The Ecosystems Center
1991 Annual Report

Marine Biological Laboratory
Woods Hole, Massachusetts
Looking across tundra at foothills of Brooks Range, Alaska.

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The Ecosystems Center, located at the Marine Biological Laboratory in Woods Hole, Massachusetts, is dedicated to the study of natural systems and the application of the knowledge thus gained to the management of natural resources. Founded in 1975, the center has become MBL’s largest year-round program. It operates as a collegial association under the leadership of co-directors John Hobbie and Jerry Melillo; the 11 scientists who comprise its senior staff make all major decisions by consensus.

Although funding for research projects comes primarily from competitive government grants, vital support for administration, research and educational activities also comes from a reserve fund created with grants from private sources, including foundations and corporations.

Investigators at The Ecosystems Center study the structure and functioning of ecological systems, or ecosystems. Ecosystems can vary greatly in size. Some are defined by natural boundaries, some by the questions researchers ask. But each is a basic unit of nature that encompasses both organisms and their environment, linked through a variety of biological, chemical and physical processes. Among the types of ecosystems studied at the center are estuaries, lakes, streams, temperate and tropical forests, arctic tundra and areas of the coastal ocean.

Ecosystem structure is defined not only by the species present and their abundance, but also by the distribution of such elements as carbon or nitrogen among the system’s various components, living and non-living. Ecosystem function is defined by processes that control species and their abundance and channel the movement of energy and materials among components and across system boundaries. The processes that govern the way ecosystems function are themselves controlled by a variety of environmental factors, such as the presence or absence of organisms, temperature or the availability of water and nutrients. Describing the complex set of interactions among organisms, processes and controls is essential to understanding the way ecosystems work and predicting their response to changing conditions.

Center investigators are particularly interested in the effects of disturbance on ecosystems at all levels, local, regional and global. Questions that guide their research include: How will the world’s terrestrial ecosystems respond to elevated levels of carbon dioxide and associated changes in climate? How does the chronic deposition of airborne compounds affect biological and chemical processes in the forests, lakes and streams of eastern North America? Will more nutrients be released from the soil into arctic lakes and streams if the depth of permafrost in the arctic tundra changes? What impact would such an increase have on the plants, insects and fish that live in these bodies of water?

The research projects described in this report are divided into five categories: arctic, temperate, tropical, coastal and global. Center scientists undertake studies in diverse geographic regions and on different scales. But their work is unified by similarities in the questions they ask, the methods they use and the mathematical models they employ to test their understanding and predict the effects of environmental change over long periods of time and on the large scale.

The carryover of information from one research site to another is immense; the long-term result of applying a common set of tools to research in a wide range of contexts will be an improved understanding of how ecosystems function and interact at all levels. This understanding will benefit efforts to preserve and manage resources wisely.

Tools that enable scientists at The Ecosystems Center to address these large-scale questions include models and databases. Center scientists are currently using a global model to see how climate change will affect the exchange of carbon and nitrogen between the atmosphere and the vegetation. The center’s geographic information system (GIS) program for storing and organizing data also contributes to the effort to model responses of terrestrial ecosystems to changing climate conditions. Such a system enables the staff of the center to incorporate a tremendous amount of information from such sources as instruments mounted on satellites or aircraft. This
sort of information collected over long periods of time and large areas of the
earth makes it possible for center scientists to extrapolate from the results of
small-scale studies to large regions of the globe.

It is difficult for one researcher to have all of the skills necessary to
study ecosystems. Center scientists work together, bringing to their joint
projects skills in terrestrial and aquatic ecology, microbiology, chemistry,
remote sensing, botany, zoology, physiology, mathematics and computer
modeling. They also work with investigators from other institutions. One of
the strengths of The Ecosystems Center is the ability of its scientists to
interact closely over the years; the constant challenge and stimulation are
invaluable.

The center's facilities include aquatic, terrestrial, chemical and mass
spectrometer laboratories, a plant growth chamber and several controlled
temperature chambers. Projects share the aquatic and terrestrial labs,
where field samples are prepared and experiments using radioisotopes,
microscopy and other techniques are performed. The chemistry lab is a
common resource for all of the center's projects. It contains such
instruments as an automated nutrient analyzer, gas chromatographs and an
ion chromatograph. The center's mass spectrometer facility is used for
analyzing ratios of isotopes of carbon, nitrogen and sulfur. The plant growth
facility has three large chambers, each with light, temperature, humidity and
atmosphere controls.

Although the National Science Foundation (NSF) funds most of the
center's research projects, investigators also receive support from the
Department of Energy (DOE), the Environmental Protection Agency (EPA),
the National Oceanic and Atmospheric Administration (NOAA) and the
National Aeronautics and Space Administration (NASA). The center has also
received support for research from the Exxon Foundation and from the Massachusetts
Water Resource Authority (MWRA) as well as seed money for new scientific directions
from the Andrew W. Mellon Foundation.

The Ecosystems Center is conducting several innovative educational programs. The
Texaco Foundation has provided funds for training a group of Puerto Rican students in
the methods and concepts of ecology. A similar internship program is getting underway
in Brazil. The Exxon Corporation is supporting young scholars who work with center
staff members on research projects at field sites in both North and South America. The
Clowes Fund has provided a three-year grant for a series of workshops designed to
introduce graduate students to the concepts and uses of mathematical modeling in
ecology.

One of the reasons to carry out research in ecology is to satisfy intellectual
curiosity about the way the world we live in works. Another is to provide a sound
foundation for environmental policy and management. Basic research conducted at The
Ecosystems Center will help answer questions with practical applications such as these:
What happens to streams or bays when the levels of nutrients flowing into them rise?
What effect do the gases released from forests have on global climate? How can we
manage forests to optimize removal of carbon dioxide from the atmosphere?

Staff members at The Ecosystems Center contribute to the search for answers to
such questions in a number of ways. Several center scientists are providing information
to EPA modelers on forest production of trace gases such as methane, oxides of
nitrogen or sulfur compounds for a model of trace gas production and consumption in
forest ecosystems. This model will be used to predict greenhouse gas concentrations in
the atmosphere over the next century. Another scientist at the center is advising EPA on
a project to restore vegetation at construction and drilling sites in northern Alaska. Yet
another is serving on a review committee for EPA’s Environmental Monitoring and
Assessment Program (EMAP). Several other center investigators have conducted studies
in Massachutes Bay that are providing valuable information for state officials
responsible for assessing the possible effects of the proposed Boston sewer plant and
offshore outfall.

Center scientists are members of a wide variety of governmental and non-
governmental committees and boards. They serve on NSF, NASA, NOAA, EPA,
Department of Agriculture and National Research Council committees, on the Scientific
Committee on Problems of the Environment and on committees of the International
Geosphere-Biosphere Programme. One senior staff member serves on the executive
commitee of the MBL; another is on the board of the Association of Ecosystem
Research Centers and the Arctic Research Consortium of the U.S. (ARCUS). Several are
members of Ecological Society of America committees.
The Role of Process Studies in Understanding Ecosystems

The fundamental goal of research at The Ecosystems Center is to understand the way ecosystems work. We want to know about their structure and function and about ways that disturbances, both natural and manmade, alter these two characteristics. In order to understand the way ecosystems work and how disturbances affect structure and function, we focus much of our research on processes and especially on those mechanisms that transfer energy and materials in and out of an ecosystem and among its components.

By focusing on particularly important mechanisms, or processes, we break up a complex system into smaller, more manageable pieces for study. Mathematical models allow us to reassemble these pieces of a system and have these processes interact as they do in a real ecosystem. This process-oriented approach to analyzing ecosystems is essential to our ability to predict the consequences of environmental change.

Basic ecosystem processes include photosynthesis, respiration, uptake of nutrients and decomposition. These processes and the rate at which they occur are each controlled by a specific set of environmental factors, such as temperature, amount of sunlight, the moisture in the soil and the concentrations of nutrients necessary for plant growth. Our understanding of the controls that regulate various ecosystem processes allows us to model ecosystems mathematically and predict the ways in which environmental change will alter their functioning. Modeling, in turn, allows us to analyze the effects of multiple processes acting simultaneously.

But models are always simplifications of reality. To find out whether we have included the right processes and whether the models we have created are applicable, we test their predictions against field experiments and refine them if necessary.

Center scientists study controls on ecosystem processes in a variety of geographic regions and at several scales. Descriptions of some of these studies form the research reports in the following pages.

- In the Arctic, we are studying the way temperature controls the rate of carbon dioxide (CO₂) production and nitrogen mineralization in soils. We are also using ¹⁵N, a stable isotope of nitrogen, to see how filamentous algae control the downstream movement of ammonium in arctic streams.
- In temperate forests, we are investigating the effect of acid precipitation on the process of immobilization. In temperate lakes, we are measuring the way oxygen and organic matter control the rate of removal of sulfur and acid by sediments.
- In tropical forests, we are measuring the release of nitrous oxide (N₂O) at various soil moisture levels. We are also studying the effects of clearcutting on soil processes and N₂O emissions.
- In coastal estuaries, we are investigating the relative effects of sources of dissolved organic carbon on bacterial production. We are also studying the way sediment oxidation levels and nitrate concentration in the water column control the process of denitrification in coastal waters.
- Many processes and controls interact in the center's global models; one key control on the amount of carbon stored in an ecosystem is the amount of nitrogen and other vital elements supplied from outside an ecosystem relative to the amount supplied by recycling within an ecosystem.

There are many advantages to studying a single process and the factors that control it over a wide variety of ecosystems. For one thing, we can see how the process responds to the same control with a wide range of values as well as to different controls. An example of how this approach works comes from our study of the effects of soil temperature on CO₂ release from temperate forests. Data from Harvard Forest in Massachusetts covered a certain set of temperatures. Data from other temperate forests expanded the temperature range of the data set. All of the data agreed, and we were able to use a single mathematical relationship to describe CO₂ flux at different temperatures for temperate forests around the world. This relationship also successfully predicted the results of experiments in which forest soil temperature was raised by 5°C. The ability to predict the effect of temperature on CO₂ flux rates in temperate forests suggests that knowledge of soil temperatures alone, derived from widely available air temperature measurements, would allow us to make global estimates of effects of future increases in air temperature on the flux of CO₂ from forest soils to the atmosphere.

Another advantage to studying processes and controls over a range of ecosystems is the insight gained about multiple controls over a single process. For example, field research on sediments from a large number of lakes led center scientists to hypothesize that sulfur removal is controlled both by the oxygen content of the overlying water and
the amount of organic matter available to sediment microbes. In experiments with lake sediments in the laboratory, we found that the sediments took up the greatest amount of sulfur when organic matter was added and oxygen removed.

Because this process of sulfur uptake also generates alkalinity, it mitigates to some extent the effects of acidification from anthropogenic sources. Eutrophication caused by human activities increases available organic matter and decreases oxygen in the bottom waters of lakes, which in turn leads to removal of sulfur and neutralization of acidity.

The results of process studies are often applied to solving environmental problems. For many decades, minimally treated sewage from Boston and surrounding communities has flowed into Boston Harbor. The corresponding rate of nitrogen addition per square kilometer is among the highest for any estuary. In 1995, a secondary treatment plant is scheduled to begin operations, and the effluent will be redirected into the deep waters of Massachusetts Bay. Our ability to predict the ecological effects of changing the location of the outflow depends upon estimating how much of the nitrogen currently entering Boston Harbor is changed into harmless nitrogen gas by the process of sediment denitrification. Center scientists studying the controls on the process of denitrification in the sediments of the harbor and the bay are finding that maximum denitrification occurs when organic matter addition is moderately high and when circulation and mixing provide a moderate supply of oxygen to the sediments.

