The Ecosystems Center
1992 Annual Report
These small greenhouses are used in experiments designed to measure trace gases such as carbon dioxide and methane emitted from tundra soils and vegetation under varying temperature conditions at the Toolik Lake field station in Alaska.

## Credits

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<thead>
<tr>
<th>Role</th>
<th>Name</th>
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<tbody>
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</tbody>
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**Cover Photography:**

- **Top Left:** A fence separates pastures of different ages that were created from cleared rain forest at Fazenda Nova Vida in Rondônia, a province in the western Brazilian Amazon. The trees in the photo are remnants of the original forest. Photo by Chris Neil.
- **Top Right:** Researchers seine for winter flounder in Waquoit Bay. The fish are used for studies of the effects of eutrophication on fish populations. Photo by Linda Deegan.
- **Bottom:** Debbie Repert, a research assistant for the arctic Long-Term Ecological Research (LTER) project at Toolik Lake, uses an electronic meter to measure the velocity of water flow in Oksrukuyik Creek, Slope Mountain, in the northern foothills of the Brooks Range in Alaska, is in the background. Photo by John Hobbie.
<table>
<thead>
<tr>
<th>Page</th>
<th>Title</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>Introduction to The Ecosystems Center</td>
</tr>
<tr>
<td>6</td>
<td>Integrating Ecology</td>
</tr>
<tr>
<td>8</td>
<td>Comparative Studies and Whole-Ecosystem Experiments Yield Insights Into the Effects of Development on Coastal Ecosystems</td>
</tr>
<tr>
<td>11</td>
<td>Sulfur Cycling in Lakes: Understanding the Role of Competing Processes in Neutralizing Acid Deposition</td>
</tr>
<tr>
<td>13</td>
<td>Microbes and the Fate of Organic Matter in Aquatic Ecosystems: Top-Down or Bottom-Up Control?</td>
</tr>
<tr>
<td>15</td>
<td>Modeling Element Interactions as Controls on Carbon Storage in Terrestrial Ecosystems</td>
</tr>
<tr>
<td>17</td>
<td>Forests to Pastures: Assessing the Environmental Consequences of Changing Land Use in the Amazon Basin</td>
</tr>
<tr>
<td>21</td>
<td>Predicting the Impact of Changes in Climate and Atmospheric Carbon Dioxide on Terrestrial Net Primary Production</td>
</tr>
<tr>
<td>24</td>
<td>Using Nitrogen Isotopes in Studies of Forest Ecosystems</td>
</tr>
<tr>
<td>26</td>
<td>Education at The Ecosystems Center</td>
</tr>
<tr>
<td>28</td>
<td>Events and Activities of 1992</td>
</tr>
<tr>
<td>32</td>
<td>Staff of The Ecosystems Center</td>
</tr>
<tr>
<td>34</td>
<td>Seminars at The Ecosystems Center During 1992</td>
</tr>
<tr>
<td>35</td>
<td>1992 Publications of The Ecosystems Center</td>
</tr>
<tr>
<td>38</td>
<td>Research Grants in Effect During 1992</td>
</tr>
<tr>
<td>40</td>
<td>Sources of Support for Research and Education</td>
</tr>
</tbody>
</table>
Introduction to The Ecosystems Center

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 problems of sustaining and managing the Earth’s resources. Founded in 1975, the center 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, corporations and individuals.

Investigators at The Ecosystems Center study the structure of ecological systems, or ecosystems, and their function, or the way they work. Ecosystems vary greatly in size. Some are defined by natural boundaries, some by the questions researchers ask. But each is a 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 lakes, streams, temperate and tropical forests, arctic tundra, coastal estuaries and ocean shelf waters.

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 living and non-living components. Ecosystem function is defined by the rates of processes, such as predation or photosynthesis, 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 factors, such as the presence and absence of organisms, the 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 environmental change on ecosystems at all levels, local, regional and global. A wide variety of questions guides their research. How will the world’s terrestrial ecosystems respond to elevated levels of carbon dioxide and associated changes in climate? How does atmospheric deposition of acidic compounds affect biological and chemical processes in the forest, lakes and streams of eastern North America? How will changes in climate and land use affect the flow of organic matter and nutrients into estuaries? Will an increase in the depth of the summer thaw in the soil of the arctic tundra make more nutrients available to plants? Will these nutrients flow into streams and lakes, affecting the food web in these bodies of water?

Although center scientists undertake studies in diverse geographic regions and on different scales, they ask similar questions in these different contexts. Their work is also unified by similarities in the processes they measure; 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 project and site to another is immense. By studying one process, such as the decomposition of soil organic matter, in a wide range of temperature and moisture conditions, one can predict its rate in an unstudied system with some degree of confidence. 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.

Among the tools that Ecosystems Center scientists use are models and geographic information systems (GIS). They are currently using a global model to see how changes in climate and concentrations of carbon dioxide in the atmosphere will affect the growth of vegetation. They are also using a GIS program to store and organize data on types and characteristics of vegetation for a grid made up of 56,000 parcels of equal area that cover the entire land surface of the Earth. Information from each of these GIS units is used in a model of plant growth that is run 56,000 times in the process of developing predictions about the response of different types of vegetation to a variety of potential climate scenarios.

It is difficult for one researcher to have all of the skills necessary to study whole ecosystems. Center scientists work with each other and with investigators from other institutions, bringing to their joint projects skills in terrestrial and aquatic ecology, microbiology, chemistry, remote sensing, botany, zoology, physiology, mathematics and computer modeling. 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 is invaluable.
Ecosystems Center researchers have participated for many years in the multi-institutional Long-Term Ecological Research (LTER) projects at Toolik Lake on the north slope of the Brooks Range in Alaska and at Harvard Forest in Petersham, Massachusetts. This year the center became part of the Land Margin Ecosystems Research (LMER) program with a four-year grant from the National Science Foundation to conduct an estuarine study in Plum Island Sound in northeastern Massachusetts. The new project will measure the amounts and types of organic matter and nutrients flowing into the sound from the uplands and will assess their effect on the aquatic ecosystem. In addition to its participation in the LMER field program, The Ecosystems Center is host to the recently established LMER coordinating office.

The center’s facilities in Woods Hole include analytical laboratories and chambers for small-scale experiments. Projects share aquatic and terrestrial laboratories 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 atmospheric controls.

Environmental Protection Agency (EPA), the National Oceanic and Atmospheric Administration (NOAA), the National Aeronautics and Space Administration (NASA) and the Department of Agriculture’s Forest Service. The center has also received funds for research from the Massachusetts Water Resource Authority (MWRA), Exxon Corporation and Texaco Foundation. The Andrew W. Mellon Foundation has provided seed money for new scientific directions, and The Clowes Fund has provided endowed support to help the center provide initial research support for young investigators.

The Ecosystems Center is conducting several innovative educational programs. Texaco Foundation has provided funds for training Puerto Rican students in the methods and concepts of ecology. The foundation is also providing support for three Brazilian graduate students who are working with Ecosystems Center staff members on a study of the effects of converting forested lands into pasture in the Amazon. Exxon Corporation is supporting young scholars who work with center staff members on research projects at field sites in Latin America. A grant from The Clowes Fund has supported a series of workshops for graduate students on the concepts and uses of mathematical modeling in ecology. The center also participates in the MBL’s Science Writing Fellowships Program, making opportunities available to journalists who want to participate in environmental field research.

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: Can we reverse the deleterious effects of eutrophication on coastal ponds and bays? What effects do the gases released from vegetation and soils have on climate variables such as temperature, rainfall or cloudiness? Are the sediments of Boston Harbor able to break down nitrates and other compounds found in sewage? Would extensive tree-planting programs help mitigate global climate effects?

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 center investigators have conducted studies in Massachusetts 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. One senior staff member is chairman of the U.S. Scientific Committee on Problems of the Environment (SCOPE) and a member of the International Geosphere-Biosphere Programme (IGBP) Scientific Committee. Another is president of the Association of Ecosystem Research Centers (AERC), a director of the Arctic Research Consortium of the U.S. (ARCSUS) and chairman of the LMER Coordinating Committee. Several are members of Ecological Society of America committees. Many members of the staff serve on committees of the MBL.
The search for solutions to the environmental problems that face our society is challenging ecologists to tackle complex questions that require the integration of diverse approaches and methods of study. These questions are not the comfortable ones that can be studied by a single scientist with the techniques and perspective of a single tradition; answering them requires research that cuts across disciplinary boundaries and addresses a wide variety of topics.

The Ecological Society of America (ESA) has addressed this challenge in its 1991 report titled The Sustainable Biosphere Initiative: An Ecological Research Agenda. This report identifies three research priorities: global change, biological diversity and sustainable ecological systems. It also recommends a set of steps toward addressing them. Each of these priorities requires research on a wide variety of topics from many different perspectives. Successful design and management of sustainable ecosystems, for example, will depend upon our knowledge of the effect of physical factors on the establishment and growth of species as well as of the effect of fluctuations in populations on productivity and the cycling of nutrients through ecosystems.

Ecologists have traditionally divided themselves into subdisciplines that focus on questions associated with particular levels of biological organization: individual organisms, populations, communities and ecosystems. But many complex questions cut across these divisions. In its discussion of cross-cutting issues, the 1991 ESA report notes that almost all questions in ecology explore the way phenomena at a given level are related to processes operating at other levels.

Although we have long recognized the need for integration in our discipline, training is still divided into population, community and ecosystem ecology. National Science Foundation funding for ecological research comes from two different sources, the ecosystems panel or the ecology panel. Textbooks are primarily oriented towards the population and community levels. Despite these academic distinctions, researchers addressing large-scale or complex questions are attempting to bring together perspectives and methods from the various subdisciplines into single studies.

The essays that follow illustrate some of the ways in which such questions are being addressed in basic research at The Ecosystems Center. Some projects are concerned with only one level of biological organization; others show the way different levels of organization can be included in a single study. Each of these studies, in one way or another, furthers the search for answers to pressing environmental problems.

Anne Giblin reports on a study of sulfur cycling in lakes that takes an ecosystem-level approach to the problem of assessing the way lakes respond to increased acid deposition from the atmosphere. She and other center researchers are studying the physical and chemical controls on the oxidation and reduction of sulfur compounds in lake sediments. Although these processes are biological, the study uses the ecosystem approach of considering only fluxes and mass balances, not the populations of microbes that transform the sulfur.

An ecosystem-level approach also characterizes a series of modeling studies, described by Gus Shaver and Ed Rastetter, of element interactions in terrestrial ecosystems and the ways in which they control carbon storage. These studies are being used to make comparative predictions of the responses of different terrestrial ecosystems to changes in atmospheric temperatures and levels of carbon dioxide.

Another lake project, this one in the Arctic, couples population and ecosystem approaches in a study of the basic mechanisms of the carbon cycle. The question is what controls the utilization of organic carbon transported from land to water. John Hobbie and his colleagues investigated the interactions of populations of bacteria and their predators to find out whether population-level processes in the lake controlled the utilization of organic carbon from the land (an ecosystem-level question).

Linda Deegan's report on her research in Waquoit Bay nicely illustrates the coupling of population- and community-level approaches with ecosystem questions.
The question is what environmental conditions favor species diversity. To answer this question, research had to go beyond ecosystem-level measurements of overall primary productivity as a response to eutrophication. The study showed that what really mattered for maintaining a diverse fish community was preserving a healthy population of eelgrass.

