposition of Sweet Chestnut Leaf Litter with Animal Food Webs of Different Complexities. Oikos 61:54-64.

Elliott, E. T., D. C. Coleman, and C. V. Cole. 1979. The Influence Of Amoebae on the Uptake Of Nitrogen By Plants In Gnotobiotic Soil. In: pp. 221-229. J.L. Harley and R. Scott Russell, eds. The Soil-Root Interface. Academic Press, London, UK:

Groombridge, B. (Ed.). 1992. Global Biodiversity: Status of the Earth's Living Resources. Chapman and Hall, London.

Hawksworth, D. L. and J. M. Ritchie. 1993. Biodiversity and Biosystematic Priorities: Microorganisms and Invertebrates. CAB International, Wallingford, UK.

Heal, O. W., J. C. Menaut, and W. L. Steffen , Eds. 1993. Towards a Global Terrestrial Observing System: Detecting and Monitoring Change in Terrestrial Ecosystems (GTOS): AB Digest 14 and IGBP Global Change Report 26, UNESCO, Paris and IGBP, Stockholm.

Heal, O. W., S. Struwe, and A. Kjoller. (in press) Diversity of Soil Biota and Ecosystem Function. In: B. Walker et al., eds. Global Change and Terrestrial Ecosystem. IGBP, Vol. 1. Cambridge University Press, Cambridge, UK.

Hendrix, P.F., R. W. Parmelee, D. A. Crossley, Jr., D. C. Coleman, E. P. Odum, and P. M.

Groffman. 1986. Detritus Food Webs in Conventional and Non-tillage Agroecosystems. BioScience 36:374-380.

Huston, M. 1993. Biological Diversity, Soils and Economics. Science 262:1676-1680.

Lavelle, P., E. Blanchart, A. Martin, A. V. Spain, and S. Martin. 1992. Impact Of Soil Fauna on the Properties of Soils in the Humid Tropics. In: R. Lal and P.A. Sanchez, eds. Myths and Science Of Soils Of The Tropics. SSSA Special Publication No. 29, Soil Science Society of America, Madison, WI, USA.

Marmonier, P., P. Vervier, J. Gilbert and M. J. Dole-Olivier. 1993. Biodiversity in Ground Waters. Trends in Ecology and Evolution 8:392-395.

National Research Council. 1993. A Biological Survey for the Nation. National Academy Press, Washington, D.C.

Moore, J. C. and P. C. de Ruiter. 1991. Temporal and Spatial Heterogeneity of Trophic Interactions within Below-ground Food Webs. Agriculture, Ecosystems and Environment 34: 371-397

National Research Council. 1993. Research Priorities in Tropical Biology. National Academy Press, Washington, D.C.

National Science Board. 1989. Loss of Biological Diversity: A Global Crisis Requiring International Solutions. National Science Foundation, Washington, D. C.

O'Donnell, A. G., M. Goodfellow and D. L. Hawksworth. 1994. Theoretical and Practical Aspects of the Quantification of Biodiversity among Microorganisms. Phil. Trans. R. Soc. Lond. B. 345:65-73

Schlesinger, W. H. 1991. Soil Warming Experiments in Global Change Research. The Report of a Workshop Held in Woods Hole, Massachusetts, September 27-28, 1991. National Science Foundation Ecosystem Studies Program, Washington, D.C.

Stanford, J. A. and J. V. Ward. 1992. Emergent Properties of Ground Water Ecology: Conference Conclusions and Recommendations for Research and Management. In: pp 409-415. Proceedings of the First International Conference on Ground Water Ecology. U.S. Environmental Protection Agency and American Water Resources Association, Washington, D. C.

Stanford, J. A. and J. J. Simmons, (Eds). 1992. Proceedings of the First International Conference on Ground Water Ecology. U.S. Environmental Protection Agency and American Water Resources Association, Washington, D. C.

Systematics Agenda 2000. 1994. Systematics Agenda 2000: Charting the Biosphere. American Museum of Natural History, New York.

Swift, M. J., O. W. Heal and J. M. Anderson. 1979. Decomposition in Terrestrial Ecosystems. Blackwell, Oxford, UK.