While the data on these processes are valuable, they only cover a few square meters at the 10 measurement sites scattered over the harbor and nearby bay. In order to estimate the total denitrification in different parts of the harbor-bay complex, we must apply our site data to a larger scale. An approach under consideration is, first, to prepare a map of the harbor-bay sediments divided according to the amounts of organic matter. Concentrations are generally high in the inner harbor sediments and low in the bay sediments. Next, we plan to incorporate the process and control data into a mathematical model of nitrogen movement. The model will produce rates of denitrification for a series of sediment types, each with a different amount of organic matter in the sediment. We will then extrapolate the results to the entire harbor-bay complex by multiplying each sediment type by the total area for that type of sediment as derived from the map.

The study of processes and their controls in ecosystems is more than just another research approach used by center scientists. It is the key that allows us to model the interactions of many processes and simulate the dynamics of nutrient cycling and plant growth. This approach also allows the transfer of ecological knowledge from the study of one ecosystem to another. When we understand the relationships between processes and controls, we can predict the ecological consequences of changes that affect a controlling factor. For this reason, questions about management of ecosystems are often addressed through models that incorporate controls on important ecosystem processes.
How Arctic Ecosystems Respond to Changing Climate

A third point is that these effects of climate change on the arctic landscape will, in turn, have an impact on global climate. Changes in temperature alone, followed by changes in ecosystems throughout the arctic regions, will produce large changes in CO₂ and methane (CH₄) fluxes into the atmosphere. These key greenhouse gases have a strong influence on global temperature.

A fourth point is that changes in primary production in terrestrial and aquatic communities will affect the abundance and distribution of caribou, moose and fish, thus affecting the human population and other predators that depend on these species. The arctic landscape consists of an interlocking mosaic of communities and ecosystems, all of which are responsive to climatic change.

INTERACTION OF ARCTIC COMMUNITIES AND THEIR BIOGEOCHEMICAL CYCLES WITH GLOBAL CLIMATE CHANGE

Figure 1 shows how terrestrial, riparian, stream, and lake communities of the Arctic are linked by the flow of water, nutrients, and organic matter. It also illustrates their impact on the atmosphere and on human populations. Global climate change affects every component of ecosystems in the Arctic.

Bruce Peterson
Effects Of Temperature Change On Microbial Respiration And Nitrogen Cycling In Arctic Soils

To understand how the landscape functions and how it may respond to changing climate, Ecosystems Center scientists have been looking at the ways in which carbon and nutrient cycling are altered by disturbance. In one series of experiments, Knut Nadelhoffer, Anne Giblin and Gus Shaver studied the role of temperature in controlling rates of microbial CO₂ production and nitrogen mineralization in arctic soils (Figure 2). The researchers incubated soils from heath, tussock and wet sedge sites at 3°, 9° and 15°C in the laboratory, where they were able to collect all of the evolved CO₂ and the inorganic nitrogen.

They were surprised to find that a temperature increase from 3° to 9°C had no effect on CO₂ production from microbial respiration, while a further boost to 15°C doubled the rate. Nitrogen mineralization did not respond as much as CO₂ to temperature increases, and soils with the highest rates of ammonium and nitrate production had the lowest rates of CO₂ production. These differences probably reflect differences in organic matter quality in the soils beneath different vegetation types. Respiration does not follow the standard pattern of change for metabolic processes with increases in temperature, and CO₂ and nutrient changes are not linked in a simple way. Units of the landscape with different types of vegetation will therefore contribute to changes in CO₂ and nutrient cycles in different ways as soil temperature changes. Thus models of CO₂ and nutrient transfer for the tundra must account for the heterogeneous distributions of terrestrial vegetation and soils in the landscape.

Figure 2. Respiration and nitrogen mineralization of soil organic matter (SOM) from dry heath, moist tussock and wet sedge tundra ecosystems. We incubated soils in the laboratory for 13 weeks at 0.06 MPa moisture tensions and 3°C, 9°C or 15°C. Bars show (A) cumulative microbial respiration (CO₂-C production) and (B) cumulative nitrogen mineralized (NO₃⁻-N plus NH₄⁺-N leached).

Gus Shaver surveys the ice, revealed by stream erosion, that underlies the tundra around the Toolik Lake research site in Alaska.
Controls On Nitrogen Flux In Arctic Streams

While most nitrogen mineralized in tundra soils is recycled on land, some inevitably moves downslope with soil waters into streams and rivers. The fate of this nitrogen was the focus of a tracer experiment designed by Bruce Peterson and George Kling on the Kuparuk River last summer. Bruce and George added ammonium chloride labeled with $^{15}$N, a stable isotope of nitrogen that occurs in very small amounts in nature, to the control (unfertilized) reach of the Kuparuk. Their aim was to trace the fate of natural ammonium, which seeps downhill in soil solution into the river. They added the tracer continuously for six weeks, and by the fifth week, most components of the river ecosystem showed uniform labelling with $^{15}$N (Figure 3). The resulting distribution of $^{15}$N in components of the river ecosystem provides a picture of how stream processes control the downstream movement of nitrogen. The rapid decline in the $^{15}$N content of filamentous algae as one goes downstream indicates rapid removal; ammonium travels on average about one kilometer before it is taken up by the algae. Uptake of ammonium and nitrification are primarily responsible for the decline, since dilution from tributaries is negligible in this stretch of the river.

The high $^{15}$N content of certain insect species, such as mayflies (Baetis) and chironomids (Orthocladius), shows that their growth is tightly linked to algal production. Other species, such as black flies (Prosimilium) and caddisflies (Brachycerinus), contain much lower levels of $^{15}$N, indicating that they consume only small amounts of algae. Black flies are filter feeders, which collect fine particles swept downstream with the current. The $^{15}$N content of black flies shows a peak at a location 800 meters below the place where the $^{15}$N tracer was added. A simple model calculation shows that fine particles, including algae, sloughing from riffle rocks travel about 800 to 1,000 meters before being removed from the water by settling or by filter feeders. This experiment allows scientists to determine what controls the rate at which nitrogen moves downstream in dissolved and particulate form as well as the pathways for nitrogen flow in the food web of the river.

The ability of scientists to predict how climatic changes will alter ecosystems depends on synthesizing results of these soil-warming and nutrient-tracing experiments and many others into models of the landscape that incorporate the linkages and changes illustrated in Figure 1. Arctic regions provide a natural laboratory where climatic changes are occurring most rapidly and in which terrestrial and aquatic ecosystems are particularly amenable to the study of whole-ecosystem responses. Because climate change is a global phenomenon, however, similar challenges exist everywhere.

The demands of working and thinking across ecosystem and disciplinary boundaries, of dealing with several interacting elements simultaneously and of extrapolating from small-scale studies to regional and global levels are presenting unprecedented challenges for environmental scientists. Humanity is performing an experiment in global change, however, that appears likely to outstrip even our most determined efforts to understand these changes before they are history. A wise society would act now to slow the rate of change and by doing so achieve a better chance for both understanding and survival on a changing planet.


Figure 3. The downstream distributions of $^{15}$N values for algae, epilithon and insects after five weeks of continuous addition of trace-level $^{15}$N-NH$_4$. The tracer is easily detectable in all taxa 5 km downstream.
The Uplands and the Estuaries: Tracing the Effects of Human Activity on Coastal Ecosystems

The ecosystems of the densely populated coastal regions are especially susceptible to the effects of human activities. Development in the upland basins that drain into the sea has a direct impact on the health and functioning of coastal ecosystems. These regions are also particularly vulnerable to potential effects of global climate change such as sea-level rise. In an effort to address these issues, Ecosystems Center scientists Linda Deegan, Brian Fry, Anne Giblin, John Hobbie, Chuck Hopkinson and Bruce Peterson have developed a broadly integrated research program that focuses on change in coastal ecosystems.

The basic premise of the coastal research program is that activities in the upland portion of coastal drainage basins are strongly linked to processes and conditions downstream in the wetlands, open waters and sediment systems of estuaries as well as in the open ocean (Figure 1). They are linked through the water, nutrients, organic matter and sediments that flow downstream.

The runoff of organic matter and nutrients from forested lands differs immensely from that of agricultural lands or settled areas. Thus human activity changes the quantity and quality of the materials that flow downstream into the estuaries. Over the long term, changes in climate and the regular addition of airborne contaminants will also influence the nature of upland runoff into the estuary.

The increased flow of nutrients and organic matter from the uplands into the estuaries leads to increased algal production and noxious blooms, shifts in habitats, altered fish communities and decreases in estuarine fisheries. Extreme overloading can deplete the oxygen dissolved in the water and produce vast fish kills.

At the broadest level, our research efforts are focused on understanding cause-and-effect relationships between human activities, quality of habitats and the structure and productivity of the food web in coastal ecosystems. We are focusing our research on three areas: the amount of runoff of water, nutrients and organic matter from agricultural, residential and forested uplands; the effect of these upland inputs on the trophic structure, production and efficiency of estuarine systems; and the effect of upland inputs on the distribution and quality of estuarine habitats and the production of fish and shellfish.

Two general questions guide our research program: What is the relative importance to estuarine ecosystems of organic carbon and nitrogen inputs from watersheds with differing uses?

Figure 1 represents a conceptualization of some of the important linkages between estuarine ecosystems at the land-sea interface and the adjacent oceans and uplands. Understanding and predicting the long-range effects of human activity on the complex web of relationships that structures the marine environment requires a broad research program that integrates phenomena occurring at a wide range of time and space scales.
Does the interaction of inorganic nutrients with the quantity and quality of organic carbon and nitrogen play an important role in determining the trophic structure, production and efficiency of estuaries?

The interaction between inorganic nutrients and the quantity and quality of organic matter inputs from land determines, in part, the structure of estuarine food chains and the production of higher trophic levels. Increased levels of inorganic nutrients generally stimulate production of large phytoplankton cells, such as diatoms, which provide high-quality food for zooplankton, small invertebrates and shellfish. This short food chain is an efficient way to produce commercially valuable fish and shellfish.

Overloading estuaries with dissolved organic matter, on the other hand, stimulates bacterial production. Because of their small size, bacteria are at the bottom of a long and inefficient food chain with many links between the microorganisms and the top predators. More than 95% of the carbon in food consumed by bacteria can be lost as carbon dioxide (CO₂) as it moves up the food chain.

All forms of organic matter, furthermore, are not equal in their ability to stimulate production. The rate and efficiency of bacterial growth and nutrient regeneration decrease as the quality of the organic matter supply decreases. Growth on a low-quality organic substrate is slight and inefficient. The lower the quality of the substrate, the more CO₂ must be given off through respiration before sufficient nitrogen is available to build biomass with the proper ratio of carbon to nitrogen. The productivity of the entire food chain is correspondingly lower.

**Bacterial Utilization Of Dissolved Organic Carbon**

Bacterial utilization of dissolved organic carbon (DOC) is a key process in the transfer of energy in estuarine ecosystems. Understanding this process is essential to our ability to describe the flow of organic matter from various sources and their relative importance. These sources include uplands, estuarine algae, marsh grass and oceanic phytoplankton. Using a new stable isotope tracer approach, Ecosystems Center scientists Brian Fry and Bruce Peterson have teamed up with microbial ecologist Dick Wright of Gordon College to study bacterial use of easily consumed (labile) DOC in estuaries.

The results of our field surveys, measurements of bacterial production and DOC utilization, bacterial stable isotope analyses and laboratory experiments have led us to a new view of the cycle of DOC in the Plum Island Sound estuary of northern Massachusetts. Rather than showing a steady decrease along the salinity gradient from the upper estuary to the sea, DOC distributions show substantial additional inputs along the way.