Basic physiological knowledge about tropical plant species is helping researchers ask ecosystem-level questions about the origins of carbon stocks in tropical soils. Jerry Melillo reports on a study, undertaken in cooperation with colleagues in Brazil and the United States, of the effects of converting Amazonian forests to pasture on both soil fertility and the release of carbon dioxide into the atmosphere. Using known differences in the ratios of carbon isotopes in plant tissues of different origins, they are calculating the relative contributions of grasses and trees to soil carbon stocks throughout the Amazon Basin. This information will help researchers to quantify the flux of carbon from soils and vegetation into the atmosphere as well as to evaluate the sustainability of pastures in the Amazon.

In his report on the Watershed Manipulation Project in eastern Maine, Knute Nadelhoffer describes another large-scale study that makes use of a stable isotope (¹⁵N) to trace the flux of an element (nitrogen) through the components of an ecosystem. This ecosystem-level approach, which focuses on processes that make use of nitrogen inputs, is coupled with measurements of the amounts of nitrogen retained in the foliage and wood of four different species of trees as well as soils. The aim of the study is to understand the effects of increased nitrogen deposition from atmospheric sources on temperate forests and the waters downstream from them. Knowledge of the different levels of nitrogen retained in different components of the ecosystem can be used to make predictions about nitrogen retention in other watersheds throughout New England.

David McGuire reports on a modeling study that asks how the net primary production of the world’s terrestrial ecosystems will be affected by changes in climate and atmospheric carbon dioxide levels. The model described operates at the ecosystem level of organization, utilizing interactions among ecosystem processes such as photosynthesis, nutrient cycling and plant respiration. The limitation of this model is that it does not allow different ecosystems to shift from one region to another in response to changes in climate. The next step is to combine this ecosystem process model with a species change model, such as BIOME from Colin Prentice at the University of Lund.

All of the basic questions we are asking at The Ecosystems Center are allied to practical questions of concern to society. In answering these questions, we combine ecological approaches, from physiological studies of individual plants to the investigation of ecosystem processes, in almost every project. Distinctions between ecological studies at the level of the individual, the population, the community and the ecosystem are becoming blurred. Research driven by complex questions, especially that stimulated by issues important to society, requires an integrated view of ecology that uses the approaches appropriate for each question and ignores artificial boundaries among ecology’s subdisciplines.
The highly productive ecosystems of the coastal zone, situated where the land, rivers and ocean meet, are uniquely vulnerable to the effects of changing climate and increasing human population. Pollution from excess nutrients and toxic substances, decreases in the flow of freshwater and sediments, and dredging have taken a toll on habitats, diversity of species and fisheries harvests, threatening the very resources that encourage settlement by the sea.

The diverse pressures on the coastal zone underscore the need to improve our understanding of these systems and our ability to predict their response to environmental changes. We have traditionally studied coastal zone problems in isolation, treating them as peculiar to a particular area. But understanding one system in detail does not necessarily help us understand how another system will respond to the same stress. We need to develop a view of coastal ecosystems that is based on an understanding of underlying mechanisms and of controls on processes common to different systems.

Comparative studies of whole ecosystems and experimental manipulations, widely used in lake and forest ecosystems, are helping us expand our knowledge of the basic patterns of response to change in coastal ecosystems. Comparison of common features among coastal ecosystems can produce a broader view of the mechanisms that control basic estuarine processes. Focusing on a few key variables will often yield a new understanding of an important process.

Human use of upland areas (lands that drain into an estuary and its tributaries) affects aquatic systems in many ways. Estuaries are linked to upland areas by the flow of water, sediments and nutrients. Development in a watershed generally increases the flow of nitrogen into estuaries. Because productivity in estuaries is limited by the availability of nitrogen, this increase in nitrogen flow has a strong influence on many aspects of estuarine function, including fisheries production.

Linda Deegan of The Ecosystems Center and John T. Finn of the University of Massachusetts at Amherst conducted a comparative study of the relationship of fish abundance to development in several coastal ponds with similar natural characteristics but different levels of development in the surrounding uplands. All three ponds were located within the Waquoit Bay National Estuarine Research Reserve on the south shore of Cape Cod. The entire watershed of Timms Pond is within a state park and has no development. Although most of the watershed of Sage Lot Pond is within a protected park, there are a few houses and a golf course in the upland area. Residential development occupies more than 57% of the watershed surrounding Hamblin Pond.

In our study, we demonstrated that fish abundance declined in a predictable pattern in response to development (Figure 1). We found that Hamblin Pond and, to a lesser extent, Sage Lot Pond were characterized by high densities of macroalgae, low...
light penetration, lack of oxygen and low eelgrass abundance. Fish abundance and number of species were low in these two ponds and considerably higher in Timms Pond.

We think that the following chain of events takes place as development increases:

1. Residential development in the watershed brings about a high flow of nitrogen from septic systems and lawns into coastal waters.
2. Increased nutrients cause algal blooms and loss of eelgrass.
3. The loss of eelgrass and increase in macroalgae bring about changes in food webs and loss of nursery areas for fish species.
4. The cumulative effect is a decline in fish and shellfish production.

Comparative whole-ecosystem studies cannot establish these hypothesized cause-and-effect relationships as fact. We can develop empirical patterns, and we can establish the distribution of these patterns by studying large numbers of ecosystems. We are then in a position to use experimental approaches to test our hypotheses about the mechanisms that explain the relationships observed in comparative studies.

Figure 2: The diagram shows the results of a $^{15}$N tracer experiment in a coastal pond community dominated by macroalgae. The macroalgae were initially labeled with $^{15}$N. They had a $\delta^{15}$N value of approximately +600 o/oo after a week. Next, the whole pond community was exposed to the labeled macroalgae in a screened enclosure. Only small amphipods and polychaete worms developed $\delta^{15}$N values that indicated a link with the macroalgae. Most of the small fish typical of eelgrass beds had $\delta^{15}$N values that indicated dependence on epiphytes or eelgrass rather than the large algae.

Whole-ecosystem experiments provide some of our most reliable information on the effects of perturbations in ecosystems. In order to test our understanding of the way upland development affects fish in eelgrass ecosystems, for example, we have conducted a series of experiments with eelgrass (Zostera marina) and macroalgae. In one experiment, we removed macroalgae from a portion of an eelgrass bed and compared these treatments to nearby reference areas. The diversity and abundance of fish and shellfish and the density of eelgrass increased in the ecosystems from which the macroalgae had been removed.

In a separate experiment, we evaluated the changes in the food web caused by the invasion of macroalgae. Eelgrass and associated epiphytes form the base of the food web in undisturbed eelgrass systems (Figure 2), providing a source of food for small invertebrates such as amphipods, copepods and snails. These organisms are eaten, in turn, by the small fish. In an eelgrass system dominated by macroalgae, small invertebrates eat the macroalgae. The complex physical structure of the algae, however, gives the invertebrates a refuge from predation by small fish. Unlike the eelgrass/epiphyte food web, the macroalgal food web ends with the invertebrates and does not provide food for the fish.

We tested this hypothesis by using $^{15}$N, a stable isotope of nitrogen, to trace nitrogen through the macroalgal food web. In order to introduce the tracer and differentiate the macroalgae from all other potential food sources, we grew the algae in a solution of nitrogen that was composed almost entirely of $^{15}$N. These macroalgae had a $\delta^{15}$N value of approximately +600 o/oo, which is dramatically different from the value of +4 o/oo to +6 o/oo for epiphytes or eelgrass.

The macroalgae were placed in a small screened enclosure in the pond and the enclosure stocked with the typical animals from the eelgrass ecosystem. At the end of one week, the isotopic value for the different components of the food web
clearly showed that very little of the nitrogen from the macroalgae was reaching the small fishes in this system (Figure 2). Only the amphipods and the polychaete worms that live in the algae had δ¹⁵N values that indicated consumption of the macroalgae. The δ¹⁵N values for the fish indicated that they were dependent upon the eelgrass/epiphyte food chain.

The results of these two whole-ecosystem experiments suggest that our basic understanding of the mechanisms behind declines in the fish populations associated with eelgrass ecosystems is probably correct. Unfortunately, only a handful of such experiments have been carried out in coastal ecosystems. One reason is that it is difficult to find unaltered ecosystems to use as controls along crowded and already developed coastlines. In addition, many experiments that we might propose are no longer allowed by law. The few pristine ecosystems left are often set aside as preserves; deliberately altering them to mimic an “impacted” condition at the ecosystem level is, properly, not allowed. Experimental attempts to restore impacted ecosystems to their pristine state is an alternative that holds promise.

Assessing The Status of Buzzards Bay: A Cooperative Effort

Researchers interested in understanding how aquatic ecosystems respond to disturbances can learn a great deal from studying estuaries that have been affected by human activities. We can compare conditions near a source of pollution with those outside its area of influence, and we can compare current and future observations with data from the past. In this way, we can analyse the impact of human activity on the health of coastal ecosystems over time and space.

Buzzards Bay is an example of a coastal system that is affected by pollution from both toxic substances and excess nutrients. Studies conducted in 1978 indicated that most of Buzzards Bay was still relatively free of pollution from industrial and residential activities. By 1989, however, it was clear that pollutants were having an impact on the smaller bays and coastal ponds that border Buzzards Bay. As residential density around the bay has increased, the flow of nutrients from septic systems, fertilizer and other sources has enriched the coastal waters and increased primary productivity. Higher levels of nutrients stimulate growth of algae and consumption of oxygen, producing unhealthy conditions for fish and shellfish.

In cooperation with scientists from the Lloyd Center for Environmental Studies and the University of Massachusetts at Dartmouth, Ecosystems Center researchers Jane Tucker, Anne Giblin and John Hobbie are measuring primary productivity at three stations in Buzzards Bay. We are using ¹³C, a radioisotope of carbon, to measure the rate at which carbon is taken up during photosynthesis. One goal of this project is to measure primary production in Buzzards Bay over an entire year. Another is to determine the importance of nutrients in this estuary. In order to make this determination, we are comparing the changes in productivity that we are observing with changes in the nutrient concentrations and light levels that are being measured by our colleagues at the University of Massachusetts.

These measurements will provide a baseline for comparison with data collected in the future as progress is made on the task of cleaning up sources of pollution around Buzzards Bay. Studies such as this collaborative effort can provide resource managers with a way to assess the effectiveness of policies designed to reduce the pollution of coastal waters.
For the past five years, Ecosystems Center researchers Anne Giblin, Brian Fry, Bruce Peterson, Jane Tucker, Kathleen Regan, and Mark Dornblaser have been studying the response of lakes to an increase in the deposition of sulfuric acid from the atmosphere. We have focused our attention on the changes in the sulfur cycle within the lake that may play a role in neutralizing this acid. This question is important because of the impact of acidity on the diversity of species in lakes. As lake waters increase in acidity, one major consequence is that fish species lose their ability to reproduce and eventually die out.

The microbial process of sulfate reduction can counter some of the effects of acid deposition. During sulfate reduction, microbes decompose organic matter by reducing sulfate to sulfide. This process consumes hydrogen ions, thereby neutralizing some of the acid that is entering lakes from the atmosphere. For the neutralization to be permanent, however, the sulfide must be bound to iron or to organic matter and buried in the sediments. When sulfide comes in contact with oxygen, it is reoxidized to sulfate and acidity is regenerated.