Szegi, J., ed. 1984. Soil Biology and Conservation of the Biosphere, Vol. I and II. Akademiai Klado, Budapest, Hungary.

Verhoef, H.A. and L. Brussard. 1990. Decomposition and Nitrogen Mineralization in Natural and Agroecosystems: The Contribution of Soil Animals. Biogeochemistry 11:175-211.

[Return to the top of the document]

WORKSHOP PARTICIPANTS

Professor J.M. Anderson, Rothamsted International, Rothamsted Experimental Station, Harpenden, Herts AL5 2JQ, Phone: 0582-763133, FAX: 0582-469688

Professor C. Arme, NERC, Terrestrial & Freshwater Sciences, Polaris House, North Star Avenue, Swindon SN2 1EU, Phone: 0793-411500, FAX: 0793-411502

Dr. J. Balandreau, Universite Claude Bernard, 43, Boulevard du 11 Novembre 1918, Bat 741 - 4e 69622, Villeurbanne Cedex, FRANCE, Phone: 72/44-8200, FAX: 72/43-1223

Dr. Valerie Behan-Pelletier, Biosystematics Research Center, Agriculture Canada, CEF, Ottawa, Ontario, K1A OC6, Canada, Phone: 613/996-1665, FAX: 613/947-5974, Email: behanv@ncccot2.agr.ca

Dr. David Bignell, Queen Mary & Westfield College, School of Biological Sciences, Mile End Road, London E1 4NS, Phone: 071/975-5555, FAX: 081/983-0973

Dr. Steve Blackmore (HOST), Keeper of Botany & Associate Director - Life Sciences, Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD, Phone: 071/938-8992, FAX: 071/938-9232, Email: sb@nhm.ac.uk

Dr. Caroline Bledsoe, Department of Land, Air & Water Resources, Hoagland Hall, University California, Davis, CA 95616-8627, FAX: 916/752-1552, Email: cbledsoe@lternet.edu

Dr. Thomas Duncan, Museum Informatics Project, Information Systems & Technology, 2111 Bancroft Way, Rm. 501, University Calif., Berkeley, CA 94720, Phone: 510/642-6533, FAX: 510/643-8856, Email: tdunc@buttercup.berkeley.edu

Dr. James Edwards, Executive Officer, Directorate for Biological Science, National Science Foundation, 4201 Wilson Boulevard, Arlington, VA 22230, Phone: 703/306-1400, FAX: 703/306-0343, Email: jledward@nsf.gov

Dr. Paul Eggleton, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, Phone: 071/938-9459, FAX: 071/938-8937, Email: pe@nhm.ac.uk

Dr. E. T. Elliott, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, Phone: 970/491-5645, FAX: 970/491-1965, Email: tede@nrel.colostate.edu

Dr. Alastair Fitter, Department of Biology, University of York, York YO1 5DD, Phone: 0904-432814, FAX: 0904-432860, Email: ahfi@vax.york.ac.uk

Dr. Diana Freckman, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, Phone: 970/491-2504, FAX: 970/491-1965, Email: dfreckman@lternet.edu

Dr. James Gosz, Director, Division of Environmental Biology (DEB), National Science Foundation, 4201 Wilson Boulevard, Arlington, VA 22230, Phone: 703/306-1480, FAX: 703/306-0367, Email: jgosz@lternet.edu

Dr. Sheridan Haack, U. S. Geological Survey, Water Resources Division, 6520 Mercantile Way, Suite 5, Lansing, MI 48911, Phone: 517/887-8909, FAX: 517/887-8937, Email: skhaack@srvrdmilns.er.usgs.gov

Dr. W. Hallwachs, Department of Biology, University of Pennsylvania, Philadelphia, PA 19104-6018, Phone: 215/898-5636, FAX: 215/898-8780, Email: whallwac@sas.upenn.edu

Dr. J. Harris, Environment and Industry Research Unit, University of East London, Romford Road, London E15 4LZ, Phone: 081/590-7722 x 9459, FAX: 081/849-3499, Email: harris@whimain.uel.ac.uk

Professor David L. Hawksworth, International Mycological Institute Bakeham Lane, Egham, Surrey TW20 9TY, Phone: 0784-470111, FAX: 0784-470909, Email: imi@cabi.org

Professor O.W. Heal, Institute of Terrestrial Ecology, NERC, Monks Wood, Abbots Ripton, Huntingdon PE17 2LS, Phone: 01487-773381, FAX: 01487-773590.