**Figure 2.** Dissolved organic carbon (DOC) and bacterial activity at various salinities (ppt) in the Plum Island Sound estuary. a) The typical midsummer concentrations of total DOC from various sources. Also shown are the δ¹³C values (%o) of DOC for these sources. b) Bacterial production in summer. c) Total labile DOC concentrations during the summer, as determined by microbial growth assays. d) The source of labile DOC as determined by the δ¹³C composition of the assay bacteria.

DOC in the estuary comes from at least five different major sources with four different carbon isotope compositions (Figure 2a). The bulk of the DOC in the upper estuary comes from upland watersheds and from tidal freshwater cattail (Typha) marshes. We have also found an upstream chlorophyll peak; however, where DOC from algae accumulates to levels well in excess of background concentrations. In mid-estuary, DOC from tidal salt marshes creates a second peak. In the coastal ocean, most of the DOC is derived from marine phytoplankton.

Studies of the growth and isotopic composition of the bacterial populations in the Plum Island Sound estuary indicate that labile DOC is distributed differently from bulk DOC. Bacterial production is highest in mid-estuary (Figure 2b). In experiments in which natural bacteria were inoculated into freshly filtered estuarine water, we found a net bacterial biomass production of only 5-10 micromoles per liter (μmol/l) of carbon before growth ceased. Assuming a 50% growth efficiency, this result indicates an available pool of labile DOC of only 10-20 μmol/l of carbon or roughly 1% to 5% of the total DOC (Figure 2a & 2c).
The isotopic composition of the bacteria growing in this water reflects that of DOC produced locally by algae and marshes (Figure 2d) rather than that of the bulk DOC pool. Bacteria in the upper estuary are relatively low in $^{13}$C, an isotope of carbon that occurs in very small amounts in nature, and obtain DOC from algae. The bacteria in mid-estuary are relatively rich in $^{13}$C, reflecting the composition of DOC derived from Spartina salt marshes. The isotopic composition of bacteria found in the most saline portion of the estuary is intermediate in value, reflecting the primary dependence of these bacteria on DOC derived from oceanic phytoplankton.

The focus of this research is on the relative importance of the various sources of organic carbon that fuel the secondary production of bacteria in estuaries. The important controls on this process are both direct and indirect. The rate of supply and the quality of the DOC available to the bacteria are the two most important direct controls on bacterial production; the most important indirect controls are the human activities that determine land use and the dynamics of water, nutrient and organic matter runoff into estuaries.

**Denitrification In Coastal Sediments**

Coastal ecosystems are heavily loaded with nutrients. The flow of excess nitrogen into estuaries from sources such as sewage or agricultural runoff can lead to increased primary production, toxic algal blooms, low oxygen levels in the water and even anaerobic conditions. Denitrification, the reduction of nitrate ($\text{NO}_3^-$) to nitrogen gas ($\text{N}_2$), is an important process in coastal waters because nitrogen is converted from a form that stimulates algal production to a form that does not.

Ecosystems Center scientists Anne Giblin and Chuck Hopkinson have been conducting studies in the coastal region around Boston Harbor, which experiences one of the highest levels of nitrogen loading of any estuary in the world. Questions that guide their research include: How much of the nitrogen currently entering Boston Harbor is denitrified in bay bottom sediments? How much will be denitrified after 1995 when the sewage outfall is redirected into deep Massachusetts Bay waters that are cold year round? Will the inorganic nitrogen loading of the bay actually increase if the water is not "cleansed" via passage through Boston Harbor? What effects will the input of sewage into Massachusetts Bay have in remote locations, such as the northern shore of Cape Cod?

Controls on the denitrification process in marine sediments are complex and inter-related; they include rates of organic matter loading, temperature and the nitrate and oxygen concentrations in the water above the sediments. Building on earlier studies conducted in Buzzards Bay and the nearshore region of coastal Georgia, Anne and Chuck are evaluating the importance of two factors controlling denitrification: the degree of sediment oxidation, and the concentration of nitrate in the overlying water.

The degree of sediment oxidation is an important factor controlling denitrification because it determines whether or not $\text{NO}_3^-$ is produced, and whether microbes must use nitrate instead of oxygen to support their metabolism. Denitrification in coastal sediments proceeds through a two-step "coupled" process. Ammonium produced in the sediments from decomposing organic matter is oxidized (nitrified) to $\text{NO}_3^-$. The nitrate then diffuses into deeper portions of the sediments lacking oxygen where it is reduced (denitrified) to $\text{N}_2$.

As illustrated in Figure 3, we predict that the amount of nitrogen that is denitrified is highest at an intermediate level of sediment oxidation. When sediments are only slightly oxidized, denitrification is low and limited by the low rate of nitrification. Nitrate is produced when sediment oxidation levels are high, but the microbes use oxygen instead of nitrate to support their metabolism. Thus denitrification is low.

**Figure 3. Experimental results and theoretical models of the rate of denitrification in riverine, estuarine and oceanic sediments at various degrees of sediment oxidation.**
Figure 4 illustrates how we think additions of organic matter and NOs concentration in the water above the sediments influence denitrification. Under conditions of high sediment oxygen demand (SOD) associated with high organic matter loading or low bottom-water oxygen concentrations, the denitrification fluxes are greater than when oxygen demand is low or bottom-water oxygen concentrations are high.

These studies of the nitrogen cycle in Boston Harbor and Massachusetts Bay will provide baseline information on the various inputs and transformations of nitrogen needed to characterize this coastal ecosystem. They will also give us the information necessary to understand the controls on certain critical processes in the estuarine nitrogen cycle. This knowledge will improve our ability to predict future effects of human activities on natural resources, information that is essential for better management of the ecosystems at the land-sea interface.

Ecosystems Center staff members participating in studies of coastal ecosystems during 1991 included: Gary Banta, Linda Deegan, Brian Fry, Robert Garritt, Anne Giblin, John Hobbie, Charles Hopkinson, Meredith Hullar, Bosse Normman, Daniel Padien, Bruce Peterson, Susan Soupe, Kristin Tholke, Jane Tucker and Sam Wainright.
Environmental Change in Temperate Zone Ecosystems

In the northern hemisphere, the burning of fossil fuels in factories, homes and vehicles releases tremendous amounts of carbon, nitrogen and sulfur into the atmosphere (Figure 1). These emissions affect the terrestrial and aquatic ecosystems of the northern temperate regions in a variety of ways. Gaseous nitrogen and sulfur from combustion are transformed into nitric and sulfuric acids in the atmosphere and eventually deposited over large areas of North America and Europe, where they influence the cycling of elements within terrestrial ecosystems as well as the flow of these elements from terrestrial to aquatic systems. Increases in the atmospheric levels of "greenhouse gases" such as carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) are likely to promote an overall warming of the global climate. This warming will also have an impact on ecosystem processes in the soils and vegetation of the temperate regions.

Researchers at The Ecosystems Center are conducting long-term, large-scale experiments in both terrestrial and aquatic ecosystems in order to study the effects of a changing environment on key processes in temperate-zone ecosystems.

Figure 1. In the northern hemisphere, the burning of fossil fuels releases carbon, nitrogen and sulfur into the atmosphere, contributing to greenhouse warming as well as the deposition of nitric and sulfuric acids over large areas of North America and Europe. Atmospheric warming and acid deposition affect terrestrial and aquatic ecosystems in a number of ways. In the diagram, concentrations of nitrate, sulfate and acidity are given in microequivalents per liter for precipitation, forest soil solutions and ions in lake water. We have multiplied the precipitation values by 3.6 to account for the loss of water by evapotranspiration. Both nitrate and acidity interact with soil processes so that little reaches aquatic ecosystems. In contrast, soils do not retain sulfate, and most of the amount in precipitation reaches lakes and streams. Numbers in boxes are average values for Cape Cod, compiled from a variety of sources.
The effects of disturbances on ecosystem processes in plants, soils, sediments and surface waters are frequently subtle and slow to appear. But small changes in critical processes build up over time and can eventually alter ecosystem behavior and interactions among ecosystems.

We do not yet have an adequate understanding of how climate warming and the regular deposition of nitrates and sulfates will influence ecosystem processes in the temperate regions. One effect of climate warming, for example, will be increased soil temperatures, which will affect the rate at which soil microbes cycle elements. Since biological productivity in the forests and other terrestrial ecosystems of temperate regions is often limited by the amount of nitrogen that is available in the soil, nitrogen from atmospheric sources is likely to have a significant influence on terrestrial ecosystem processes. These processes, in turn, will play a major role in determining the ultimate fate of the nitrogen. Biological demands for sulfur, in contrast, are low in most terrestrial ecosystems. Retention of sulfate (SO$_4^{2-}$) in forest ecosystems is regulated primarily by geochemical factors. Only a small fraction of the excess sulfate deposited annually from the atmosphere is retained in forest ecosystems; the rest leaches into the groundwater and ends up in lakes and streams.

**Temperature And Carbon Dioxide Emissions From Forest Soils**

Temperature has a strong influence on the process of soil respiration, a process that is closely linked to the cycling of elements in forests. Increases in soil respiration could lead to greater rates of nitrogen and sulfur cycling between forest vegetation and soils. As a result of a number of field studies in temperate forest ecosystems, scientists have concluded that the relationship between CO$_2$ emissions from soils and soil temperature can be described by an exponential equation. The rate of CO$_2$ emissions increases at a constant percentage as temperature increases.

As scientists began to develop a mathematical model of ecosystem responses to climate change, it became evident that temperate forests could be exposed in the future to temperatures higher than they had ever experienced before. Will future soil respiration responses to temperature increases fit the same exponential equation used to describe the relationship under current climate conditions?

To answer this question, Ecosystems Center scientists Jerry Melillo and Paul Steudler, postdoctoral research associate William Peterson and consultant Frank Bowles designed and implemented a large field experiment in a mixed deciduous forest at the Harvard Forest in Petersham, Massachusetts. The purpose was to study the effects on soil processes of increasing soil temperature by 5°C. We established 18 plots of 36 square meters each. The total included experimental plots heated by means of buried cables; disturbance-control plots, in which heating cables were installed but the heat not turned on, and control plots.

We found that the CO$_2$ emissions produced by the elevated temperatures of the experimental plots did fit the exponential equation described above (Figure 2). The data show that the CO$_2$ emission rate increases 2.5 times for every 10°C rise in temperature. The relationship observed between soil temperature and CO$_2$ flux for the soil-warming experiment is consistent with data from hardwood forests around the world, allowing us to make global estimates of CO$_2$ flux from hardwood forests.

We also observed a strong correlation between the daily average air and soil temperature during the snow-free period of the year at Harvard Forest. These observations strengthen our ability to make global estimates by allowing us to use widely-available weather data to predict CO$_2$ flux. To demonstrate the utility of this approach, we predicted the CO$_2$ flux for the soil-
warming site using the air temperature measured at the Harvard Forest (Figure 3). For the period between June and November, the mean of the twelve actual CO₂ flux measurements agreed well with the mean of the daily predictions.

The clear trend of exponential increases in soil respiration with increases in soil temperature has implications for other ecosystem processes. Increased soil respiration could lead to increased cycling of nitrogen and sulfur and weathering of soil minerals, thereby increasing rates of nutrient cycling within forests and the flow of nitrogen, sulfur and acidity into aquatic ecosystems.

**Immobilization Of Nitrogen In Decomposing Forest Litter**

Ecosystems Center scientists Knute Nadelhoffer and Jerry Melillo are studying the effects of atmospheric deposition on ecosystem processes in collaboration with John Aber of the University of New Hampshire as part of the Bear Brooks Watershed Study. We have been simulating atmospheric nitrogen deposition at this site in Maine since 1988 by spraying large forest plots with dilute nitric acid solutions. Along with several other research teams, we are studying the effects of these additions on critical processes such as tree growth, nitrogen uptake by tree tissues and the decomposition of leaf litter.