Scientists have generally assumed that increasing sulfate concentrations in lake waters would result in an increase in sulfate reduction rates in the sediments, thereby increasing sulfide storage. We have found, however, that a substantial quantity of sulfide stored in lake sediments over the summer months can be reoxidized during the fall when lake waters mix after a summer stratification. The quantity of sulfur stored in sediments is the net difference between the gross sulfate reduction rate during the summer and the sulfide oxidation rate in the autumn. In order to improve our understanding of what controls the level of sulfur storage in lakes, we need to understand how the balance between sulfate reduction and sulfide oxidation changes with changing concentrations of sulfate in the water column.

We have been measuring the effect of sulfate concentration on sulfur storage over two months in a laboratory experiment by manipulating sulfate concentrations in lake water over sediment cores. The experiment was run at two sulfate concentrations: 70 μM, which is the ambient sulfate concentration in the lake water, and a high sulfate level of 260 μM. By measuring changes in the sulfate concentration in the water, we could measure sulfur storage. When sulfate concentrations in the overlying water were at the ambient value, there was no net change in the sulfate concentration in the water (Figure 1a) and no change in the amount of sulfur stored in the sediment. At the higher sulfate concentration, we observed a small amount of storage of sulfur (about 150 micromoles per square meter per day).

![Figure 1: The upper panel (a) shows sulfate concentrations in lake water over sediment cores measured over a period of two months. Arrows indicate complete exchange of overlying water for fresh water with same sulfate concentration. Lower panel (b) shows fraction of 34S sulfate, a stable isotope tracer, in lake water over sediment cores measured over two months. Arrows indicate water exchanges for fresh water with same 34S fraction.](image-url)
Did these results mean that sulfate reduction rates were zero when sulfate in the overlying water showed no change from ambient conditions? In order to measure the process of sulfate reduction, we added a stable isotope tracer (^{34}SO_{4}^{2-}) to the water. Although the total sulfate concentration did not change, we saw a rapid decline in the amount of tracer in the overlying water (Figure 1b). This drop takes place because sulfate reduction removes sulfate enriched in ^{34}S from the water, while sulfide oxidation adds sulfur with a lower isotopic content to the water from the sediments. By measuring the dilution of ^{34}SO_{4}^{2-} in the water, we could calculate that the rate of gross sulfate reduction in this experiment was approximately 352 micromoles per square meter per day (Table 1). The high rate of sulfate reduction was balanced by a high rate of oxidation of sulfides in the sediments, resulting in no net change in sulfate concentration in the water.

Observing the dilution of the same tracer in our high sulfate experiment, we found that the rate of gross sulfate reduction was similar to that occurring in the 70 \( \mu \text{M} \) sulfate concentration treatment (approximately 342 \( \mu \text{mol} / \text{m}^2 / \text{d} \)). As Table 1 shows, however, the rate of sulfide oxidation was somewhat lower. The small increase in sulfur storage that we observed in the high sulfate treatment was the result of a decrease in sulfide oxidation rather than any increase in sulfate reduction.

Our results demonstrate that rates of gross sulfate reduction in lake sediments can be much higher than the rate of disappearance of sulfur from lake waters would indicate. In order to predict the ability of a lake to neutralize acid, we need to understand how both processes, sulfate reduction and sulfide oxidation, respond to changing inputs of acidity and sulfur.

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Table 1: Rates of sulfide oxidation and production as determined by isotope dilution and by change in the concentration of sulfate in the lake water over sediment cores. Values are given in micromoles per square meter per day.
Microbes and the Fate of Organic Matter in Aquatic Ecosystems: Top-Down or Bottom-Up Control?

Streams and rivers transport organic matter from terrestrial sources into lakes and estuaries in amounts large enough to dominate the carbon budget of aquatic ecosystems. Microbes decompose a portion of this organic material; another portion is stored permanently in sediments, and the remainder flows downstream and eventually into the open ocean. Because microbes are responsible for any decomposition that takes place, an understanding of the factors that control the fate of this organic matter can best be gained through studies of the growth of aquatic bacteria.

Ecologists have two theories about the control of microbial growth. The "bottom-up" theory says that control comes from the rate of supply of the substrate, the usable organic matter itself. The "top-down" theory, on the other hand, says that growth of microbes is controlled by the organisms that limit the bacteria populations through grazing or viral disease.

Ecosystems Center researchers John Hobbie and Michele Bahr worked with former center staff member George Kling, now of the University of Michigan, and Parke Rublee of the University of North Carolina at Greensboro on an arctic lake experiment designed to test these two control theories. Organic matter for the experiment was leached from dead leaves and blades of litter gathered from the surface of the tundra. After five days of soaking, the particulate organic matter was filtered off and the brown-stained water added to two large chambers filled with water from Toolik Lake in Alaska.

The chambers, one made of clear plastic (light bag) and one of black plastic (dark bag), each contained 4,900 liters of Toolik Lake water and an additional 120 liters of water rich in organic matter. A dark bag containing only Toolik Lake water served as the control (Figure 1). The added organic matter changed the dissolved organic carbon (DOC) from 5 to 6 mg per liter in the bags and the particulate organic carbon (POC) from 0.1 to 1.2 mg per liter.

Figure 1 shows an experiment carried out in 5,000-liter bags incubated in a lake in Alaska during June and July 1991. All three bags contained lake water; in addition, the experimental light and dark bags each contained 1 milligram per liter dissolved organic carbon (DOC) leached from terrestrial plant material. A black cover was used on the two dark bags.
The bacteria responded rapidly to the added organic matter (Figure 2). Their growth, measured by the incorporation of the amino acid leucine into bacterial protein, peaked rapidly and then fell to low levels within six days. Growth in the control bag did not change. Some 60% of the added organic matter was quickly decomposed in the experimental chambers, while the control bag showed little appreciable change in the organic matter originally in the lake water. Microbial growth was controlled from the bottom up, by the supply of usable organic matter.

Bacterial numbers did not appear to control the rate of growth. In other words, there was no evidence of top-down control. There were roughly 300% more bacteria in the light bag than in the dark experimental bag (Figure 2), even though the bacterial growth was about the same in both bags.

On the other hand, top-down factors exert tremendous control over the numbers of bacteria. Why were the numbers of bacteria so different in the light and dark bags? The explanation comes from measurements of the microbial food web. There are three trophic levels in the bags: The bacteria are at the bottom level; they are consumed by small colorless protozoan flagellates, and the flagellates, in turn, are consumed by larger protozoan ciliates and rotifers. Evidently these large ciliates and rotifers need more food than the flagellates can provide, for they only survive in the light bag where photosynthetic algae provide an additional food source (Figure 2).

The sequence of controlling events is as follows: when the large ciliate grazers are present (as in the light bag), they hold the small flagellates to relatively low numbers. The bacteria, therefore, are able to maintain high numbers. When these large grazers are absent (as occurred in the dark bag), the small bacteria-eating flagellates become abundant and hold the numbers of bacteria down.

Both bottom-up and top-down controls are important in this microbial system. But only the bottom-up controls, that is, the rate of supply of usable substrate, affect the rate of microbial growth and the rate of microbial decomposition of the organic matter from terrestrial sources. The center's Land Margin Ecosystem Research project will test this generalization in a completely different ecosystem by using the same techniques and experiments in water from Plum Island Sound.

Figure 2. Bacterial productivity in nanograms of carbon per liter per hour (2a), number of ciliates per liter (2b) and number of bacteria in millions per milliliter (2c) in light and dark experimental bags incubated in a lake in Alaska.

Ecosystems Center staff members carried out a variety of arctic research projects, such as the one described in this report, during 1992. They include Michele Bahr, Linda Deegan, Brian Fry, Heidi Geyer, Anne Giblin, John Hobbie, Loretta Johnson, David Jones, James Laundre, Robert McKane, Georgia Murray, Knute Nadelhoffer, Patricia O'Hara, Nancy Parmentier, Bruce Peterson, Edward Rastetter, Deborah Repert and Gus Shaver.
Many research projects at The Ecosystems Center address the question of what controls the flux of carbon between terrestrial ecosystems and the atmosphere. Understanding the way this exchange is controlled is important because carbon accumulation in the atmosphere, in the form of greenhouse gases like carbon dioxide, has a major impact on global temperature. By storing or releasing carbon held in vegetation and soil organic matter, terrestrial ecosystems have the potential to influence significantly the accumulation of carbon in the atmosphere.

One approach to this issue is to study the way various processes, such as photosynthesis or soil respiration, control the flux of carbon between terrestrial ecosystems and the atmosphere. An alternative approach is to study controls on the total amounts of carbon held in terrestrial vegetation and soil organic matter. Center investigators Edward Rastetter, Gus Shaver, Jerry Melillo and Robert McKane have taken the latter approach in a series of studies using the center's General Ecosystem Model (GEM).

The principal assumption behind these modeling experiments is that carbon accumulation in terrestrial ecosystems is constrained by plant and soil requirements for other elements, like nitrogen. The accumulation of carbon in terrestrial vegetation and soil organic matter requires the uptake and incorporation of at least 14 or 15 different elements in addition to carbon. All of these elements are essential, although their exact proportions in vegetation and soil organic matter may vary depending on climate, relative element availability and the type of vegetation or soil. Nevertheless, there are definite limits to the possible variation in the proportions or ratios of these elements in various ecosystem components.

These limits on the variability of element ratios define a set of conditions that regulate ecosystem carbon stocks and limit their potential for change. For example, if the carbon-to-nitrogen (C:N) ratio of a given type of vegetation is 50:1 and the maximum possible C:N ratio is 100:1, then the carbon content of the vegetation could increase by a factor of two even if there were no change in its nitrogen content. On the other hand, if the maximum possible C:N ratio is 50:1, then no increase is possible in the carbon content of the vegetation without a corresponding increase in nitrogen content.

Element ratios also vary among the major organic matter pools within ecosystems. For example, C:N ratios in vegetation may vary from about 30:1 in herbaceous vegetation to more than 600:1 in some forests. Soils, however, almost always have lower C:N ratios; the range is from 8:1 to 50:1. The consequence of this variation is that the total carbon stocks of ecosystems are strongly influenced by the distribution of nitrogen between vegetation and soils. For a given total nitrogen stock, the total carbon stock will be highest when most of the nitrogen is held in the vegetation.

Our analysis of ecosystem element ratios has led us to the hypothesis that constraints on change in terrestrial carbon stocks can be analyzed in terms of three principal factors. We suggest that changes in terrestrial carbon stocks should be constrained by:

1. Limits on the ratios of carbon to other vital elements within plant and soil organic matter pools;
2. Limits on the distribution of vital elements among organic matter pools with different characteristic ratios of carbon to other vital elements;
3. Limits on the total amounts of vital elements other than carbon in the ecosystem.

We examined this three-part hypothesis using our General Ecosystem Model (GEM) of carbon-nitrogen interactions. The model was used to develop predictions of the change in carbon stocks in arctic tundra and temperate deciduous forest ecosystems following a doubling of atmospheric carbon dioxide (CO₂) concentration or an increase in air temperature of 5°C. The use of a model of interactions between carbon and nitrogen to examine our hypothesis is appropriate because nitrogen is considered to be the limiting element for most temperate and high-latitude ecosystems.
The model's predictions suggest that different mechanisms are responsible for bringing about changes in carbon stocks in response to increased CO₂ versus increased temperature (Figure 1). When CO₂ was doubled, both ecosystems stored carbon as a result of increased carbon-to-nitrogen ratios in the vegetation and the soils. When the temperature was increased by 5°C, the shift of nitrogen from soils to vegetation (from a pool with a low C:N ratio to a pool with a high C:N ratio) caused the forest to store carbon. This effect was partially offset in this temperature-change scenario by a transient decrease in the C:N ratios within both vegetation and soils.

