On the cover: Chronic nitrogen inputs lead to conifer forest decline in the nitrogen saturation experiment, which began 15 years ago at the Harvard Forest. Foliar biomass has been greatly reduced in the pine stand receiving high-N additions (bottom) compared with the control (top). Photographs by D.R. Foster.
# Long Term Ecological Research at Harvard Forest

March 29, 2004

Audrey Barker Plotkin, Julie S. Pallant and Linda Hampson, Editors

## Long Term Ecological Research at Harvard Forest

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## Harvard Forest Ecology Symposium

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LONG-TERM ECOLOGICAL RESEARCH AT HARVARD FOREST

Background and Framework for Long-Term Research

In 1907 Harvard University acquired nearly 3,000 acres of land in the central Massachusetts town of Petersham to establish the Harvard Forest as a center for research and education in forest ecology, conservation, and management. In the ensuing century of investigations, students, faculty, and visiting researchers came to rely heavily on accumulated and continuing historical studies as a complement to intensive field and laboratory work and as a source of insight into important processes that have shaped the land, its people, and its biota. By developing long-term studies of the past and present, we can uncover events and processes that are infrequent in occurrence, we can examine physical and biological processes that unfold over long periods of time, and we can sift through the many changes and factors that have operated in the landscape over time in order to identify those that are critical for interpreting modern conditions and dynamics (Figure 1, Table 1).

This long-term approach to ecological research was a central driver in the selection of research directions when we teamed together with colleagues from several Harvard departments, the University of New Hampshire, the Ecosystem Center at the Marine Biological Laboratory, and the University of Massachusetts in 1988 to form the Harvard Forest Long Term Ecological Research (LTER) program. In particular, we applied our understanding of the history of the land, modern forest dynamics, and projections for future changes in the regional and global environment to select a suite of important disturbances, stresses, and forest ecosystem processes to investigate in detail. The broad objective of these studies was to develop information and approaches that will answer fundamental ecological questions and to generate data and perspectives that have broad application to major environmental and conservation issues.

A sketch of the history of New England's land and people highlights the major changes that shape the present landscape and the key objectives of our investigations.

Table 1. Design of the Harvard Forest LTER Program

<table>
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<tr>
<th>Research Approaches</th>
<th>Disturbances, Stresses, and Environmental Processes Investigated</th>
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</thead>
<tbody>
<tr>
<td>1. Reconstruction of ecosystem dynamics using paleoecology, historical ecology, and modeling to evaluate long-term trends, to study infrequent processes, and to understand the development of modern conditions.</td>
<td>1. Climate change</td>
</tr>
<tr>
<td>2. Measurement of modern ecosystem structure, composition, processes, and dynamics on permanent plots, through remote sensing, and through eddy flux measurements of atmosphere-biosphere exchanges to define current conditions and rates.</td>
<td>2. Hurricane and lesser windstorms</td>
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<td>3. Experimental manipulations of ecosystems and controlled environment studies on individual plants and populations to evaluate and compare patterns of response and to collect integrated measurements on multiple processes.</td>
<td>3. Fire</td>
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<td>4. Integration through modeling, comparative studies, regular meetings, annual symposia, and synthetic publications.</td>
<td>4. Native and introduced pathogens</td>
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<tr>
<td>5. Application to ecological theory, conservation biology, environmental policy, and forest management.</td>
<td>5. Land-use: aboriginal, Colonial, and current</td>
</tr>
<tr>
<td>6. Changes in atmospheric chemistry and deposition.</td>
<td>6.</td>
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</tbody>
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Spatial Scales of Investigation

1. Site - 1 km - Harvard Forest
2. Landscape - 10 km - Petersham, MA
3. Sub-region - 100 km - Central Massachusetts
4. Region - 1000 km - New England and New York
5. Disturbances, Stresses, and Environmental Processes Investigated

Education Integrated with Research

1. Summer Research Program for Under-graduates and Graduate Students (15-20 students/yr)
2. Informal Education Program through the Fisher Museum (> 5,000 visitors/yr)
3. Graduate Programs through diverse institutions at the MS and PhD level (5-15/yr)
4. Bullard Fellowship Program for mid-career scientists (4-8/yr)
5. Conferences, Symposia and Workshops (> 1000 participants/yr)
Figure 1. Spatial scales of investigation in the Harvard Forest LTER program.
Overview of Environmental and Forest Dynamics in Central New England

The landscape of central New England has been highly dynamic over the past few thousand years as environmental factors that control forest structure, composition and ecosystem processes have changed continuously, though at variable rates (Figure 2; Foster and Zebryk 1993, Fuller et al. 1998). The broad-scale physiographic template has been relatively unaltered since the last glaciation shaped the gentle hill and valley topography and left a variable thickness of till and stratified deposits some 13,000 years ago. However, climate, on a century to millennial time frame, has undergone continual change in temperature, precipitation and their seasonal distribution. Even over the last century there exist annual variation, short-lived changes, and lengthy trends that are relevant to forested ecosystems, and the physical processes and biotic constituents that shape them (Aber et al. 1995).