One example of a key process is the immobilization of nitrogen in decomposing litter. During decomposition, microbes take up inorganic nitrogen from precipitation and soil solutions and convert it into organic forms. As the nitrogen in the decomposing litter increases, less is available for plants. What effect does the addition of nitrogen have on the process of immobilization during decomposition?

In order to address this question, teams of investigators added 56 kilograms of nitric acid per hectare per year to experimental forest plots. After one year, litter decomposing on the experimental plots immobilized more nitrogen than did litter decomposing on control plots (Figure 4). Although the mass of beech litter decreased at equal rates on both control and experimental plots, the nitrogen content of litter decomposing on experimental plots was greater than on control plots. After one year, spruce litter retained about 70% of its initial nitrogen on control plots and about 90% on the experimental plots. Nitrogen content doubled in maple wood chips decomposing on the treated plots.

Our studies show that immobilization during decomposition serves to retain at least some of the nitrogen deposited on forest ecosystems from the atmosphere. Continued deposition and immobilization will produce humus that is increasingly rich in nitrogen. Two questions remain to be answered over a longer period of time: Will more nitrogen become available to plants through mineralization from this nitrogen-rich humus? Will more nitrogen and acidity leach out of the soils and into streams and lakes?

**Sulfur And Acidity In Lakes And Streams**

Lakes and streams receive much of their water from the flow of groundwater that has been "processed" within forest soils. Some 75% of the water in precipitation that falls on the forests is lost through evaporation and transpiration before it reaches the groundwater. Because they are not taken up as they pass through the soil, solutes such as chloride and sulfate become more concentrated in the groundwater flowing into surface bodies of water. Biological processes in the soil take up a certain amount of the nitrate in precipitation, on the other hand. These processes, along with soil weathering, reduce the amounts of nitrate and acidity entering lakes and streams (Figure 1).

Biological processes within lakes remove some of the sulfate and nitrate that flows into them via the groundwater. These processes, such as the sulfate reduction that takes place
in the sediments of lakes, also generate alkalinity, which reacts with hydrogen ions to neutralize the acidity of incoming water. Ecosystems Center scientists Anne Giblin, Bruce Peterson and Brian Fry have been making measurements in lakes and conducting laboratory experiments in order to understand what controls the process by which sediments take up sulfur from the water.

Over the past several years we have been monitoring changes in lake water during the summer. Once the lake waters become stratified by temperature, the bottom water can no longer mix with the atmosphere; microbial respiration decreases oxygen levels in the bottom water and the sediments of the lake bottom. In most lakes, sulfate concentrations in the bottom water also decrease over the summer, especially after the oxygen is depleted, because microbes in the lake sediments use sulfur for respiration.

What will happen to the chemistry of lakes if levels of sulfate flowing into them change? As part of our investigation of this question, we carried out field and laboratory studies designed to find out what controls the rate at which microbes in the sediment remove sulfate from the water. We first tested the idea that the initial sulfate concentration in the water was the most important factor controlling the rate at which lake sediments take up sulfate and remove it from the water. Finding no relationship between sulfate concentration and sulfate uptake in 12 different lakes (Figure 5), we concluded that the sulfate concentration in the overlying water was not the sole factor regulating sulfate uptake by lake sediments.

We next performed a series of laboratory experiments to see whether other factors such as oxygen, iron or organic matter could be important in determining rates of sulfur uptake. We brought intact sediment cores from the lake bottom back to the laboratory. Some of these samples served as controls, while the rest were treated in three different ways. We added organic matter to the sediments in the first set of samples and organic matter plus iron to the second set. In the case of the third set, we added organic matter to the sediments and removed oxygen from the overlying water. All the sediments that received additions of organic matter took up more sulfate from the overlying water than the controls (Figure 6a). Organic matter had even a greater effect on generating alkalinity and thus reducing the acidity of the overlying water (Figure 6b). The lake sediments took up the greatest amount of sulfate and generated the most alkalinity when we added organic matter and removed the oxygen from the water.

The final step is to develop a mathematical model of the controls on the rate at which lake sediments remove sulfur and acid from the water. As we make measurements in lakes with different levels of productivity and carry out laboratory experiments with different sulfate concentrations, we can begin to put the numbers into our conceptual diagram. Similar experiments performed with nitrate will help us predict the capacity of lakes to respond to the changing nitrate inputs that may result from changes in nitrogen cycling in terrestrial ecosystems.

**Figure 5.** The rate at which deep-water sediments take up sulfate versus sulfate concentrations in the overlying water at the beginning of the summer. The sediments came from three lakes in the Finger Lakes region; basins of Trout Lake, Wisconsin: a lake in the Adirondack Mountains, and three ponds on Cape Cod. We incubated each sediment core in the laboratory at 10°C.

**Figure 6.** Total uptake of sulfate (Fig. 6a) and the total amount of alkalinity generated (Fig. 6b) during three weeks of 10°C incubation of sediment cores collected from Mountain Lake, Nova Scotia. We held the sediment either with no treatment (control) or with additions of algal carbon (+C), algal carbon plus iron (+C, Fe), or algal carbon and anoxic incubation (+C, Anox).

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*Ecosystems Center staff members who participated in studies of temperate zone forests, soils and lakes during 1991 were: Mark Castro, Jonathan Chapman, Mark Dombolser, Martha Downs, Todd Drumley, Steve Fafinsky, Brian Fry, Anne Giblin, David Kicklighter, Jerry Melillo, Catherine Michmerhuizen, Michelle Mikesky, Knute Nadelhoffer, Kathleen Newskirk, William Peterjohn, Bruce Peterson, Kathleen Regan, Andrea Ricca, Paul Steudler and Jane Tucker.*

*Kathy Newskirk, Frank Bowles*
Pilot study plot in Woods Hole for long-term soil-warming experiment currently underway at Harvard Forest.
Ecosystems Center scientists are studying the effects of human activities on the biogeochemistry of tropical forests in Latin America. One focus of this research is the exchange of greenhouse gases between tropical forest soils and the atmosphere. We seek to determine what environmental factors control fluxes of nitrous oxide (N₂O) and methane and to understand how changes in land use affect the processes that control the fluxes of these gases. This information will be used in ecosystem models to predict the fluxes of greenhouse gases in the future as a result of the cutting of forests or the abandonment of pastures.

One dramatic result of the rapid population growth in the tropics is the clearcutting of forests and their conversion into agricultural and pasture lands. In a wet tropical forest in eastern Puerto Rico, Jerry Meillio, Paul Steudler and Mark Castro, a postdoctoral research associate at The Ecosystems Center, measured greenhouse gas fluxes in clearcut and control plots. The clearcutting increased the emissions of N₂O for up to 17 months after the disturbance (Figure 1). The highest rate occurred four months after the clearcut. Soil nitrate concentration and the rate of nitrification peaked at the same time.

N₂O is produced by two microbial processes, nitrification and denitrification. As ammonium is transformed to nitrate in the process of nitrification, some fraction of the nitrogen can be released into the atmosphere as N₂O. In addition, the process of denitrification uses nitrate as a substrate to produce both N₂O and nitrogen gas (N₂). We know that clearcutting enhances the production of N₂O, but we do not know which of these two processes, nitrification or denitrification, is more important.

Although we have some clues about the control of these processes, we still need to learn a great deal more about the biological and chemical processes underlying this large flux of N₂O. We can also make a general prediction that additional clearcutting of tropical forests will increase the atmospheric concentration of N₂O. But many questions remain to be answered before we know just how important these fluxes are to

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**Figure 1.** Fluxes of nitrous oxide (N₂O) from soils at clearcut and reference sites in the Luquillo Experimental Forest of eastern Puerto Rico over a period of 17 months. Four months after the sites were cleared, N₂O emissions were more than 55 times greater in the cut plot than in the reference plot. We collected emissions with trace gas sampling chambers located on the forest floor.
Figure 2. Fluxes of nitrous oxide (N₂O) to and from soils in a 30-year-old dry forest in northeastern Puerto Rico at various levels of soil moisture. We measured fluxes with a static chamber technique six times over a year during both wet and dry seasons.

the total atmospheric buildup. For example, we need to know whether this effect occurs in dry forests as well as wet, and whether it is a general phenomenon of all tropical forests.

We have also been able to study the effect of one particular control, moisture, on the exchange of N₂O in a different forest in Puerto Rico, a dry tropical forest on the northeastern end of the island. This forest, with a rainfall of about 165 centimeters a year, is quite dry for part of the year and becomes fairly wet during the hurricane season in late summer and fall. When the exchange of N₂O was measured over a year, we found that the soil was a sink for N₂O at moisture levels between 5% and 15%. Above these moisture levels, the soil was a source for N₂O, and the rate of release rapidly increased as the soil moisture increased (Figure 2). The biological processes responsible for both the uptake and release need further study; one interpretation is that microbial consumption of N₂O occurs at the same time as production and that the balance between these two processes is controlled by soil moisture.

Studies of trace gas exchange in tropical forests are just beginning. To further the general understanding of the effect of land-use changes on the rates of gas transfer, scientists from the center are pursuing these studies in both Puerto Rico and Brazil in cooperation with scientists from these countries.

Ecosystems Center staff members who participated in studies of tropical ecosystems during 1991 were: Mark Castro, Jonathan Chapman, Jerry Melillo, Michelle Miliefsky, Chris Neill and Paul Steudler.
The global carbon cycle has long been a research topic at The Ecosystems Center. We initially focused our attention on the consequences of changes in land use on the global carbon cycle. These changes, which include the burning of tropical forests, logging and the conversion of forests to agriculture, have contributed many billions of tons of carbon to the atmosphere. Some of that carbon has been recaptured from the atmosphere as trees have grown on abandoned farmlands or pastures. Nevertheless, current land-use practices are releasing a net of about 1.6 billion metric tons of carbon into the atmosphere each year. This flux and the approximately 5.4 billion metric tons of carbon released each year from the burning of fossil fuel are the major sources of the increase in atmospheric carbon dioxide (CO₂).

Natural processes of removal partially balance these anthropogenic sources of atmospheric carbon. For example, the ocean absorbs about two billion metric tons each year. Recent evidence suggests that terrestrial ecosystems may be storing an additional 1.6 billion metric tons each year above and beyond that associated with the regrowth of forests on abandoned farmlands. This additional terrestrial sink of carbon has become a major focus of research at The Ecosystems Center that will improve both our understanding of the global carbon cycle and our ability to predict the effects of climate change in the future.

For each square meter of land, the annual additional terrestrial sink of carbon is very small, too small to be measured directly as a change in the size of trees or in the amount of organic matter in soils. Information about the controls on processes that make up the carbon cycle can be used in mathematical models, however, to infer changes in the terrestrial carbon sink.

The first model we developed was the Terrestrial Carbon Model (TCM). It was used to investigate the carbon exchanges associated entirely with land-use changes and regrowth of vegetation (Table 1). This model was based upon empirical observations of the effects of burning, logging and regrowth on carbon storage within ecosystems.

In order to make better use of our knowledge of plant and ecosystem processes, we next developed the Terrestrial Ecosystem Model (TEM), which can be used at regional and global scales. TEM uses information on climate, soils and vegetation to make monthly estimates of important carbon and nitrogen fluxes and pool sizes. This information is entered in a 0.5° latitude by 0.5° longitude grid that covers all of the continents.

This process-based approach is shared by a more detailed model, the General Ecosystem Model or GEM. We use this model to predict the way carbon storage at particular sites has changed as CO₂ concentrations, temperature and nitrogen deposition rates have changed over hundreds of years.