The 5°C temperature increase caused the tundra to store carbon for two reasons: a shift in nitrogen from soils to vegetation and an increase in the C:N ratios of the vegetation and soils. Temperature increased C:N ratios in the tundra ecosystem because of a stimulation of photosynthesis at higher temperatures. This effect was not manifested in the forest ecosystem because of the high proportion of non-photosynthetic tissue in the forest and the stimulation of respiration in these tissues.

Both tundra and deciduous forest ecosystems have small nitrogen inputs relative to the internal cycling of nitrogen. Therefore only small increases in carbon storage could be attributed to new nitrogen in our modeling experiment if we assumed that nitrogen inputs and outputs were the same as those measured in field studies (Figure 1). When we experimented with multiplying the initial nitrogen inputs and outputs in these simulations by a factor of 10, however, additional nitrogen uptake became possible. The substantial increases we noted in carbon storage could be attributed to uptake of this newly added nitrogen (Figure 2).

Our approach to studying the ratios of carbon to other elements in terrestrial ecosystems and their consequences for carbon storage is turning out to be quite useful for analysis, prediction, testing of hypotheses and comparison of ecosystems.

We are currently working with this method to identify differences among ecosystems with respect to the three factors listed above. We are using those differences to develop predictions about which ecosystems should be responsive to particular kinds of disturbances and which ecosystems are likely to store or lose carbon in the future.

**Figure 1:** Partitioning the simulated change in total ecosystem carbon storage among three factors and their interaction. The solid line shows the net change in carbon storage. The line with short dashes shows the change in carbon storage associated with changes in the C:N ratios of vegetation and soils. The dotted line shows the change associated with nitrogen input from outside the system. The line with long dashes shows the change associated with a shift in nitrogen from soils to vegetation, and the chained line shows the change associated with the interactions of all three factors. Ecosystems were in equilibrium with CO₂ and temperature at year 0. At the beginning of the third year, CO₂ was doubled (left), or temperature was increased by 5°C (right). Upper graphs are for hardwood forests; lower graphs are for tundra.

**Figure 2:** Partitioning the simulated change in total ecosystem carbon storage among three factors and their interaction after increasing both the inputs and losses of inorganic nitrogen by a factor of 10. Simulations are otherwise identical to those portrayed in Figure 1.
Forests To Pastures: Assessing The Environmental Consequences Of Changing Land Use In The Amazon Basin

Each year millions of hectares of tropical forest are converted to agricultural land. The country with the highest rate of conversion is Brazil, where more than half the clearing of forests is undertaken to create pastures. Despite the large area involved, we do not fully understand the environmental consequences of this change in land use. How does the conversion of forest to pasture in the Amazon Basin affect the release of carbon dioxide (CO₂) into the atmosphere? This question has direct implications for global climate change because CO₂ helps trap heat in the atmosphere. How does this change in land use affect soil fertility? The answer to this question is relevant to the issue of the sustainability of pastures in the Amazon Basin.

Jerry Melillo, Paul Steudler and Christopher Neill of The Ecosystems Center at Marine Biological Laboratory (MBL) are working with Carlos Cerri, director of the Centro de Energia Nuclear na Agricultura (CENA) at the University of São Paulo, and his research team as well as David Skole and his colleagues from the Complex Systems Research Group at the University of New Hampshire to address these questions. We call our collaborative study “Flor-Past Brasil,” from the Portuguese words for forest (floresta) and pasture (pastagem).

Our study of the carbon budget of the Amazon Basin has four major components: estimation of the rate of deforestation for conversion to pasture and other purposes, estimation of the carbon stocks in the vegetation and soils that existed before deforestation, determination of the fate of the carbon in the felled trees, and determination of changes in the carbon stocks of the vegetation and soils of pastures of various ages. We are integrating these components into a carbon flux model.

Skole has been using a series of images taken over time from the LANDSAT satellite to determine the rate of forest clearing in the Amazon Basin. He has estimated that the total area cleared by the end of the 1980s was about 25 million hectares, or about 6% of the forest in the basin. He also estimates that the average annual clearing rate in the Brazilian Amazon during the 1980s was about 1.7 million hectares, an area slightly smaller than Massachusetts. Most of the clearing has taken place in a crescent along the perimeter of the basin running from the northeast to the southwest. We are currently trying to separate the clearing of land for pasture from other uses.

Our research team has begun to develop estimates of soil carbon stocks before land was converted to pasture and to

Gas sampling chambers, such as the one shown here, are used to measure the release of trace gases from soils in Brazilian forests and pastures. The base of the chamber is permanently emplaced in the soil to a depth of 1 centimeter. The top of the chamber, shown at the left, is attached to the base during 20-minute measurements of changes in trace-gas concentrations.
organize and store these data in a geographic information system (GIS). Working with our colleagues at CENA and the University of New Hampshire, we have built a GIS database that contains information on carbon stocks from approximately 1,200 soil pits distributed throughout the Brazilian Amazon. These data were originally collected from 1972 to 1984 as part of the RADA MBRASIL project, a survey of the natural resources of the Amazon Basin conducted by the Brazilian government.

We have combined these data on soil carbon stocks with a classification of Brazilian soils to produce a map of soil carbon distribution in the basin (Figure 1). We estimate that the basin contains a total of $47 \times 10^{12}$ g C (47 billion metric tons of carbon) in the top meter of soil. We are currently making a similar estimation for forest vegetation carbon stocks.

We will use the data on pre-conversion carbon stocks for soil and vegetation to set the initial conditions for the MBL terrestrial carbon model (TCM), an empirical model that simulates the year-by-year time course of carbon release and sequestration caused by land-use changes. The model accounts for carbon released to the atmosphere through the burning of slash and for carbon removed from sites through harvesting. The harvested carbon is assigned to decay pools in the model with turnover times depending on the uses of the harvested wood.

The model also describes changes in carbon stocks resulting from changes in land use, whether from forest to agricultural uses such as pasture or from agriculture back to forest. Change in carbon stocks associated with conversion of forested lands to agriculture, for example, follows the pattern shown in Figure 2 in each part of the Amazon Basin, although the numbers vary according to the soil and vegetation carbon stocks in that part of the basin.

The soil response curve in the TCM that describes the conversion of forest to pasture is not well documented for the Amazon Basin. We are therefore undertaking a field study to determine how soil carbon stocks change when forest is converted to pasture. We are studying soil carbon stocks in a sequence of pastures and forests of different ages that grow in several types of soils in Rondonia, a Brazilian state in the western Amazon. Our early results indicate that soil carbon stocks in the pastures are generally equal to or greater than those in the original forest (Figure 3). Other reports in the literature suggest a loss of soil carbon when tropical forests are converted to pastures. We are expanding our studies to see whether our findings stand up to further test.

In our pasture carbon studies, we have been able to use an analysis of stable carbon isotopes to calculate the relative contributions of carbon derived from forest trees and from pasture grasses to the total carbon stocks of the soils. This calculation is possible because forest trees produce plant tissue that has a different ratio of two carbon isotopes ($^{13}$C to $^{12}$C) than does the tissue produced by the pasture grasses that grow in Rondonia.

As the trees and grass decay to produce soil organic matter, the carbon component of the organic matter retains the isotopic composition of the source material. Our analyses suggest that in 20-year-old pastures, the surface 30 centimeters of soil organic matter is about one-third "new" carbon derived from grasses and two-thirds "old" carbon of forest origin (Figure 4).

We have yet to make basin-wide carbon flux estimates with the MBL/TCM using the new data described above on deforestation rates, pre-disturbance soil and vegetation carbon stocks and the changes in soil carbon stock when forests are
Figure 2. Idealized response curves in the MBL/TCM model. The top curve shows the changes in vegetation carbon stock associated with the conversion of woody vegetation to pasture vegetation. The middle curve shows three (a-c) possible patterns of change in soil carbon stocks associated with the conversion of forested land to agricultural (pasture or crop) land. The bottom curve shows changes in carbon bound up in woody material from trees felled during deforestation.

Figure 3. Stocks of carbon (closed circles) and nitrogen (open circles) in the top 30 centimeters of soil in pastures of different ages in Ouro Preto, Rondônia.

Figure 4. The relative contributions of carbon derived from forest and pasture in the top 30 centimeters of soil in pastures of different ages in Ouro Preto, Rondônia. Closed circles indicate total soil carbon, and open circles indicate soil carbon derived from forests. The relative contributions were determined from the total carbon stock in the upper 30 cm, the $\delta^{13}$C of the soil and the $\delta^{13}$C of the initial tree and grass tissues.

converted to pasture. When we do, we expect to find that deforestation in the Amazon Basin results in an annual net flux of carbon to the atmosphere of between 0.2 and 0.3 x $10^{3}$gC ($200$ to $300$ million metric tons), with the clearing of forest for pasture responsible for a significant fraction of net flux. Although this estimate would be lower than those we and others have previously reported, it still represents a large loss of carbon from the land into the atmosphere.

Our work indicates that pasture soils may be accumulating nitrogen, especially during the first decade following clearing (Figure 3). Although we do not yet know the source of the added nitrogen, we think that it is fixed from the air by free-living microbes that inhabit the soil in the rooting zone of the pasture plants.

Carlos Cerri, director of CENA and Jerry Melillo.
Pasture soils may be suitable sites for nitrogen fixation for two reasons (Figure 5). First, the productive pasture grasses make available to the microbes easily usable carbon compounds in the form of organic matter given off by the roots and litter from fine-root decay. The microbes use this carbon as an energy source in the nitrogen-fixing process. Second, the burning associated with forest clearing adds ash to the soil, making it less acidic. The reduction in acidity, in turn, makes phosphorus more available. An adequate supply of phosphorus is essential for the growth of the nitrogen-fixing microbes.

During the next two years, we will continue to make field measurements of soil carbon and nitrogen stocks in forests and pastures in Rondônia and elsewhere in the Amazon Basin to see whether the patterns of carbon and nitrogen accumulation we have seen in pasture soils are widespread. We also plan to evaluate the effects of conversion of forest to pasture on phosphorus availability. With information on soil carbon, nitrogen and phosphorus in hand, we will have a scientific basis for evaluating the sustainability of pastures in the Amazon Basin.

Figure 5. A conceptual model showing how conversion of forest to pasture creates conditions suitable for nitrogen fixation by free-living soil microbes. Plants with $C_4$ carbon fixation mechanisms process CO$_2$ more efficiently than $C_3$ plants.

Ecosystems Center staff members participating in studies of tropical ecosystems during 1992 include Mark Castro, Jonathan Chapman, Jerry Melillo, Michelle Miliefsky, Christopher Neill and Paul Steudler.
Scientists who study terrestrial ecosystems use the term "net primary production" (NPP) to refer to the net amount of carbon captured by land plants. It represents the difference between the carbon fixed during photosynthesis and that released to the atmosphere during respiration. Understanding the way terrestrial NPP responds to changes in climate and in carbon dioxide (CO₂) concentrations in the atmosphere is essential to our ability to predict the impact of changes in these variables upon terrestrial ecosystems.