Dr. Samuel James, Department of Biology, Maharishi International University, 1000 North Fourth Street, Fairfield, IA 52557-1056, Phone: 515/472-1146, FAX: 515/472-1167, Email: sjames@miu.edu

Dr. Dan Janzen, Biology Department, University of Pennsylvania, 415 South University Avenue, Philadelphia, PA 19104-6018, Phone: 215/898-5636, FAX: 215/898-8780, Email: dJanzen@sas.upenn.edu

Dr. Leonard Krishtalka, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213, Phone: 412/622-3232, FAX: 412/622-8837, Email: krishtalkal@clp2.clpgh.org

Dr. Jack Lattin, Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, OR 97331-2907, FAX: 503/737-3643, Email: Jlattin@lternet.edu

Professor J. Lynch, University of Surrey, Guildford, Surrey GU2 5XH, Phone: 0483-300800, FAX: 0483-576978

Professor Robert M. May, Department of Zoology, Oxford University, South Parks Road, Oxford OX1 3PS, Phone: 0865/271/170, FAX: 0865/310/447

Dr. Steve McGrath, Soil Science Department, Rothamsted Experimental Station, Harpenden, Herts AL5 2IQ, Phone: 0582-763133, FAX: 0582-760981, Email: mcgrath@bbsrc.ac.uk
Dr. A. G. O'Donnell, Department of Agriculture & Environmental Science, The University, Newcastle upon Tyne, NE1 7RU, Phone: 091/222-6920, FAX: 091/222-6920, Email: tony.odonnell@newcastle.ac.uk

Dr. Parke A. Rublee, Department of Biology, 312 Eberhart Bldg., University of North Carolina at Greensboro, Greensboro, NC 27412, Phone: 910/334-5391, FAX: 910/334-5839, Email: rubleep@goodall.uncg.edu

Dr. Tim Seastedt, INSTAAR, University of Colorado, Boulder, CO 80309-0450, Phone: 303/492-3302, FAX: 303/492-6388, Email: tims@culter.colorado.edu

Dr. Carol Shearer, Department of Plant Biology, 505 S. Goodwin St., University Illinois, Champaign, IL 61821, Phone: FAX: 217/244-7246, Email: ashearer@uiuc.edu

Professor Janice Sprent, Department of Biological Sciences, University of Dundee, Dundee DD1 4HN, Phone: 0382/344279, FAX: 0382/322318, Email: jis@biol.sc.dundee.ac.uk

Dr. Kelley Thomas, School of Biological Sciences, University of Missouri, Kansas City, 5100 Rockhill Road, Kansas City, MO 64110-2499, FAX: 816/235-5158, Email:

kthomas@vax1.umkc.edu

Dr. R. Thomas, Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, Phone: 071/938-9301, FAX: 071/938-8754, Email: r.thomas@nhm.ac.uk

Professor Bernard Tinker, Department of Plant Sciences, Oxford University, South Parks Road, Oxford OX1 3RB, Phone: 0865/792750

Professor Michael B. Usher, Scottish Natural Heritage, 2 Anderson Place, Edinburgh, EH6 5NP, Phone: 031/446-2401, FAX: 031/446-2406

Professor Keith Vickerman, Department of Zoology, University of Glasgow, Glasgow G12 8QQ, Phone: 041/339-8855, FAX: 041/307-8016

Dr. Kristiina Vogt, Yale University, School of Forestry and Environmental Studies, 370 Prospect Street, New Haven, CT 06511, FAX 203/432-5942, Email: kdvogt@lternet.edu

Observer

Dr. James T. Callahan, Ecosystem Studies Program, National Science Foundation, 4201 Wilson Boulevard, Arlington, VA 22230, Phone: 703/306-1483, FAX: 703/306-0367; Email: jcallaha@nsf.gov

[Return to the top of the document]