Table 1

| Terrestrial Carbon Model (TCM): | A bookkeeping model that keeps track of carbon in more than 50 types of ecosystems over time as they lose and regain carbon after changes in land use. |
| Terrestrial Ecosystem Model (TEM): | A process-based model with six pools and 12 fluxes that runs each month with input from a geographic information system (GIS) with 0.5° by 0.5° grid cells over all of the continents. |
| General Ecosystem Model (GEM): | A process-based model with 19 pools that uses data from a single site and inputs representing the past and future climates and nitrogen deposition rates. |
availability for much of the temperate forest region in North America. When temperature is elevated, in contrast, NPP shows a progressively larger response to increases in CO₂. The release of nitrogen from soil organic matter at elevated temperatures allows the vegetation in most locations to incorporate some of the elevated CO₂ into production.

Figure 1. Increases in annual net primary production (NPP) of temperate forests predicted by the Terrestrial Ecosystem Model (TEM) as a result of doubling carbon dioxide (CO₂) concentration (from 350 ppm to 700 ppm) and increasing temperature by 2°C and 5°C. Increased temperature enhances the effects of increased CO₂ because nitrogen release from decomposing soil organic matter is stimulated by higher temperatures. The resulting increase in available nitrogen fertilizes plant production.

Figure 2. A conceptual model of the links between the carbon (solid arrows) and nitrogen (dotted arrows) cycles in terrestrial ecosystems. Vegetation takes up carbon dioxide (CO₂) through the process of net primary production (NPP). This uptake of carbon is closely tied to the uptake of inorganic nitrogen from the soil. Both carbon and nitrogen enter the soil as litter, where the flux of these elements is tightly linked. Carbon is given off from soils as CO₂ through the process of decomposition (DECOMP); the nitrogen associated with it is transformed (mineralized) from organic to inorganic form, thus becoming available to plants. The nitrogen cycle can be supplemented by inputs from outside the ecosystem via nitrogen fixation by soil bacteria or deposition from the atmosphere. The total carbon stored in the ecosystem can be increased by three means: increasing nitrogen inputs and thereby stimulating the growth of vegetation, moving nitrogen from soils with low carbon to nitrogen ratios (C:N) to vegetation with higher C:N ratios, and increasing the C:N ratios of either vegetation or soils.

The General Ecosystem Model

The potential for carbon sequestration (or loss) by terrestrial ecosystems depends almost certainly upon the interactions of the carbon cycle with the cycles of other vital elements like nitrogen. Interactions between the carbon and nitrogen cycles are complex and have ramifications on a diversity of ecosystem properties from tissue function, on the fine scale, to whole system carbon storage, on the coarse scale. We have tried to generalize from these complex interactions to identify the key properties controlling carbon storage. We can conceptualize changes in carbon storage in terrestrial ecosystems in terms of three key biogeochemical properties (Figure 2).
One control is the amount of nitrogen and other vital elements supplied from outside the ecosystem relative to the internal recycling of these elements. As shown in this figure, the cycles of carbon and nitrogen in ecosystems are tightly linked. The amount of carbon stored in an ecosystem can be increased by increasing the supply of nitrogen from outside the ecosystem. An ecosystem with a ready, external supply of vital elements, such as nitrogen, can store carbon without redistributing its internal resources or changing the concentrations of vital elements in its tissues. The more open an ecosystem is to external sources of vital elements, the more responsive its carbon-storage capacity should be to disturbances like long-term changes in CO₂ and climate.

Working in collaboration with colleagues Gus Shaver, Knut Nadelhoffer and Jerry Melillo, Ecosystems Center scientist Edward Rastetter and postdoctoral research associate Robert McKane used the General Ecosystem Model (GEM) to simulate changes in carbon storage in a hardwood forest in central Massachusetts. The simulation was based on a reconstruction of changes in CO₂ concentration, temperature and nitrogen deposition between 1740 and 1984. The rate of nitrogen deposition in rainfall, an important control on forest carbon storage, has increased dramatically at this site as a result of industrial development during that period. Our model predicts that the increased deposition increased carbon storage by approximately 1,800 grams per square meter (18 metric tons per hectare) over the last 250 years (Figure 3).

Another control on carbon storage capacity is the distribution of carbon, nitrogen and other vital elements between vegetation and soils. Figure 1 shows the difference in chemistry between vegetation and soils. The ratio of carbon to nitrogen in vegetation ranges from about 30 to 600 (by mass), depending largely on the amount of woody tissue; the ratio in soils ranges from about 8 to 50, depending on many factors including temperature and the degree of water saturation.

This wide difference between vegetation and soils is significant for nitrogen-limited ecosystems. If nitrogen from the soil organic matter (with a low carbon to nitrogen ratio) is taken up and incorporated into the vegetation (with a high carbon to nitrogen ratio), there will be a net storage of carbon in the ecosystem, even without the addition of nitrogen from outside sources. If, on the other hand, nitrogen moves from vegetation to soils, the ecosystem will have a net loss of carbon because the same amount of nitrogen is now associated with a smaller amount of carbon. The greater the difference in the carbon to nitrogen ratios of vegetation and soils, the higher the potential for storing carbon by moving nitrogen from soils to vegetation.

To illustrate the importance of the redistribution of nitrogen, we simulated the responses of a coniferous forest in Oregon to reconstructed changes in CO₂ concentration, temperature and nitrogen deposition between 1740 and 1984. Because this site is on the west coast, the amount of nitrogen deposited on it in rainfall has increased very little. Temperature, on the other hand, has increased significantly over the last 250 years.

Our model predicts that this temperature increase stimulated decomposition of soil organic matter, which increased the transformation of nitrogen from organic to inorganic forms. Most of this nitrogen was taken up and incorporated into the vegetation. Our model also predicts that an increase in carbon storage on the order of 2,000 grams per square meter (20 metric tons per hectare) has occurred at this site since 1740. The net movement of nitrogen from soils to vegetation accounted for a large portion of this increase (Figure 4).

Our simulations of the forests in Massachusetts and Oregon suggest that the increased deposition of nitrogen in the Massachusetts forest and the release of nitrogen from soil organic matter in the Oregon forest have resulted in decreased carbon to nitrogen ratios in vegetation. The stimulation of productivity by nitrogen in these two ecosystems has increased.
the amount of litter, which has increased the carbon to nitrogen ratios of the soils. The model predicts that this increase only accounted for about 10% of the increase in carbon storage in these two ecosystems. If the level of CO₂ in the atmosphere continues to increase, however, increases in carbon to nitrogen ratios in both vegetation and soils could contribute significantly to carbon storage by terrestrial ecosystems.

Our results lead us to believe that terrestrial ecosystems have a high capacity to store carbon. Most terrestrial ecosystems are likely to be sinks for CO₂ as a result of projected changes in atmospheric CO₂ concentration and temperature. The strength of these sinks will be strongly affected by interactions between the carbon cycle and cycles of other vital elements like nitrogen.

Further research will be necessary to determine the limits of carbon storage in the biosphere and the capacity of management schemes to enhance this type of carbon storage. The biosphere will not solve the problem of rising CO₂ emissions, however. A comprehensive solution must include management of terrestrial ecosystems for carbon storage, reductions in the use of fossil fuels and an end to the explosive growth of human populations.

_Ecosystems Center staff members participating in global modeling projects during 1991 included: John Hobbie, David Jones, David Kicklighter, David McGuire, Robert McKane, Jerry Melillo, Knute Nadelhoffer, Edward Rastetter and Gus Shaver._

**Figure 4.** Simulated changes in the total amount of carbon stored in the H.J. Andrews Ecosystem in Oregon over the last 250 years and the associated changes in the amounts of nitrogen in soils and plants and in the entire ecosystem. Simulations were run with the General Ecosystem Model (GEM) using reconstructed records of carbon dioxide in the atmosphere, temperature and nitrogen deposition in rainfall and dust. The increase in carbon storage at this site is predominantly a result of increased temperature, which caused a net movement of nitrogen from soils with low carbon to nitrogen ratios into plants with high carbon to nitrogen ratios.
Education at The Ecosystems Center

Although Marine Biological Laboratory and its various programs do not grant degrees, The Ecosystems Center is actively involved in education in a variety of ways. In addition to serving as adjunct professors, guest lecturers and doctoral thesis committee members at a number of educational institutions, members of the staff conduct workshops and participate in courses given at MBL. Senior staff members supervise the work of half a dozen postdoctoral fellows, who spend an average of two years apiece doing research at the center. Several visiting scientists and students come to work on projects at the center each year, some for just a month or two and some for as much as two years.

Anne Giblin and John Hobbie hold adjunct professorships at Boston University. Gus Shaver is a senior research associate at the University of Alaska. Linda Deegan was recently promoted to associate adjunct professor at the University of Massachusetts at Amherst. Postdoctoral research associate Chris Neill holds an adjunct appointment with Bard College, where he taught a graduate-level course in ecosystem ecology last summer.

Several center staff members are collaborating with colleagues in Puerto Rico and Brazil to train students in these countries in the methods and principles of ecosystem ecology. These young scholars will view the Ecosystems Center and research sites in North America during the course of their training as well as working with center scientists on projects of their own at field sites in the tropics.

A. David McGuire, a postdoctoral researcher with the U.S. Forest Service, is a visiting scientist at The Ecosystems Center. He is participating in a joint Ecosystems Center/Forest Service project on the response of vegetation to changes in climate, environmental chemistry and land use. Working with center staff members Jerry Melillo and David Kicklighter, he is using the Terrestrial Ecosystem Model (TEM) developed at the center to study the potential effects of changes in temperature and atmospheric CO2 on the productivity of forests in North America. Dave completed his doctorate in biology at the University of Alaska at Fairbanks in 1989.

Swedish researcher Bosse Norman came to The Ecosystems Center as a visiting scientist in September 1991. During his year here, he has been working with Brian Fry and Meredith Hullar on the development of techniques with 13C, a stable isotope, for measuring bacterial consumption of dissolved organic carbon (DOC). The aim of their effort is to develop a direct method for sampling the 13C in bacteria that will help scientists trace and quantify the sources of DOC consumed by bacteria. Bosse received his doctorate in physiological chemistry in 1987 from the University of Umeå, where he has a research staff position in the department of microbiology.

University of Umeå graduate student Ulla Li Zweifel joined Bosse for several weeks during the fall. The aim of her visit was to compare the methods and instruments used for analysing DOC at her home university with those used at the center.

Boston University Marine Program graduate student Gary Banta, a research assistant at The Ecosystems Center since 1984, was awarded a NATO post-doctoral fellowship for a year in Denmark at Odense University beginning July 1991. He will receive his doctorate from Boston University in May 1992. Gary worked on decomposition processes in marine systems with center scientists Anne Giblin and John Hobbie, who served on his thesis committee. His thesis research was on the effect of benthic macrofauna, temperature, oxygen and organic matter inputs on decomposition and nitrogen cycling in coastal sediments.

Research associate George Kling moved to Ann Arbor in September to join the department of biology at the University of Michigan as an assistant professor. He came to The Ecosystems Center as a postdoctoral fellow in 1987 after receiving his doctorate in zoology at Duke University, where he conducted his thesis research on the crater lakes of Cameroon, West Africa. He revisited the African crater lakes in January 1991 to make measurements of CO2 buildup and to meet with Cameroonians about plans to set up a monitoring and remediation plan designed to prevent further CO2 eruptions.

Postdoctoral research associate Sam Wainright has received an appointment as an assistant professor in the Marine and Coastal Sciences Department at Rutgers University. Since his departure from the center in June, he has been working as a research fellow in the Boston University Marine Program at MBL.

Texaco fellows from Puerto Rico and their advisors on a visit to forest research sites in New England. They are, from the left, Gerardo Millan Ramos, Dr. Clyde E. Ashbury, Luis Mina Babilonia, Francisco Calderon, Luis Ramon Ordonez, Samantha Arzon-Cintron and Dr. Gary A. Toranzos.
During his last year at the center he worked with Bruce Peterson and Brian Fry on a study of bacterial utilization of dissolved organic carbon in the Parker River estuary. Sam earned his doctorate in zoology at the University of Georgia, where he worked on the microbial food web off the coast of Georgia.