The first estimates of terrestrial productivity were made by simply multiplying the mean NPP values of different types of ecosystems by the area of their distribution and then adding up the results. More refined estimates became possible with the development of equations that link NPP values with environmental variables, such as temperature and precipitation. These models allow more specificity because the environmental variables they use are associated with geographic locations. But they provide little insight into the way NPP is controlled by ecosystem processes such as photosynthesis, respiration, decomposition and nutrient cycling. The next step was the development of dynamic process models that describe how processes are affected by environmental variables and how they interact. These models have the potential for showing how processes that affect NPP will interact under future climatic conditions.

In collaboration with Berrien Moore, Charles Vörösmarty and Annette Schloss of the University of New Hampshire, Ecosystems Center researchers Jerry Melillo, David McGuire and David Kicklighter have used the Terrestrial Ecosystem Model (TEM) to make the first process-based estimate of NPP for the world’s terrestrial ecosystems (Figure 1). The model, developed at The Ecosystems Center, uses information on soils, vegetation and climate variables such as temperature, precipitation, cloudiness and solar radiation to make monthly estimates of important transfers of carbon and nitrogen in ecosystems. The data sets used in TEM are organized into 0.5° latitude by 0.5° longitude parcels that cover the vegetated surfaces of the globe.

We applied the model to more than 56,000 of these parcels in order to develop a total terrestrial NPP estimate for current climate conditions and atmospheric CO₂ levels. The result was a global terrestrial NPP of 53 x 10¹⁵ gC (53 billion metric tons of carbon) per year. The model indicates that more than half of the total terrestrial NPP, 30 x 10¹⁵ gC (30 billion metric tons of carbon) per year, occurs in the tropics (Figure 2). Most of the

![Diagram of Atmospheric Carbon Dioxide Cycle](image)
tropical NPP takes place in forests, which generate 36% of total terrestrial NPP in spite of the fact that they cover only 14% of the land surface. Temperate forests, which cover 11% of the land surface, account for 17% of total terrestrial NPP.

In order to simulate changes in terrestrial productivity under various climatic conditions, we used the output from four global climate models to run TEM. These forecasts describe climate under conditions of doubled atmospheric CO₂. We also ran TEM with current climate conditions and doubled CO₂.

Under conditions of doubled CO₂ and current climate, TEM predicts that total terrestrial NPP will increase by 16%. The response varies widely among ecosystems. Northern ecosystems, such as tundra and boreal forests, show little response; tropical forests show a substantial response, and temperate forests show intermediate response. The model predicts that the availability of inorganic nitrogen in the soil will limit NPP most in northern regions, less in temperate regions and least in tropical regions. These results suggest that tropical forests are most able to incorporate higher levels of CO₂ from the atmosphere into production.

For changes in both CO₂ levels and climate, the predicted change in total terrestrial NPP ranges between 20% and 26%, depending on the climate forecast. The overall changes in NPP for vegetation in northern, temperate and tropical regions are similar in magnitude. The relative contribution of climate conditions and CO₂ levels to the predicted responses, however, varies among the regions.

For all four of the climate scenarios, temperature increases are predicted to be greatest towards the poles and least in the tropics. The predicted responses in both northern and temperate ecosystems reflect primarily the effects of elevated temperature in enhancing the availability of inorganic nitrogen in the soils of these regions. TEM predicts that the newly available nitrogen will give vegetation in these regions an increased capacity to incorporate CO₂ into production. In tropical regions where vegetation is generally less limited by nitrogen availability, the predicted responses are dominated by the effects of elevated CO₂.

Although the predicted global and regional responses of NPP to elevated CO₂ levels are generally similar for all of the climate scenarios, responses differ at smaller spatial scales. For example, when we ran TEM with the climate conditions predicted by the Oregon State University (OSU) global climate model, our model predicted that NPP would decrease throughout much of Indonesia (Figure 3). For the other three climate scenarios, TEM predicts that NPP would increase in most locations in Southeast Asia. The predicted decrease that occurs with the OSU climate scenario is associated with a predicted increase in cloudiness of 12.5% for tropical forest areas in the region.

The results of the modeling studies with TEM indicate that interactions among ecosystem processes play an important role in the ability of vegetation to incorporate a higher level of CO₂ from the atmosphere into production. Because these
Figure 3. Predicted responses of annual net primary production (NPP) in Southeast Asia to doubled CO₂ for different climate scenarios as determined by the Terrestrial Ecosystem Model. The simulations of climate that correspond to a doubling of atmospheric CO₂ concentration include two from the Geophysical Fluid Dynamics Laboratory in Princeton, New Jersey (GFDL 1 and GFDL Q), one from the Goddard Institute of Space Studies in New York (GISS), and one from Oregon State University (OSU) in Corvallis.

Interactions appear to vary from region to region, process-based models that are organized geographically are required to assess how changes in climate and CO₂ concentrations can affect NPP. The TEM approach represents an important advance because it provides scientists and policymakers with an opportunity to explore the effects of climate change on the properties and processes of ecosystems in a quantitative and geographically specific way.

Staff members at The Ecosystems Center participated in a number of modeling studies, such as the ones described in this report, during 1992. They include John Hobbie, David Jones, David Kicklighter, David McGuire, Robert McKane, Jerry Melillo, Knute Nadelhoffer, Bruce Peterson, Edward Rastetter, Gus Shaver and Paul Steudler.
Using Nitrogen Isotopes in Studies of Forest Ecosystems

Investigators at The Ecosystems Center are making novel use of stable (non-radioactive) isotopes as tracers in several large-scale experiments. One such experiment is the Watershed Manipulation Project at the Bear Brooks Watersheds site in eastern Maine (BBWM). In cooperation with colleagues at the University of New Hampshire and the University of Maine, Knute Nadelhoffer, Marty Downs, Brian Fry and Jerry Melillo are studying the effects of nitrogen deposition from atmospheric pollutants on forests in the watershed.

Our aims are to identify the forest processes that make use of these inputs of nitrogen and to predict how much additional nitrogen forests can retain before the excess is released into drainage waters as nitrate. This question is important for two reasons: the flow of nitrate increases the acidity of waters downstream; it also depletes the forest of valuable nutrients such as calcium, magnesium and potassium.

Since 1990, we have applied nitrogen fertilizer by helicopter every other month to a 10-hectare forested watershed at the BBWM site to simulate nitrogen deposition (Figure 1). The rate of nitrogen application (roughly 25 kg per hectare per year in the form of ammonium) is similar to rates of nitrogen deposition in forests downwind from major sources of industrial emissions in the Northeast United States and elsewhere. In 1991 we started "spiking" the fertilizer with \( ^{15}N \), a stable isotope of nitrogen normally present at extremely low levels in natural materials. This \( ^{15}N \) tracer has allowed us to measure the amounts of fertilizer taken up by different components of the forest ecosystem and to estimate the overall capacity of this ecosystem to retain nitrogen.

How is the tracer used? More than 99% of the nitrogen in biogenic materials is \( ^{14}N \). Because natural \( ^{15}N \) levels are very low and relatively uniform, we can estimate the movement of fertilizer labelled with \( ^{15}N \) into ecosystem components. For example, the nitrogen in plant tissues and soils in the BBWM forest contains between 0.365% and 0.369% \( ^{15}N \). The nitrogen we added to the forest catchment in 1991 was 0.437% \( ^{15}N \). By measuring changes in the \( ^{15}N \) content of plants and soils, we can find out where the added nitrogen is retained in the watershed.

Small variations in nitrogen isotope composition can be more simply described by using the "delta" notation, in which \( ^{15}N \) contents are expressed as per mil (o/oo) deviations from the atmospheric nitrogen standard of 0.3663% \( ^{15}N \). With this notation, the \( ^{15}N \) values of plants and soils range from -3 to +6 o/oo; the fertilizer nitrogen, on the other hand, has a \( ^{15}N \) value of +192 o/oo. If increases in \( ^{15}N \) can be detected following fertilizer application, the amount of labelled fertilizer entering plant tissues or soils is easily calculated using mass balance techniques. With the highly sensitive instruments available in The Ecosystems Center's stable isotope facility, we were able to detect increases in \( ^{15}N \) values of wood, leaves and soils at sampling points distributed within the fertilized watershed. Isotope analysis showed that the \( ^{15}N \) values of wood in the four most common tree species increased by 3.5 to 4.5 o/oo, following four applications of labelled fertilizer in 1991 (Figure 2). We used similar increases in \( ^{15}N \) values and estimates of nitrogen pool sizes in other ecosystem compartments to trace the movements of the labelled fertilizer and to estimate total nitrogen retention in the forest (Table 1).

This preliminary set of analyses showed that surface soil was the most important "sink" for nitrogen, retaining about 67% of the nitrogen additions. Vegetation of the four dominant tree

<table>
<thead>
<tr>
<th>Ecosystem Component</th>
<th>N Pool (kg/ha)</th>
<th>pre-treatment ( ^{15}N ) (o/oo)</th>
<th>post-treatment ( ^{15}N ) shift (o/oo)</th>
<th>N Retained (kg/ha/yr)</th>
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<tr>
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<td>11.3</td>
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<td>4.4</td>
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<tr>
<td></td>
<td>8</td>
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<tr>
<td>TOTAL ECOSYSTEM</td>
<td></td>
<td></td>
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<td>12.5</td>
</tr>
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</table>

Table 1. Estimated retention of nitrogen fertilizer labeled with \( ^{15}N \) in compartments of the forested catchment at the Bear Brooks site. About 16.8 kg N/ha (\( ^{15}N=192 \)) was added in four equal applications from April 1991 through October 1991. Nitrogen retained in each compartment is proportional to the nitrogen pool size and the increase in \( ^{15}N \) after treatment.
Figure 1: The dashed lines mark two catchments (watersheds) at the Bear Brooks Watersheds site in Maine. Both catchments are located on a southeast-facing slope and drained by streams that persist throughout the year (dark lines). The shaded catchment was treated with fertilizer labeled with $^{15}$N during 1991; the other served as a control. Filled triangles show sampling locations in the fertilized area.

species retained about 7% of the added nitrogen. Overall retention was about 75% of the total nitrogen applied during the 1991 growing season (12.5 of a total of 16.8 kg N/ha).

We plan to complete our sampling and $^{15}$N analyses of materials from the fertilized watershed during the coming year. These efforts will help us improve our estimate of the amount of nitrogen retained by the forest ecosystem and to rank more precisely the strengths of various components as nitrogen sinks, increasing our understanding of the way plant and microbial processes interact to control nitrogen retention on the large scale. We could not undertake these sorts of experiments without the highly sensitive techniques for analyzing $^{15}$N afforded by our modern mass spectrometer facility or the collaborative efforts that permit large-scale manipulations such as we have described here.

Ecosystems Center staff members are undertaking a variety of studies, such as the one described here, in ecosystems of the temperate zone. Participants include Mark Castro, Jonathan Chapman, Mark Dornblaser, Martha Downs, Todd Drumme, Robert Garratt, Brian Fry, Anne Giblin, David Kicklighter, Jerry Melillo, Michelle Miliefsky, Knute Nadelhoffer, Kathleen Newkirk, William Peterjohn, Bruce Peterson, Kathleen Regan, Andrea Ricco, Paul Steudler and Jane Tucker.
Education at The Ecosystems Center

Although The Marine Biological Laboratory does 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 members of doctoral committees at a number of colleges and universities, members of the staff conduct workshops and participate in courses given at MBL. Senior staff members supervise the work of half a dozen postdoctoral research associates, who spend an average of two years apiece working at the center. Visiting scientists and students come to work on projects each year, some for just a month or two and some for as much as two years.

The Ecosystems Center also participated in MBL’s Science Writing Fellowships Program last summer. One of the fellows, staff writer Heather Dewar of The Miami Herald, accompanied investigators to the Long-Term Ecological Research (LTER) site at Toolik Lake in Alaska for a first-hand look at ecological field research in the Arctic.

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 is an adjunct associate professor at the University of Massachusetts at Amherst.

Postdoctoral research associate Chris Neill holds an adjunct appointment at the Graduate School of Environmental Studies at Bard College, where he teaches graduate-level courses in ecosystem ecology every other summer.

Michael Miller of the University of Cincinnati spent three months at The Ecosystems Center as a visiting scientist during 1992. During his stay in Woods Hole, he worked on nutrient data collected during expeditions to the LTER site at Toolik Lake in Alaska.

Swedish researcher Bosse Normann spent a year at The Ecosystems Center as a visiting scientist during 1991-92. He worked with Brian Fry and Meredith Hullar on the development of techniques using $^{13}$C, a stable isotope, to measure bacterial consumption of dissolved organic carbon (DOC). The aim of their effort is to develop a method for sampling the $^{13}$C 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.

A postdoctoral researcher with the U.S. Department of Agriculture Forest Service during his first two years at The Ecosystems Center, A. David McGuire has now joined the center as a research associate. He received his doctorate in biology at the University of Alaska at Fairbanks in 1989. 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 CO$_2$ on the productivity of tropical and temperate ecosystems. Dave recently received an award from the USDA Forest Service for outstanding performance in his postdoctoral research.

Bob McKane

Mark Castro was appointed a research associate at The Ecosystems Center in October 1992. He came to the center initially as a postdoctoral research associate in 1990 after receiving his doctorate in environmental sciences from the University of Virginia, where he studied the factors controlling the flux of sulfur gas between temperate forest soils and the atmosphere. With Jerry Melillo and Paul Steudler, Mark is currently studying the effects of atmospheric deposition on nutrient cycling and trace gas fluxes at the LTER site at Harvard Forest. Mark and Jerry are also conducting a study with colleagues at the University of Florida on the effects of management practices on nutrient cycling in slash pine plantations at a site near Gainesville.

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. Bob is also working with Gus Shaver and Loretta Johnson on a large-scale stable isotope tracer experiment in arctic tundra in which he is studying the way interspecific competition for nitrogen structures a tundra plant community.

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 as a postdoctoral research associate in October 1990. He has been working with center staff members Jerry Melillo, Paul Steudler and Kathy Newkirk and Frank Bowles of Research Designs on a soil-warming experiment in Harvard Forest. The project focuses on the effect of increased temperatures on the availability of nutrients and on trace-gas emissions from soils. Although Bill has accepted a position as assistant professor in the biology department at West Virginia University as of January 1993, he will continue to work with Ecosystems Center staff members on soil-warming projects in New England and in northern Sweden.
Christopher Neill, appointed a postdoctoral research associate at The Ecosystems Center in November 1991, received his doctorate in forestry and wildlife management at the University of Massachusetts at Amherst in January 1992. His thesis research was on the effects of flooding on plant growth and nitrogen cycling in prairie marshes in Manitoba. Chris is currently working with Jerry Melillo, Paul Steudler and Brazilian researchers from the Centro de Energia Nuclear na Agricultura (CENA) of the University of São Paulo at Piracicaba on a study of the effects of changes in land use on soil fertility and trace-gas emissions in the Brazilian Amazon. During 1992, he spent four months working with colleagues in Brazil, partly at Fazenda Nova Vida, a remote field site in the western Brazilian state of Rondônia, and partly in São Paulo.

Loretta Johnson joined the staff of The Ecosystems Center as a postdoctoral research associate in May 1992 after a semester of teaching at the University of Connecticut, where she received her doctorate in 1991 in ecology and environmental biology. For her doctoral research, Loretta studied decomposition in peatlands in northeastern Maine and in Sweden. She is currently working with center staff members Gus Shaver and Bob McKane on a stable isotope tracer experiment, using nitrogen-15 to track the flow of nitrogen in various forms through arctic tussock tundra plants and soils. She is particularly interested in the partitioning of nitrogen over time between vegetation as a whole and soils and soil microbes.

Training Students in Latin America

With support from Texaco Foundation and Exxon Corporation, Jerry Melillo, Paul Steudler and Chris Neill are collaborating with colleagues in Puerto Rico and Brazil to train students in these countries in the methods and principles of ecosystem ecology. A number of these young scholars have visited The Ecosystems Center during the course of their training as well as working with center scientists on projects of their own at field sites in the tropics.

For 1992, Texaco awarded a six-month fellowship to Lynette Y. Garces Rivera, an undergraduate biology major at the University of Puerto Rico at Rio Piedras, for her senior research project on microbial populations of nitrifiers and denitrifiers in mature tropical forests and abandoned pastures of various ages. Her adviser is Prof. Gary Toranzos of the University of Puerto Rico.

The Texaco Fellowship Program is also providing support for three graduate students in Brazil, where The Ecosystems Center has a close working relationship with the Centro de Energia Nuclear na Agricultura (CENA) of the University of São Paulo at Piracicaba. Prof. Carlos Cerri, director of CENA, visited The Ecosystems Center in 1991 to work with staff members and plan the Brazil program. The three Texaco fellows are working with Ecosystems Center staff members in both the laboratory and the field; two of them have also visited the center and other research facilities in the U.S. to learn new techniques.

Jener Leite de Moraes received his undergraduate degree in agricultural engineering from the University of São Paulo and his master's degree from CENA, where he is currently a doctoral candidate. He spent a month in the U.S. during 1992 learning techniques for data analysis in a Geographic Information System (GIS), skills he is applying to an analysis of soils data for the Amazon Basin. He is currently setting up a GIS at CENA with help from The Ecosystems Center.

Brigitte de Paula Eduardo worked with scientists at The Ecosystems Center during March 1992 on techniques for analyzing organic matter in tropical soils. She received her bachelor's degree in biology and her master's degree in agronomy from the University of São Paulo. She is currently studying the carbon dynamics of tropical forests and pastures as part of her doctoral work at CENA.

Marisa de Cassia Piccolo earned her undergraduate degree in industrial chemistry from the Universidade Metodista de Piracicaba and her master's degree from CENA, where she is currently a doctoral candidate. She spent two months during 1992 at Fazenda Nova Vida in Rondônia, working with Ecosystems Center researchers on experiments to determine methods of measuring patterns of soil nitrogen availability in pastures of varying ages.

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 southeastern 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. She has completed this work, which will form a part of her dissertation.

Alvaro Velez, a master's candidate in the Department of Agronomy and Soils at the University of Puerto Rico at Mayaguez, is currently studying the effects of transforming sugar cane fields to pasture on soil carbon and nitrogen stocks, rates of nitrogen mineralization and nitrification and trace gas fluxes. His research is supported by grants from Exxon and the USDA Forest Service.

Under Linda Deegan's supervision, four students conducted studies in Waquoit Bay during 1992 as part of an eelgrass recovery project funded by NOAA's Estuarine Reserve Program. Undergraduates John Harrison of Brown University, Brad Colvin of Southampton University and Chris Capone of the University of Massachusetts at Amherst studied macroalgal production, the response of the eelgrass to removal of the large algae and changes in predation on winter flounder. UMass-Amherst graduate student Tania Lewandowski also studied fish response to removal of macroalgae.

Many Ecosystems Center staff members share their expertise with Falmouth's public and private schools. Kris Tholke, Hop Garritt, John Hellrich, Brian Fry and Knute Nadelhoffer served as judges this year for science fairs at Falmouth Academy and Falmouth High School. Anne Giblin assisted an FHS student with his project as well.

Others have participated in activities sponsored by the Woods Hole Science and Technology Education Partnership, a consortium of area schools, research institutions and businesses. Kris Tholke and Hop Garritt participated in a poster session at Falmouth High School in May 1992, where they presented a poster on stable isotopes in pilot whales. Hop also presented a poster on macrophyte metabolism in the Hudson River. As part of the partnership's Women in Science program, Kathy Regan, Heidi Geyer, Meredith Hullar and Ecosystems Center consultant Beth Schwarzman spoke to Falmouth school system students about their work and how they chose careers in science. Beth also serves on the executive committee of the partnership.

Leslie Redmond, Hop Garritt, Kristin Tholke
Ecosystems Center Events and Activities

Highlights of 1992

Ecosystems Center Joins The LMER Program

The Ecosystems Center became part of the National Science Foundation’s Land Margin Ecosystem Research (LMER) program this year with the establishment of a fifth LMER site in Plum Island Sound estuary north of Boston. Chuck Hopkinson is serving as chief scientist for the new LMER project. Other investigators are Linda Deegan, Brian Fry, Anne Giblin, John Hobbie and Bruce Peterson from the center, Jack Finn from the University of Massachusetts at Amherst and Robert Buchsbaum of Massachusetts Audubon Society. John is also chairman of the LMER coordinating committee.

In addition to its participation in the field program, The Ecosystems Center is host to the newly established LMER coordination office. Deborah Scanlon has joined the center staff as executive assistant for this office.

The center was well represented at the 1992 scientists’ meeting of the LMER program, held in November at the Marine Biological Laboratory (MBL). The three-day event included four workshops as well as plenary sessions. Anne Giblin served as chairman of the workshop on vertical coupling between sediments and the water column in coastal ecosystems. Jane Tucker and Linda Deegan also took part in this session. Chuck Hopkinson participated in the workshop on coupling between land and water; John Hobbie attended the session on the use of Geographic Information Systems (GIS) in LMER projects, and Bruce Peterson joined the workshop on biological-physical modeling.

As a member of the LMER coordinating committee, Chuck attended a meeting in July in Fairbanks, Alaska, as well as the one in Woods Hole in November.

Workshop on Northern Herbivory

Along with John Bryant of the University of Alaska, Gus Shaver organized an NSF-sponsored workshop on the role of herbivores in arctic and boreal ecosystems. The meeting, held Nov. 9 and 10 at MBL, attracted researchers from Canada, Sweden and Finland as well as the United States. Other participants from The Ecosystems Center were Linda Deegan, Bruce Peterson and Ed Rastetter.

LMER Workshops and Meetings

Researchers participating in the Harvard Forest Long-Term Ecological Research (LMER) program got together in Petersham during January to report on their current and future projects. Speakers at the third annual ecology symposium included Ecosystems Center staff members Mark Castro, Dave Kicklighter, Kathy Newkirk, Bill Peterjohn and Paul Steudler, who gave presentations on methane uptake in forest soils, estimating regional fluxes of carbon dioxide and methane between forest soils and the atmosphere, the Harvard Forest soil-warming experiment and trace gas fluxes from a simulated hurricane blow-down. Others attending or contributing from the center were Frank Bowles, Jon Chapman, Marty Downs, Todd Drummey, Dave McGuire, Bob McKane, Jerry Melillo, Michelle Milieski, Knute Nadelhoffer and Andy Ricca.

The Arctic LMER research group held its annual meeting in Woods Hole during March. Nancy Parmentier of The Ecosystems Center organized the meeting. Other participants from the center were Michele Bahr, Linda Deegan, Brian Fry, Heidi Geyer, Anne Giblin, John Hobbie, Jim Laundre, Knute Nadelhoffer, Bruce Peterson, Gus Shaver and Ed Rastetter and Debbie Repert.