Mark Castro joined The Ecosystems Center staff as a postdoctoral research associate in July 1990 after completing his doctorate in environmental sciences at the University of Virginia. His thesis was on the factors controlling the flux of sulfur gas between temperate forest soils and the atmosphere. He is currently working with Jerry Melillo and Paul Steudler. Mark is involved in studies of the effects of atmospheric deposition and a simulated hurricane on nutrient cycling and trace gas fluxes at the Long-Term Ecological Research (LTER) site at Harvard Forest. He is also participating in field projects at the LTER site in Puerto Rico, where he is looking at the effects of hurricanes and land-use changes on soil nitrogen cycling and the exchange of trace gases between the atmosphere and the soils.

Robert McKane was appointed a postdoctoral research associate at the center in July 1990. He received his doctorate in soil sciences from the University of Minnesota, where he studied nitrogen and carbon cycling in old-field succession. He is currently working with Ed Rastetter and other center researchers on the General Ecosystem Model (GEM) project. Ed and Bob are simulating the effects of nitrate deposition and temperature change on the storage of carbon in the vegetation and soils of northern temperate ecosystems.

After completing his doctorate at Duke University, where he studied nitrogen loss from desert ecosystems in southwestern United States, William Peterjohn joined The Ecosystems Center staff as a postdoctoral research associate in October 1990. He is working with Jerry Melillo, Paul Steudler, Kathy Newkirk and center consultant Frank Bowles on a soil-warming experiment in Harvard Forest. The project focuses on the effect of increased temperatures on the availability of nutrients and trace-gas emissions from soils.

Christopher Neill was appointed a postdoctoral research associate in November 1991 after he completed work for his doctorate in forestry and wildlife management at the University of Massachusetts at Amherst. His thesis research was on the effects of flooding on plant growth and nitrogen cycling in prairie marshes in Manitoba. Working with Jerry Melillo and Paul Steudler on a new field project in the Brazilian state of Rondonia, he is studying the effects of land-use changes on soil fertility and trace-gas emissions from plots that were converted from forest to pasture and later abandoned at varying times in the past.

With support from Texaco Foundation, scientists at The Ecosystems Center are working with colleagues in Puerto Rico and Brazil to introduce the methods and concepts of ecosystem ecology to researchers and students in these countries. Accompanied by Prof. Gary Toranzos and Dr. Clyde Asbury of the University of Puerto Rico, Texaco fellows Gerardo Millan Ramos, Luz Mina Babilonia, Luiz Ordenez, Francisco Calderon and Samantha Arzon-Cintron visited the center and research sites at Harvard Forest and Hubbard Brook Experimental Forest in October 1990.

Ecosystems Center staff members made six trips to Puerto Rico during 1991 to work with the Texaco fellows in the field and laboratory and to consult with local researchers about the program. The Texaco fellows in Puerto Rico have focused on biogeochemical processes in the wet forest areas of the island. With support from the Texaco Fellows Program, Francisco Calderon participated in the 1991 MBL, summer course on molecular probes and is going on to graduate school in microbial ecology at Michigan State University.

The program is expected to continue with the appointment of several new Texaco fellows in 1992 in both Puerto Rico and Brazil. Prof. Carlos Cerri, director of the Centro de Energia Nuclear na Agricultura of the University of Sao Paulo at Paracicaba, visited The Ecosystems Center during 1991 to work with the staff and plan future Texaco Fellowship Programs in Brazil.

As part of the Exxon Environmental Education Program, Ecosystems Center staff members have worked with young U.S. Forest Service scientists to understand carbon and nitrogen cycling in the dry tropical forests of southwestern Puerto Rico. During 1991, University of Puerto Rico graduate student Sandra Molina studied the effects of forest clearing for agriculture on these key element cycles. Her research will be widely useful, since dry tropical forests are under heavy development pressure throughout the world. This work will form a part of her thesis research.

The Ecosystems Center has also played host for the past three years to a group of teachers enrolled in Southern Connecticut State University's Institute for Science Instruction and Study (ISIS) program. They are participating in a certificate program designed by the university's science faculty to help high school science teachers keep up with developments in their fields.

The ISIS Fellows arrived at the Marine Biological Laboratory March 15 and 16 for a weekend of lectures by Woods Hole scientists and a tour of The Ecosystems Center. Several center staff members participated in the program. John Hbbie spoke on the uses of stable isotopes in ecological research; Knute Nadelhoffer discussed the biology of forest decline, and Anne Giblin conducted the tour of the labs. Ed Rastetter spoke on modeling the terrestrial portion of the global carbon cycle, and Chris Neill introduced the visitors to the ecology of North American prairie marshes.

Kathy Regan

Many Ecosystems Center staff members have shared their expertise with Falmouth's public and private schools in a variety of ways. Kris Tholke, Hap Garritt, John Helfrich, Sue Sape, Brian Fry, Knute Nadelhoffer and Anne Giblin served as judges this year for science fairs at Falmouth Academy and Falmouth High School.

Others have participated in activities sponsored by the Woods Hole Science and Technology Education Partnership, a consortium of area schools, research institutions and businesses. Jerry Melillo contributed to a workshop for science teachers, and Marty Downs, Jane Tucker, Heidi Geyer and Kathy Regan participated in Women in Science seminars at one of the Falmouth public schools. Center consultant Beth Schwarzman is on the executive committee of the partnership.
Events and Activities of 1991

Highlights of the activities of Ecosystems Center staff members during the year

Workshops

Soil Warming Workshop
The Ecosystems Center played host in September to a two-day workshop on ecosystem responses to soil warming and the development of a soil warming experiment for Long-Term Ecological Research (LTER) sites. Organizer of the conference was William Schlesinger of Duke University. Paul Steudler, William Peterjohn, Gus Shaver and Jerry Melillo were among the 40 participants who gathered to discuss previous research experiences, the effects of elevated soil temperatures on ecosystem processes and methods for conducting a large-scale soil warming experiment.

Watershed Manipulation Project Workshop
Some 45 researchers from six countries gathered at MBL during November for a workshop on the effects of nitrogen and sulfur deposition on forest nitrogen cycles and biological processes. Ecosystems Center scientist Knute Nadelhoffer organized the three-day session, one of a series of workshops on research of the EPA-supported Watershed Manipulation Project. Also participating from the center were Marty Downs, Todd Drummey, Brian Fry, David Jones, Bob McKane, Ed Rastetter and Paul Steudler.

Bernie Moller

Ecological Modeling Workshop
Ed Rastetter led a second ecological modeling workshop for students interested in the use of mathematical modeling in ecosystems analysis during August. The two-day session, held at Colorado State University in Fort Collins, was designed as a follow-up to the initial workshop held in Woods Hole in November 1990. Support for this three-year project comes from The Clowes Fund. The students who had attended the first workshop presented the projects they had been working on in the interim. Among them were Bob McKane and Dave McGuire, who presented talks on various modeling projects at The Ecosystems Center. Other participants from the center were John Hobbie and Gus Shaver.

LTER Workshops
Researchers participating in the Harvard Forest Long-Term Ecological Research (LTER) program got together in February to report on their current and future research activities at the Harvard Forest Annual Ecology Symposium. Paul Steudler, Bill Peterjohn, Jerry Melillo and Knute Nadelhoffer attended and presented papers on effects of nitrogen additions on red pines and mixed hardwoods, long-term impact of organic matter inputs on soil and ecosystem developments, and soil warming and trace gas fluxes.

The Arctic LTER research group held its annual workshop in Woods Hole in March. Participants from the center included Gus Shaver, John Hobbie, Brian Fry, Bruce Peterson, Linda Deegan, Knute Nadelhoffer, Anne Giblin and Ed Rastetter. Bernie Moller participated in the Arctic LTER data managers' meeting in Albuquerque in August.

Jim Laundre, Todd Drummey

Workshop on Measurement of DOC and DON in Natural Waters
Brian Fry, Chuck Hopkinson and visiting scientist Bossie Norman took part in a week-long workshop in July on the measurement of dissolved organic carbon (DOC) and nitrogen (DON) in natural waters. The workshop, which brought scientists and instrument company representatives together to review issues and make recommendations for improving analytical protocols and research, took place at the University of Washington in Seattle. Chuck served as chairman of the DON group at the workshop.

Other Conferences and Workshops
During October, Anne Giblin and John Hobbie participated in an Institute of Ecosystem Studies workshop in Millbrook, New York, convened to discuss new areas of research in the lakes of the Antarctic dry valleys. During May, John also participated in the Fourth Cany Conference at the Institute of Ecosystem Studies. The topic of the meeting was human environmental change.

Ed Rastetter gave a talk on carbon storage in response to changes in carbon dioxide, temperature and nitrogen deposition at a workshop on carbon cycling in boreal forests, held in September at Corvallis, Oregon.

During February, Gus Shaver participated in a planning workshop for the development of a U.S. consortium for wetlands and climate change research that was held at the Pacific Northwest Laboratories in Richmond, Washington.

In March, Linda Deegan was invited to speak on her experience with using an index of biotic integrity as a means of measuring the health of estuaries. Her presentation was part of a workshop on estuaries in Columbia, Maryland, that was sponsored by the Environmental Protection Agency's
Environmental Monitoring and Assessment Program (EMAP). She also gave a talk in December at the winter flounder workshop in Milford, Connecticut, sponsored by the National Marine Fisheries Service. Knute Nadelhoffer participated in a Nitrogen Saturation Experiment (NITREX) workshop on plot and catchment-scale 15N experiments held in Amsterdam, The Netherlands, in January.

Meetings and Lectures

Brian Fry was invited to be a keynote speaker at a meeting on the microbial ecology of pelagic environments in Helsingor, Denmark, Aug. 18-23. The title of his address was “The Nutrition of Bacteria in Estuaries: Stable Isotopes as Tracers of DOC Production and Consumption.”

Knute Nadelhoffer and Jerry Melillo participated in Gordon Research Conferences during July. Jerry spoke at the Applied Environmental Microbiology conference, and Knute attended a conference titled “Hydrological, Geochemical and Biological Interactions in Forested Catchments,” where he served as co-chairman and discussion leader for a session on the interaction of biological processes and geochemical and hydrological responses in forested catchments.

Bruce Peterson presented a talk on the long-term fertilization of an arctic river at the annual meeting of the North American Bentholological Society in Albuquerque during May. He also attended the Northeast Shelf Ecosystem Symposium at the University of Rhode Island in August.

Several researchers from The Ecosystems Center presented papers at the annual meeting of the American Society of Limnology and Oceanography (ASLO) in Halifax in June. Anne Giblin discussed the importance of labile carbon in sulfur storage by lake sediments. Chuck Hopkinson spoke on storm and wave-mediated nitrogen and phosphorus fractionation and release from shallow shelf sediments. Sam Wainright gave a paper on long-term changes in the trophic level of haddock on Georges Bank using stable isotope analysis. Jane Tucker and Gary Banta also attended the meeting.

George Kling was invited to present a paper on stable isotopes and ecosystem-level experiments at the American Chemical Society meeting in Atlanta during April.

Linda Deegan and Chris Neill gave talks at the New England Estuarine Research Society meeting in Yarmouth, Nova Scotia, in May. Anne Giblin and Jane Tucker also attended.

The Ecosystems Center was well represented at the annual Ecological Society of America meeting in San Antonio, Texas, in August. Ed Rastetter and Bob McKane presented a paper on reconstructing historical patterns of carbon sequestration with a general model of ecosystem carbon and nitrogen dynamics. Gus Shaver spoke on global change and the carbon balance of arctic ecosystems. Bill Peterjohn discussed the Harvard Forest soil-warming project. Dave Kicklighter and Dave McGuire presented a paper on estimates of potential net primary productivity of ecosystems in North America, comparisons between two global models. Mark Castro gave a talk on the effects of disturbances on the exchange of trace gases between tropical soils and the atmosphere. Marty Downs presented a poster on the effects of acid additions on litter decomposition on a mixed hardwood-red spruce forest.

Paul Steudler gave a talk on methane oxidation in aerobic forest soils at an Environmental Protection Agency meeting in Athens, Georgia, in April. That same month, John Hobbie attended an EPA workshop on ecological risk assessment in Washington, D.C.

Linda Deegan was invited to speak at a session on sea grass health at the American Fisheries Society (AFS) annual meeting in San Antonio in September. She also served as a discusant for a session on the index of biotic integrity.

Chuck Hopkinson was co-author of a paper on patterns of nitrogen fixation in decaying marsh grass that was presented at the Marine and Estuarine Gradients session of the Estuarine and Coastal Science Association Symposium, held during September in Ghent, Belgium.
Shortly after the ERF meeting, John Hobbie entertained a convivial audience with his after-dinner lecture on scaling in ecosystem research at the scientific meetings of NSF’s Land-Margin Ecosystem Research program at Tomales Bay, California.

Knute Nadelhoffer gave a seminar at the department of plant ecology of the University of Bayreuth in Germany during January on plot and catchment level 15N-tracer experiments in forest ecosystems. In November he talked at the University of Toronto on the use of 15N tracers in ecosystem studies.

John Hobbie traveled to Denmark during May to participate in a review of the Danish Nitrogen, Phosphorus and Organic Matter Research Programme and to give a paper on synthesis and scale.

Paul Steudler spoke in March at Harvard University on the effects of natural and anthropogenic disturbances on soil nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. During October, he attended a NATO Advanced Research workshop on the atmospheric methane cycle, at which he presented a poster on the factors controlling methane fluxes in tropical ecosystems.

Anne Giblin gave lectures in Barcelona, Spain, during February, at San Diego State University during November, and at MBL for the Boston University Marine Program.

Bob McKane presented a seminar at the University of Minnesota in January on regulation of carbon and nitrogen cycling during old-field succession and one at The Ecosystems Center in February titled “Why are there so Many Species of Plants?”

Bruce Peterson delivered lectures at North Carolina State University and at the University of North Carolina in November, the former on the origin and fate of DOC in estuaries and the latter on biological responses to phosphorus fertilization in an arctic river.

Linda Deegan was invited to spend two days lecturing at the University of Virginia’s Environmental Sciences Department. Dave McGuire gave two talks at the Rocky Mountain Forest and Range Experimental Station on interactions between the carbon and nitrogen cycle and estimating net primary productivity for North America.

Committee Memberships

Investigators at The Ecosystems Center serve on a wide variety of national and international boards, committees and panels. John Hobbie is a member of the Polar Research Board of the National Research Council (NRC) and of the NAS/NRC panel responsible for reviewing the Environmental Protection Agency’s Environmental Monitoring and Assessment Program (EMAP). He serves on the boards of directors of the Association of Ecosystem Research Centers (AERC), the Arctic Research Consortium (ARCLUS) and The Lloyd Foundation for Environmental Studies in South Dartmouth, Massachusetts. John also serves as an assessor in the appointments board for the chair in microbial limnology at Uppsala University in Sweden.

Jerry Melillo is a member of the Scientific Committee of the International Geosphere-Biosphere Programme (IGBP) and an active participant in the planning for two IGBP core programs, Global Change in Terrestrial Ecosystems (GCTE) and International Global Atmospheric Chemistry (IGAC). He is chairman of the U.S. Committee of the Scientific Committee on Problems of the Environment (SCOPE) and a member of both the U.S. Global Change Committee of the National Academy of Sciences (NAS) and its ad-hoc committee to develop a terrestrial ecosystems action plan. Jerry also serves on committees of the Office for Interdisciplinary Earth Studies (OIES) of the University Corporation for Atmospheric Chemistry. He was invited to speak at the OIES 1991 Global Change Institute in April.

Both Gus Shaver and John Hobbie are members of the steering committee for the Land-Atmosphere-Ice Interactions section of NSF’s Arctic Systems Science Program (ARCSS).

Jerry Melillo serves on the global change advisory committee of the Electric Power Research Institute (EPRI), and Gus Shaver is a member of the review panel for EPRI’s CO2 program. Gus is also chairman of the membership committee of the Ecological Society of America.

Ed Rastetter participated during June in a panel on EPA Exploratory Research in Washington, D.C. Jerry Melillo was a speaker at EPA’s Trace Gas Fluxes Research Team meeting in August.

Anne Giblin participated in an NSF panel on facilities and equipment for research at biological field stations and marine laboratories in July. Bruce Peterson has just completed a term as a panel member for the NSF Ecosystems Program.
Chuck Hopkinson is a member of the steering committee for an NSF-sponsored working group on resolving the dissolved organic matter (DOM) problem. The group met at the University of Delaware in September and at Woods Hole Oceanographic Institution in December. Chuck was also invited to serve on South Carolina Sea Grant Consortium’s Marine Environmental Research Advisory Panel, which met in Charleston, South Carolina, in December.

Knute Nadelhoffer serves as a panel reviewer for the Department of Agriculture’s Forest, Rangeland and Crop Ecosystem Program.

George Kling serves on the steering committee of the International Volcanology Commission on Crater Lakes, which is working on organizing a joint project with the International Hydrological Sciences Commission on the biogeochemistry of crater lakes.

Ed Rastetter serves on the nominating committee of the Woods Hole chapter of Sigma Xi.

Anne Giblin is a member of the advisory committee for the Waquoit Bay National Estuarine Research Reserve and chairman of its research subcommittee. She and Bruce Peterson both serve as volunteers in the acid rain monitoring program of the Massachusetts Water Resources Authority.

Gus Shaver serves as a consultant on development of an Arctic North Slope Ecoforestation Research Strategy (ANSWERS) for the Environmental Protection Agency.

Linda Deegan serves as a consultant on evaluating the health of estuaries for VERSAR, Inc. of Columbia, Maryland, a consulting group that is developing protocols for EPA’s Environmental Monitoring and Assessment Program.

Appointments and Promotions

Brian Fry was promoted to the position of associate scientist in October 1991. He received his undergraduate degree from Cornell University in 1972 and his master’s degree and doctorate from the University of Texas at Austin in 1977 and 1981 respectively. Brian joined the staff of The Ecosystems Center as an assistant scientist in November 1985.

Knute Nadelhoffer was promoted from assistant to associate scientist in August 1991. He received both his undergraduate degree in biology and his doctorate in forestry from the University of Wisconsin at Madison. Knute came to The Ecosystems Center as a postdoctoral fellow in 1983, the year he received his Ph.D. He was appointed an assistant scientist in June 1985.

Most unusual research experience of the year

Meredith Hallor was invited to join researchers from Woods Hole Oceanographic Institution on a cruise to the East Pacific Rise during November and December to study the food web dynamics of organisms associated with the hydrothermal vents of the region. During that cruise, she had a chance to participate in a dive in ALVIN, the research submersible operated by WHOI. Meredith’s role on the cruise was to study the chemosynthetic bacteria that form the basis of the food web, using a method for measuring the stable isotope composition of the bacteria.
Staff of The Ecosystems Center

ADMINISTRATIVE STAFF
John E. Hobbie, Co-Director
Ph.D. Indiana University
Jerry M. Melillo, Co-Director
Ph.D. Yale University
John V. K. Helfrich III
Research Administrator
B.S. St. Mary's College of Maryland
Suzanne J. Donovan
Administrative Assistant
Elisabeth A. Griffin
Administrative Assistant
Martha Jesse
Receptionist

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Jerry M. Melillo, Senior Scientist
Ph.D. Yale University
Bruce J. Peterson, Senior Scientist
Ph.D. Cornell University
Gaius R. Shaver, Senior Scientist
Ph.D. Duke University
Brian D. Fry, Associate Scientist
Ph.D. University of Texas
Anne E. Giblin, Associate Scientist
Ph.D. Boston University Marine Program
Charles S. Hopkinson, Jr., Associate Scientist
Ph.D. Louisiana State University
Knute J. Nadelhoffer, Associate Scientist
Ph.D. University of Wisconsin
Linda A. Deegan, Assistant Scientist
Ph.D. Louisiana State University
Edward B. Rastetter, Assistant Scientist
Ph.D. University of Virginia
Paul A. Steudler, Research Specialist
M.S. University of Oklahoma
George W. Kling, Research Associate
Ph.D. Duke University

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Margaret C. Bowles
B.A. Bryn Mawr College
Marilyn J. Jordan
Ph.D. Rutgers University
Daniel Martin, GIS Consultant
B.S. University of Massachusetts - Amherst
Elisabeth Schwarzman
M.S. Stanford University

VISITING SCIENTISTS
A. David McGuire
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Bosse Normman
Dr. MSc. University of Umeå, Sweden

EDUCATIONAL STAFF APPOINTMENTS
Mark Castro, Postdoctoral Research Associate
Ph.D. University of Virginia
Robert McKane, Postdoctoral Research Associate
Ph.D. University of Minnesota
Christopher Neill, Postdoctoral Research Associate
Ph.D. University of Massachusetts - Amherst
William Peterjohn, Postdoctoral Research Associate
Ph.D. Duke University
Sam Wainright, Postdoctoral Research Associate
Ph.D. University of Georgia
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Gary Banta, Research Assistant
Ph.D. Boston University Marine Program
Carolyn Bauman, Research Assistant
M.S. University of Montana
Jonathan Chapman, Research Assistant
M.S. University of Wisconsin - Madison
Mark Dornblaser, Research Assistant
M.S. SUNY - Stony Brook
Martha Downs, Research Assistant
B.S. Cornell University
Todd Drummey, Research Assistant
B.S. Roger Williams College
Stephen Fafinski, Research Assistant
B.A. University of California - Santa Cruz
Robert Garritt, Senior Research Assistant
M.S. Cornell University
Heidi Geyer, Research Assistant
B.S. University of Connecticut - Storrs
Meredith Hullar, Research Assistant
M.S. University of Cincinnati
David Jones, Research Assistant
B.S. Utica College
David Kicklighter, Research Assistant
M.S. University of Montana
Karen Kracko, Research Assistant
M.S. North Carolina State University
James Laundre, Senior Research Assistant
M.S. University of Connecticut
Catherine Michmerhuizen, Research Assistant
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Michelle Miliefsky, Research Assistant
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Bernard Moller, Senior Research Assistant
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Kathleen Newkirk, Research Assistant
M.S. Virginia Polytechnic Institute
Daniel Padien, Research Assistant
M.A. Boston University
Julie Pallant, Research Assistant
B.A. Oberlin College
Nancy Parmentier, Research Assistant
B.A. University of Massachusetts - Amherst
Kathleen Regan, Research Assistant
Cleveland State University
Andrea Ricca, Research Assistant
B.A. University of Hartford
Susan Saupe, Research Assistant
M.S. University of Alaska
Carol Schwamb, Laboratory Assistant
Kristin Tholke, Research Assistant
M.S. University of Connecticut
Jane Tucker, Research Assistant
M.S. University of North Carolina
Seminars at The Ecosystems Center during 1991

January
15 Daniel Padien, The Ecosystems Center, “Stand structure and nutrient dynamics of a pinyon-juniper woodland of northern New Mexico”.
22 Inez Fung, NASA, Goddard Institute for Space Studies, New York, “3-D model synthesis of the global methane cycle”.
29 Dan Yakir, Weizmann Institute, Tel Aviv, Israel and Botany Department, Duke University, Durham, NC, “From plant cells to the biosphere using stable isotopes”.
30 Helmut Schütz, Fraunhofer Institut for Atmospheric Research, Garmisch, Germany, “The role of rice paddies in the atmospheric methane cycle”.