John and Gus also organized an Alaska field trip for the LTER coordinating committee during August. Some 40 campers made the 450-mile trip from Fairbanks to Prudhoe Bay, visiting the Toolik Lake field station along the way. Highlights of the trip were the weather, the grizzly bears, musk oxen and the Prudhoe gravel pits.

John and Ed Rastetter attended the LTER Coordinating Committee meeting, held in early March in Trout Lake, Wisconsin. John helped to organize a session on scaling at the meeting, and Ed presented a simulation that used the center’s General Ecosystem Model (GEM) to compare LTER sites.

IPCC Workshop on Biotic Feedbacks in Global Climate Systems

Knute Nadelhoffer served as a rapporteur for a session on plant responses at an international workshop on biotic feedbacks in global climate systems, held at MBL during October. The workshop, sponsored by The Woods Hole Research Center, was a review for the Intergovernmental Panel on Climate Change. Gus Shaver also participated in the meeting.

SCOPE Workshop

Jerry Melillo, Gus Shaver and Ed Rastetter participated in a modeling workshop on the effects of climate change on production and decomposition in coniferous forests and grasslands, held in Uppsala, Sweden, during September. The workshop was the final one in a series sponsored by the Scientific Committee on Problems of the Environment (SCOPE) for modelers interested in assessing and comparing the results of various grasslands and forest models. Workshop participants are currently preparing a book on their findings.

Other Modeling Workshops

Ed Rastetter led a third and final ecological modeling workshop for students interested in the use of mathematical modeling in ecosystems analysis during January. The four-day session, held in Fort Collins, Colorado, was devoted to discussing ways of developing spatial models. Dave Kicklighter and Bob McKane also participated in the workshop, attended by students from six universities or research centers.

Kathy Newkirk, Frank Bowles
Ed attended several other modeling workshops during the year. They included one on natural sinks of carbon dioxide, held in Palmas del Mar, Puerto Rico, during February under the sponsorship of the Environmental Protection Agency (EPA) and the Department of Energy (DOE); one on decomposition modeling, held in Woods Hole in April; a scaling workshop held at Wye Woods, Maryland, in September, and a global modeling workshop held in Estes Park, Colorado, in October.


Other Conferences and Workshops

Jerry Melillo and Keith Smith of the Edinburg School of Agriculture convened a workshop on trace-gas fluxes between the atmosphere and mid-latitude ecosystems at the National Center for Atmospheric Research (NCAR) in Boulder, Colorado, during September. The workshop, attended by 40 scientists from 10 countries, produced a preliminary plan for developing a mid-latitude network to further understanding of trace-gas fluxes and their controls in this region.

Paul Steudler presented a paper on trace gas exchanges and controls on gas fluxes in a slash pine forest in Florida at the EPA’s annual investigators’ workshop for the Global Climate Change Research Program, held during February in Athens, Georgia. He also served as co-chairman for a working group on measurement of trace gas fluxes at a workshop on developing a biosphere-atmosphere trace gas network (BAGNET), held at Pingree Park, Colorado, in September.

John Hobbie participated in an NSF-sponsored workshop organized jointly by the Ecological Society of America (ESA) and the Association of Ecosystem Research Centers (AERC) in Albuquerque, New Mexico, in October. The purpose of the workshop was to develop further ideas for a center devoted to synthesis in ecology.

Anne Giblin participated in several workshops on coastal research and planning during the year. She was among the speakers at a Sea Grant workshop on comparative studies of northeastern estuaries, held at the University of Rhode Island (URI) in February. She participated in a panel discussion on developing a monitoring plan at a workshop on monitoring kettle ponds, held at the Cape Cod National Seashore during March. She also presented a paper on risks to benthic communities at an EPA workshop titled “Managing Nitrogen Inputs to Near Coastal Waters,” held at URI in May.

Linda Deegan organized a session on the importance of changing fluxes in estuaries to fisheries at a joint Estuarine Coastal and Shelf Association/Estuarine Research Federation conference titled “Changes in Fluxes in Estuaries: Implications from Science to Management.” The four-day conference was held in Plymouth, United Kingdom, during September. Linda also presented a talk on flow model analysis of the effects of organic matter-nutrient interactions on estuarine trophic dynamics at the conference.

Meetings, Lectures and Other Presentations

Mark Castro made a presentation at a meeting of the National Institute for Global Environmental Change, held in January in Huntington Beach, California. His talk was on the uptake of atmospheric methane by temperate forest soils in the northeast United States during the years 1988-1991.

Several Ecosystems Center staff members made presentations at the annual meeting of the American Society of Limnology and Oceanography (ASLO), held in Santa Fe, New Mexico, in February. Anne Giblin gave a talk on controls on sulfur cycling in lake sediments. Chuck Hopkinson spoke on wave pumping effects on nitrification, denitrification and nutrient release from shallow self sediments. Bruce Peterson gave a talk on tracing dissolved organic carbon in estuaries. John Hobbie presented a paper on stable isotopes and organized a session on long-term data sets. Michele Bahr also attended the meeting.

On March 25, John Hobbie participated in a day-long “Assembly on the Arctic,” held at the National Academy of Sciences in Washington, D.C., to inform legislators, their staff members and agency officials about issues in arctic research and resource management. He gave a talk on observations, models, scales and predictions in the context of arctic terrestrial ecosystems.

Mark Dornblaser spoke at this year’s meeting of the American Chemical Society, held in April in San Francisco. His topic was the use of a stable isotope of sulfur to trace biochemical processes in lake sediment cores.

At the annual meeting of the New England Estuarine Research Society (NEERS), held in Lowell, Massachusetts, during May, Anne Giblin, Chuck Hopkinson and Jane Tucker presented a paper on metabolism and nutrient cycling in Boston Harbor sediments.

Knut Nadelhoffer presented a talk titled “Biological Sinks for Nitrogen Additions to a Forested Catchment” at the International Symposium on Experimental Manipulations of Biota and Biogeochemical Cycling in Ecosystems, held May 18-20 in Copenhagen, Denmark.

The Ecosystems Center was well represented at the annual ESA meeting, held during August in Honolulu. Knute Nadelhoffer gave an invited talk on the use of element budgets for estimating the allocation of carbon to forest roots at a symposium on forest carbon budgets. Bob McKane presented a paper on simulating biogeochemical controls on the long-term retention of nitrate in a northeastern forest using a model of ecosystem carbon and nitrogen dynamics. Bill Peterjohn and Kathy Newkirk spoke on the design of the Harvard Forest soil warming project and some early results. In his talk, Dave McGuire compared the North
American results for two global modeling studies of the effects of elevated carbon dioxide and temperature on net primary productivity in temperate forests. Dave Kicklighter talked about issues of temporal scale in estimating regional carbon dioxide fluxes from temperate forest soils.

Ecosystems Center researchers involved in studies of sediment and water-column processes in Boston Harbor presented their findings to a variety of audiences during the year. Jane Tucker presented a poster on sediment oxygen demand and nitrogen flux in Boston Harbor at the seventh annual Boston Harbor/Massachusetts Bay symposium in February. Both Jane and Anne Giblin discussed their work at the Day of Science for Woods Hole Oceanographic Institution (WHOI) Associates in September. Anne participated in a public forum on the proposed Massachusetts Bay sewer outfall in September, sponsored by the Metropolitan Area Planning Council, as well as a panel discussion for the Massachusetts Society of Professional Engineers in October. Jane gave a short talk at a cooperative research planning meeting on the effects of nutrient loading in Boston Harbor and Massachusetts Bay, held at WHOI's Coastal Research Center in December with scientists from WHOI and from the Narragansett office of the EPA.

Jerry Melillo presented a number of talks during the year on global change topics, including one at the EPA laboratory in Athens, Georgia, and another at the National Research Council (NRC) of the National Academy of Sciences (NAS).

John Hobbie attended a meeting in March at the Swedish Royal Academy of Sciences in Stockholm as a consultant on environmental research in Sweden.

Bill Peterjohn, Mark Castro

Brian Fry began a four-month trip around the world with a series of lectures in Japan during September. He spoke on the use of stable isotopes in ecosystem studies at the International Symposium on Stable Isotopes in the Biosphere, held in Tokyo, and at Kyoto University. He also discussed recent advances in the analysis of dissolved organic carbon at the Meteorological Institute in Tsukuba City and at a workshop on stable isotopes in field sciences in Otsu.

Brian also lectured at Indiana University in February on the circulation and metabolism of dissolved organic carbon in estuaries.

Marty Downs presented a paper on the immobilization and mineralization of nitrate fertilizer by decomposing litter in a mixed deciduous/evergreen forest at the annual meeting of the Soil Science Society of America in Minneapolis in November.

Knute Nadelhoffer spoke at the same meeting on using stable isotopes to trace the fate of nitrogen additions to forest ecosystems.

Bruce Peterson gave a seminar at Lehigh University on dissolved organic matter cycles in estuaries in January. He also spoke at the University of British Columbia on fertilization experiments in an arctic tundra river and at the University of Rhode Island's Graduate School of Oceanography on the topic of dissolved organic carbon in estuaries.

Loretta Johnson gave a talk during December at the University of Alberta in Edmonton. Her topic was "Collaborative Research on Canadian Peatlands: Present Status and Future Initiatives."

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 NRC and of the NAS/NRC panel responsible for reviewing the EPA's Environmental Monitoring and Assessment Program (EMAP). He is president of the Association of Ecosystem Research Centers (AERC) and serves on the boards of the Arctic Research Consortium (ARCUS) and The Lloyd Foundation for Environmental Studies in South Dartmouth, Massachusetts.

John is chairman of the steering committee for the Land-Atmosphere-Ice Interactions (LAI) section of NSF's Arctic Systems Science (ARCSS) program. Gus Shaver also served on this committee.

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 (GCET) and International Global Atmospheric Chemistry (IGAC). He is chairman of the U.S. Committee for SCOPE and a member of both the NAS Global Change Committee 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 and on the steering committee of the Northeast Center of the National Institute of Global Environmental Change.

Jerry serves on the global change advisory committee of the Electric Power Research Institute (EPRI). Gus Shaver is a member of the review panel for EPRI's carbon dioxide program.

Gus served as a member of the Cedar Creek LTER review team during 1992. He also serves on the editorial board of Ecology and Ecological Monographs and on the advisory committee for the Department of Energy's Program for Ecosystem Research.

Ecosystems Center staff members serve regularly on a variety of NSF review panels. Gus Shaver is currently on the Ecosystem Studies panel, and Chuck Hopkinson served as a member of the Ocean Sciences Biological Oceanography panel.
Chuck also serves on the steering committee for an NSF-sponsored working group charged with resolving the problem of measuring dissolved organic matter (DOM) in the ocean. He is a member of the South Carolina Sea Grant Consortium’s Marine Environmental Research Advisory Panel and the national panel charged with reviewing the Florida Sea Grant College program.

Knute Nadelhoffer served as panel manager for the U.S. Department of Agriculture’s Forest, Rangeland and Crop Ecosystems Program.

Linda Deegan is a member and past president of the board of the Southern New England chapter of the American Fisheries Society. She also serves on the selection committee for the Outstanding Contribution to Fisheries Science in New England Award.

Ed Rastetter is a member of 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 also serves on the executive committee of NEERS and on the advisory committee for WHOI’s Coastal Research Center.