February
12 Ann Buckland, Marine Biological Laboratory, “Genetic markers of plankton transport”.
19 Bob McKane, The Ecosystems Center, “Why are there so many plant species? Opposing theories and an experimental test”.
26 Fred Short, Jackson Estuarine Laboratory, Durham, New Hampshire, “What is happening to the seagrass? Pollution and disease related aspects of its decline”.

March
12 Mark Hines, Institute for the Study of Earth, Oceans and Space, University of New Hampshire, “Gaseous S exchange in Sphagnum dominated wetlands”.
26 Dale Johnson, Desert Research Institute, University of Nevada, Reno, “Nitrogen retention in forest soils - a comparison of atmospheric and fertilizer inputs”.

April
2 Scott Nixon, Graduate School of Oceanography, University of Rhode Island, “Some observations on nutrient input and the productivity of coastal marine ecosystems”.
9 Ted Loder, Department of Earth Sciences, University of New Hampshire, “Massachusetts Bay nutrient distribution -An update”.
16 Lindsey Rustad, University of Maine, “Five-year litter decay in a red spruce (Picea rubens) forest”.
30 Oliver Zafiriou, Wood Hole Oceanographic Institution, “Oceanic nitrification revisited”.

May
7 Bruno Marino, Department of Earth and Planetary Sciences, Harvard University, “C, H and O stable isotope ratios of plant cellulose as indicators of past states of the biosphere”.

June
4 Jonathan Sharp, College of Marine Studies, University of Delaware, Lewes, Delaware, “Some thoughts on the DOM controversy”.
5 Jonathan Sharp, College of Marine Studies, University of Delaware, Lewes, Delaware, “Nitrogen and phosphorous biogeochemistry of the Delaware Estuary”.

September
17 Bosse Norrman, University of Umeå, Sweden, “The Gulf of Bothnia, Northern Baltic Sea: An introDOCtion”.
24 Eric Davidson, Woods Hole Research Center, “Gross vs net rates of N mineralization and nitrification in terrestrial ecosystems”.

October
1 Chris Neill, The Ecosystems Center, “Relationships between seasonal flooding and emergent plant production in prairie whitetop (Scolochloa lestuacea) marshes”.
8 Jonathan Garber, U.S. Environmental Protection Agency, Narragansett, RI, “Development of an empirical model of estuarine eutrophication”.
15 Jack Finn, Department of Forestry and Wildlife Management, University of Massachusetts - Amherst, “Ecological modelling: 10% mathematics and 90% knowledge”.
22 Gareth Riley, School of Chemistry, University of Bristol, England, “Sources of sedimentary lipids deduced from stable carbon-isotope analyses of individual compounds”.

November
5 Steve Carpenter, Center for Limnology, University of Wisconsin, “Management experiments in a multi-use ecosystem: Lake Mendota”.
12 Gerhard Gebauer, Universitat Bayreuth, Germany, “Natural nitrogen isotope ratios in different compartments of Norway spruce from healthy and declining stands”.

December
10 Gretchen Smith, Department of Forestry and Wildlife Management, University of Massachusetts - Amherst, “Forest health monitoring in New England”.
17 Ed Rastetter, The Ecosystems Center, “Landscape modeling of barrier island ecosystems”.

Michele Bahr, Meredith Hullar


In press


Broman, D., C. Näf, C. Rolf, Y. Zebůr, B. Fry and J. Hobbie. Bioaccumulation and flux estimates of Polychlorinated Dibenzo-p-dioxins (PCDDs) and Dibenzofurans (PCDFs) for two food chains from the Northern Baltic utilizing stable isotopes of nitrogen. Environmental Toxicology and Chemistry.


Research Grants in Effect 1991

I. National Science Foundation

NSF-BSR-8702328
"An LTER program for the Alaskan Arctic"
September 1987 - August 1992
Investigators: Hobbie, Deegan, Fry, Giblin, Nadelhofer, Peterson, Rastetter, Shaver
$2,250,000

NSF-BSR-8718426
"A comparative study of the response of terrestrial ecosystems to changes in the global environment"
March 1988 - August 1992
Investigators: Rastetter, Hobbie, Melillo, Nadelhofer, Shaver
$1,364,395

NSF-BSR-8706203
"Chronic nitrogen additions to forest ecosystems: Effects on nitrogen cycling, canopy chemistry and nitrous oxide emissions" (subcontract from the University of New Hampshire)
July 1987 - June 1991
Investigators: Melillo, Steudler
$777,778

NSF-BSR-8806255
"Microbial mediation of organic carbon transformations in an emergent macrophyte-dominated habitat of the Okefenokee Swamp ecosystem" (subcontract from the University of Georgia)
July 1989 - January 1992
Investigator: Hopkinson
$25,489

NSF-BSR-8806691
"Labile dissolved organic matter in riverine saltmarsh estuaries: Origins and biological utilization"
September 1988 - June 1992
Investigators: Peterson, Fry
$916,831

NSF-BSR-8811764
"Harvard Forest: Long-Term Ecological Research" (subcontract from Harvard University)
October 1988 - March 1994
Investigators: Melillo, Nadelhofer, Steudler
$496,583

NSF-BSR-8905835
"A workshop on ideas for a center for the study of comparative ecology and scale"
March 1989 - February 1991
Investigator: Hobbie
$52,200

NSF-BSR-8918273
"The controls of sulfur storage in lake sediments by interactions among the carbon, iron, oxygen and sulfur cycles"
May 1990 - May 1993
Investigators: Giblin, Fry, Peterson
$900,000

NSF-BSR-9009190
"Biological controls on nitrate retention in northeastern forest ecosystems"
July 1990 - June 1993
Investigator: Nadelhofer
$316,601

NSF-BSR-9016141
"Development of automated instrumentation for the measurement of dissolved organic nitrogen in seawater, freshwater and soil solutions"
May 1991 - April 1992
Investigators: Peterson, Deegan, Hobbie, Hopkinson
$118,046

NSF-BSR-9019055
"Global change and the carbon balance of arctic ecosystems: The importance of carbon/nutrient interactions"
November 1991 - October 1994
Investigators: Shaver, Giblin, Nadelhofer, Rastetter
$1,212,108

NSF-BSR-9108565
"Chronic nitrogen additions to forest ecosystems: Effects on nitrogen cycling, canopy chemistry and trace gas fluxes"
September 1991 - August 1993
Investigators: Melillo, Steudler
$240,000

NSF-BSR-9108329
"Long-term intersite experiments of leaf and fine root decomposition" (subcontract from Oregon State University)
June 1991 - May 1996
Investigator: Rastetter
$53,492

NSF-OCE-8800101
"Present and past food web structure on Georges Bank: Resolution by combined C and N stable isotope analysis"
March 1988 - February 1991
Investigator: Fry
$149,998

NSF-DPP-8722015
"Changes in arctic freshwaters"
March 1988 - February 1991
Investigators: Hobbie, Deegan, Peterson
$1,430,225

NSF-DPP-9024188
"Freshwater systems"
March 1991 - February 1994
Investigators: Deegan, Hobbie, Peterson, Rastetter
$2,631,117

NSF-DIR-9115383
"Equipment and facilities for research"
September 1991 - September 1993
Investigators: Hopkinson, Fry
$141,000

II. Department of Energy

DE-FC03-90ERG1010
"National Institute for Global Environmental Change: A regional center at Harvard University" (subcontract from Harvard University)
September 1990 - June 1992
Investigators: Melillo, Nadelhofer, Steudler
$277,020

DOE-R4D
"Effects of perturbations on the tundra drainage systems" (subcontract from San Diego State University)
September 1991 - October 1992
Investigator: Shaver
$33,654

III. National Aeronautics and Space Administration

NASA NAGW-2669
"Changes in biogeochemical cycles" (subcontract from the University of New Hampshire)
January 1991 - December 2000
Investigators: Melillo, Peterson, Rastetter, Steudler
$3,399,743

NASA NAGW-1825
"Interdisciplinary program" (subcontract from the University of New Hampshire)
June 1989 - December 1992
Investigators: Melillo, Steudler
$249,566
NASA NAGW-2747
"The role of tropical deforestation in the global carbon cycle: Spatial and temporal dynamics"
September 1991 - August 1993
Investigators: Melillo, Steudler
$120,000

IV. National Oceanic and Atmospheric Administration
Estuarine Programs Office
"Effects of macroalgae on fish production in Waquoit Bay"
April 1990 - April 1991
Investigator: Deegan
$39,999

V. United States Environmental Protection Agency
CR-816363-01-0
"Watershed Manipulation Project: Nitrate mobility and nitrogen cycling" (subcontract from the University of New Hampshire)
March 1990 - February 1993
Investigator: Nadelhoffer
$300,000

CR-817734-01-0
"Factors controlling the fluxes of radiatively important trace gases from temperate forests"
July 1990 - June 1993
Investigators: Melillo, Nadelhoffer, Steudler
$607,713

CR-817688-01-0
"Factors controlling radiatively important trace gases in tundra and taiga ecosystems" (subcontract from the University of Alaska)
July 1990 - June 1993
Investigator: Nadelhoffer
$123,512

SCENV-1000-0180075
"Nitrogen cycling in Buzzards Bay sediments: Effects of eutrophication" (funded through Massachusetts Executive Office of Environmental Affairs)
January 1990 - January 1991
Investigators: Giblin, Hobbie
$16,788

VI. Miscellaneous
Massachusetts Department of Environmental Quality Engineering, Division of Water Pollution Control
"Application of the index of biotic integrity to Massachusetts estuaries"
February 1988 - September 1991
Investigator: Deegan
$116,732

The Clowes Fund
"Ecological modelling workshops"
June 1989 - June 1992
Investigators: Staff
$105,000

Texaco Foundation
"Texaco fellowships in environmental research"
June 1990 - June 1991
Investigators: Melillo, Steudler
$60,000

Exxon Corporation
"Education and research for Latin American and Caribbean scientists"
August 1989 - November 1991
Investigators: Melillo, Steudler
$25,000

Andrew W. Mellon Foundation
A program of ecological research: "A pilot study of scaling" "Land-coastal ocean linkages" "Ecological research in eastern Europe" "The global significance of tropical deforestation"
June 1990 - June 1993
Investigators: Staff
$400,000

USDA Forest Service 19-91-082
"Tropical forest nutrient dynamics and trace gas fluxes"
September 1991 - September 1992
Investigators: Melillo, Steudler
$50,000

K. G. Lloyd
"Measurement of primary productivity in Buzzards Bay"
May 1991 - April 1992
investigators: Hobbie, Giblin
$12,500
Sources of Support for Research and Education

The annual operating budget of The Ecosystems Center for 1991 increased by $165,000 over the budget of the previous year. The budget for the current year is $4,115,500. Most of the center’s income, some 85%, comes from grants for basic research from government agencies. The other 15%, roughly $617,000, comes from gifts and grants from private foundations, corporations and individuals; institutional support for administration, and income from the center’s reserve fund. These non-governmental funds provide flexibility for the development of new research projects, public policy activities and the center’s educational programs. More information about sources of support appears in the Introduction to The Ecosystems Center and in Research Grants in Effect in 1991.

The Ecosystems Center’s reserve fund, or endowment, stands at roughly $4,000,000, an increase of approximately 14% over the 1990 total of $3,500,000. Income from the reserve fund helps defray costs of operations, writing proposals, consulting for government agencies and the center’s seminar program.

The research and educational programs of The Ecosystems Center are supported by grants and gifts from private foundations, institutions and individuals as well as by grants from federal and state agencies for specific research projects. Over the years since it was founded in 1975, the center has received support from these foundations and corporations:

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