Kathy Newkirk serves on the New Hampshire membership committee of the American Society of Agronomy. She is also a member of the Association of Women Soil Scientists and serves on the association’s current issues committee.

**MBL Boards and Committees**

Ecosystems Center staff members also serve on a number of MBL boards and committees. Jerry Melillo is a trustee of the laboratory and a member of its executive committee. He was also a member of the search committee for the laboratory’s new director. John Hobbie is a member of MBL’s Scientific Advisory Council and chairman of the laboratory’s safety committee. Knute Nadelhoffer serves as a representative to the laboratory’s Council of Year-Round Scientists. Chuck Hopkinson is a member of the personnel search committee.

Ed Rastetter is chairman of the laboratory’s computer needs committee. Paul Steudler serves on the safety and research services committees. Anne Giblin is a member of the fellowship committee and diving control board. Gus Shaver is on the audit committee. Linda Deegan is a member of the marine resources committee. Jane Tucker serves on the Hay Committee, an employee group that decides upon job classifications at the MBL, and on the diving control board. John Helfrich serves on the laboratory’s staff council.

Chuck and Knute are co-chairman of The Ecosystems Center’s research committee. Paul serves on the center’s facilities committee. Jane was appointed coordinator for benthic research this year.
Staff of The Ecosystems Center

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Jerry M. Melillo, Co-Director
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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
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Elisabeth Schwarzman
M.S. Stanford University

Beth Schwarzman
Martha Jesse
Andy Ricca
Dan Martin, Nancy Parmentier
Seminars at The Ecosystems Center During 1992

January
14  Sallie Chisholm, Massachusetts Institute of Technology, “Prochlorophytes, picoplankton and ponderings about phytoplankton proportions”
21  Joe Yavitt, Cornell University, “Methane emissions from Northern peat lands”

February
4   Eric Pallant, Brown University, “Why LISA grows more corn roots”
11  Dan Campbell, University of Rhode Island, EPA, “Ecosystem integrity and health: Useful concepts for environmental management”
18  Tim Eglinton, Woods Hole Oceanographic Institution, “Stable carbon isotopic studies of macromolecular organic matter in sediments”
25  Kate Lajtha, Department of Biology, Boston University, “Ecophysiology of the saguaro cactus in the Sonoran desert of Mexico”

March
3   Brian Fy, The Ecosystems Center, “DO18C - A long road to a new method”
10  Jener Leite de Moraes, University of São Paulo, Brazil, “Carbon and nitrogen content of Amazon Basin soils”
17  Ned Fetcher, Harvard Forest, “Physiological ecology of seedling and tropical trees in differing light regimes”
24  Mike Pace, New York Botanical Garden, Institute of Ecosystem Studies, “Do trophic cascades affect microbial food webs?”
31  Bob Jeffries, Department of Botany, University of Toronto (joint MBL-BUMP speaker), “Nitrogen budget of a grazed arctic salt marsh”

April
7   Joe Montoya, Harvard University, “Stable isotopes of nitrogen in planktonic ecosystems”
14  Michael Miller, University of Cincinnati, “Biogeography of diatom communities in Ecuadorian lakes: Do lakes operate as islands?”
21  Bill Healy, U.S. Forest Service, University of Massachusetts-Amherst, “Importance of grazing in New England forests”

May
5   Brigitte Feigl de Paula Eduardo, University of São Paulo, Brazil, “Microbial biomass across a forest to pasture chronosequence”

September
22  Andrew Solow, Woods Hole Oceanographic Institution, “Bootstrapping ecological data”
29  Andrew Etherall, Institute of Hydrology, Oxfordshire, United Kingdom, “Impact of climate change on ecosystems”
29  Bill Sloan, Institute of Hydrology, Oxfordshire, United Kingdom, “Modeling nitrate in stream waters”

October
6   Sam Goward, University of Maryland, “Remote sensing in global scale ecology”
20  David Stonehill, Marine Biological Laboratory, “What is available on-line at the MBL/WHOI library and how to access it”
28  William Schlesinger, Duke University, “A global budget for atmospheric ammonia”

November
3   David McGuire, The Ecosystems Center, “Investigating the potential effects of global change on terrestrial net primary productivity with the Terrestrial Ecosystem Model (TEM)”
10  Bill Curry, University of New Hampshire, “Base cation biogeochemical dynamics in a Virginia montane watershed”
17  Jack Kelly, Battelle New England, “Boston Harbor’s nutrient coupling with Massachusetts Bay”
24  William Peterjohn, The Ecosystems Center, “The Harvard Forest soil warming experiment”

December
1   Steve Pacala, Princeton University, “Models of forest dynamics”
8   Anne Giblin, The Ecosystems Center, “Nutrient cycling in sediments from Boston Harbor and Massachusetts Bay: The importance of denitrification”
16  Mike Binford, Harvard University, “Six thousand years of Tiwanaku agroecosystems”
Publications of The Ecosystems Center for 1992


Neill, C. Life history and population dynamics of shoots of whitetop (*Scolochloa festucacea*) under different levels of flooding and nutrient supply. *Aquatic Botany* 42:241-252.


In Press


Bowden, R. D., M. S. Castro, J. M. Melillo, P. A. Steudler and J. D. Aber. Fluxes of greenhouse gases between soils and the atmosphere in a temperate forest following a simulated hurricane blowdown. *Biogeochemistry*.


Deegan, L. A. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Canadian Journal of Fisheries and Aquatic Sciences*. 50:


Fry, B. Adding ³¹⁵N to ecosystem experiments. *In: E. Wada and B. Fry (eds.), Stable Isotopes in Biological Systems*.


Hobbie, J. E. Arctic ecosystem response to change. *In: Arctic Research of the United States*.


**Chuck Hopkinson**


Van Dover, C. L. and B. Fry. Microbial sources of nutrition for the fauna of hydrothermal vents. Limnology and Oceanography.


Research Grants in Effect During 1992

I. National Science Foundation

NSF-BSR-8702328
"An LTER program for the Alaskan Arctic"
September 1987 - August 1992
Investigators: Hobbie, Deegan, Fry, Giblin, Nadelhoffer, 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, Nadelhoffer, Shaver
$1,364,395

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, Nadelhoffer, Steudler
$496,583

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: Nadelhoffer
$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: Hopkinson, Peterson
$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, Rastetter, Giblin, Nadelhoffer
$1,212,108

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

NSF-DEB-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-DEB-9209151
"The origin and biological utilization of dissolved organic carbon in riverine saltmarsh estuaries"
August 1992 - August 1993
Investigators: Peterson, Fry
$175,000

NSF-DEB-9211775
"The Arctic LTER project: Terrestrial and freshwater research on ecological controls"
Investigators: Hobbie, Giblin, Deegan, Peterson, Shaver
$3,913,750

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

NSF-DPP-9214961
"Land-water-atmosphere transfer of trace gases"
September 1992 - August 1993
Investigator: Hobbie
$117,191

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

NSF-OCE-9214461
"Plum Island Sound Comparative Ecosystem Study (PISCES): Effects of land use and organic matter-nutrient interactions on estuarine trophic dynamics"
September 1992 - August 1996
Investigators: Hopkinson, Hobbie, Deegan, Giblin, Fry
1,600,000

NSF-OCE-9216897
"Sources of DOC in the Equatorial Pacific Ocean"
October 1992 - September 1993
Investigator: Fry
$35,000
II. Department of Energy
DE-FG02-92ER61438
“Origins and fates of dissolved organic matter along the New England continental margin”
June 1992 - June 1995
Investigators: Fry, Hopkins
$778,000
Northeast Regional Center of NIGEC
“Atmosphere-biosphere feedback mechanisms in forest ecosystems”
October 1990 - June 1993
Investigators: Melillo, Steudler
$417,020
U.S. DOE
“Biological controls on soil organic matter quality and quantity” a project of the New England Regional Center of the National Institute for Global Environmental Change (NIGEC)
(subcontract from Harvard University)
April 1992 - April 1993
Investigator: Nadelhoffer
$19,000
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, 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
$130,000

IV. National Oceanic and Atmospheric Administration
Estuarine Reserve Program
“Effect of macroalgae manipulation on the fish community in an eelgrass habitat”
July 1992 - June 1993
Investigator: Deegan
$49,962
NOAA Sea Grant, R/P-47
“Benthic processing of sewage additions: Role in anoxia and nitrogen cycling”
August 1992 - July 1993
Investigators: Giblin, Hopkinson
$146,000

V. United States Environmental Protection Agency
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
“Controls on radiatively active trace gases in tundra and taiga ecosystems” (subcontract from the University of Alaska)
October 1990 - September 1993
Investigator: Nadelhoffer
$123,512

VI. Miscellaneous
Massachusetts Water Resources Authority, MWRA/SAIC
“Seasonal determination of sediment oxygen demand and nutrient flux in Boston Harbor and Massachusetts Bay”
July 1992 - December 1992
Investigator: Giblin
$84,287
Massachusetts Water Resources Research Center
“Non-point sources of dissolved organic matter to the coastal zone: An assessment in Essex County, Massachusetts”
July 1991 - June 1993
Investigator: Hopkinson
$23,954
The Clowes Fund
“Ecological modeling workshops”
June 1989 - June 1992
Investigators: Staff
$105,000
Texaco Foundation
“Texaco fellowships in environmental research”
June 1990 - June 1993
Investigators: Melillo, Steudler
$180,000
Exxon Corporation
“Education and research for Latin American and Caribbean scientists”
August 1989 - November 1993
Investigators: Melillo, Steudler
$120,000
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 1993
Investigators: Hobbie, Giblin
$25,000

Pat O’Hara, Debbie Repert
Sources of Support for Research and Education

The annual operating budget of The Ecosystems Center for 1992 increased by $704,500 over the budget of the previous year to a total of $4,820,000. Some 87% of the income of the center comes from grants for basic research from government agencies. The other 13%, roughly $626,000, comes from gifts and grants from private foundations, corporations and individuals as well as institutional support for administration and income from the center's reserve and endowment funds.

These non-governmental funds provide flexibility for the development of new research projects, public policy activities and educational programs. More information about sources of support appears in the "Introduction to The Ecosystems Center" and in "Research Grants in Effect in 1992."

The combined total of the center’s reserve fund and endowment is approximately $4,660,000, an increase of 16.5% over the 1991 total of $4,000,000. Income from these sources helps defray costs of operations, writing proposals, advising government agencies and the center's seminar program. During 1992 the center received a grant of $200,000 from The Clowes Fund to help provide endowment income for young investigators who wish to initiate new and untried research projects.

Over the years since it was founded in 1975, the center has received support from these foundations and corporations:

Atlantic Richfield Foundation
Robert Sterling Clark Foundation, Inc.
The Clowes Fund, Inc.
Charles E. Culpeper Foundation, Inc.
Arthur Vining Davis Foundations
Henry L. and Grace Doherty Charitable Foundation, Inc.
Exxon Corporation
Max C. Fleischmann Foundation
The Ford Foundation
General Electric Foundation
Grace Foundation, Inc.
The Grass Foundation
Charles Hayden Foundation
International Business Machines Foundation
Charles A. Lindbergh Fund
The Andrew W. Mellon Foundation
NL Industries Foundation, Inc.
Rockefeller Brothers Fund
The Rockefeller Foundation
Rowland Foundation, Inc.
Scherman Foundation, Inc.
Surdna Foundation, Inc.
Texaco Foundation