Reconstruction of forest dynamics suggest that natural disturbance processes, ranging from frequent small events to infrequent large and catastrophic impacts have played an important role in structuring the pattern and processes of natural ecosystems across New England (Foster 1988a). Nearly 5000 years ago a remarkably abrupt and major decline in hemlock occurred throughout its range in New England and across the Northeast, presumably as a consequence of infestation from a novel pathogen. Over the subsequent 1000-year period forest ecosystems underwent pronounced changes as hemlock gradually recovered, although with considerable regional to local variation in the response and recovery patterns (Fuller et al. 1998). The historical record of major hurricane impacts every 75-100 years leads to speculation that infrequent catastrophic disruption by tropical storms may play an important role in structuring the forest vegetation of New England over long time periods (Figures 3 and 4; Boose et al. 1994, 2001). Given the propensity for such storms to weaken over land and to exhibit relatively constrained patterns of movement across New England, it is quite possible that pronounced regional gradients and specific landscape-scale patterns of historical impact may interact with broad-scale environmental and physiographic patterns in controlling vegetation structure and composition (Foster and Boose 1995). Long-term records and the ubiquitous presence of mound and pit topography in old forest stands suggest that finer-scale disturbances such as gap dynamics, downbursts and tornadoes have contributed more local patterning to forests over the ages. The relative role of these different types and scales of physical disturbance and their spatial distribution across the landscape and region are largely unknown.

Although infrequent, perhaps occurring as rarely as once every thousand years in some regions and forest types, or ten times as frequently in others, fire has played an uncertain and variable role in New England forests (Fuller et al. 1998, Parshall and Foster 2002). The topic of fire invariably introduces the role of humans, for it is in the purposeful use of fire that aboriginal people may have exerted a widespread, though subtle impact on natural vegetation. For the New England region the general patterns of aboriginal activity are well known: a highly variable geographic pattern with dense settlements on the coast, coastal islands, and along major river valleys and sharply lower population in upland areas; a dynamic history of changing cultural patterns, seasonal activities and density that varied with climate and major changes in forest composition that altered the availability of important food sources such as nut-bearing trees and wildlife; and the late introduction of maize agriculture within the past 1000 years (Mulholland 1984, 1988). Much speculation exists on how these geographic and temporal patterns of activity interacted with and altered the natural ecosystem patterns. In particular, the extent of forest clearance for agriculture and the role of fire in pre-European times remain a major issue.

Over the past 350 years since European settlement the rate of ecosystem change has accelerated and the landscape of New England has been transformed (Foster et al. 1998, Hall et al. 2002). Despite a steadily increasing human population, major cultural and technological shifts have led to a region-wide historical pattern of extensive deforestation through the mid to late 19th century followed by broad-scale abandonment of agriculture and massive natural reforestation (Figures 5 and 6). Vast areas of New
Figure 2. The temporal setting for long-term studies in New England in relation to important biotic, cultural, and environmental changes. Biotic (vegetation) change (top) is illustrated by the varying percentages of pollen of major plant taxa from Aino Pond in north central Massachusetts (Fuller et al. 1998). Major cultural changes (middle) highlight the shift from native hunting, gathering, and horticulture to European agriculture and industry. Climate dynamics (bottom) are depicted by the long-term change in Northern Hemisphere temperature over the past 1,000 years, as reconstructed from tree-ring records and other proxies (adapted from Crowley 2000, data archived at the World Data Center for Paleoclimatology, Boulder, Colorado, USA).
England that once supported scattered, cut-over woodlots in a matrix of fields and pastures are now covered with aggrading second-growth forest that ranges across 65-85% of the uplands. Excluding northern Maine, the new forests of the New England states bear much evidence of the agricultural past of pasture, cropland, and woodlot: stonewalls separating contrasting forest stands, old cellar holes and collapsed dams, and wood trails and dirt road remnants of colonial transportation networks. As the forest area and size have recovered regionally so have the native fauna and regional ecosystem processes (Motzkin et al. 1996, 1999, Compton et al. 1998, Compton and Boone 2000). In many ways the landscape of rural New England appears more natural than at any time since the 1700s. The major question that looms is: how has this massive land-use disturbance altered the natural forest pattern and process and what legacies has it left in the new forest landscape?

In recent decades the forests and environment of New England have been exposed to more novel types of anthropogenic stress. A series of introduced pathogens - chestnut blight, Dutch elm disease, gypsy moth, beech bark disease, and hemlock woolly adelgid - has selectively weakened, defoliated or decimated major tree species across the region (Figure 7; Orwig 2002). Industrialization has led to pronounced changes in the earth's atmosphere that are leading to increased, though geographically variable, deposition of nitrogen (a major limiting nutrient in most terrestrial ecosystems) and sulphur in forms that acidify precipitation as well as the ecosystems that they impact (Figure 8; Aber et al. 1993, 1997). While photochemical reactions in the upper atmosphere deplete the tropospheric ozone layer that shields the earth from ultraviolet radiation, stagnant circulation patterns during the summer growing season bring damaging ozone episodes up the east coast to interior New England forests (Goulden et al. 1996; Munger et al. 1996). Increases in major greenhouse trace gases - CO₂, CH₄, and N₂O may be leading to a regional annual increase of temperature of 3-4°C within the next century. Meanwhile, the increase in CO₂ (as well as N and O₃) may be having subtle, though important, consequences on plant performance and ecosystem processes (Bazzaz and Miao 1993; Bazzaz et al. 1996). The interaction and comparative impact of these novel stresses with historically important disturbance processes is a major issue for ecologists and concern for natural resource managers.

As we seek to understand the current structure, composition, and process of forest ecosystems in central New England it is essential that we develop a perspective that incorporates the historically important as well as currently operative environmental factors that control these ecosystems (Foster et al. 1992, 1996). It is also important to frame questions and approaches that are regionally and societally relevant and that have general applicability to the understanding of terrestrial forest ecosystems.

 Broad Ecological Questions Concerning New England Forests

Our brief historical overview highlights many changes in the physical, biotic, and human environment of New England that have initiated a range of forest dynamics and have set the vegetation and landscape on a long-term trajectory. This overview also raises broad questions that drive our research as we seek to understand, conserve, and manage the modern landscape and anticipate future changes. Not surprisingly, these questions address fundamental issues relevant to many natural ecosystems worldwide.

1. How does the array of environmental factors and disturbance processes interact to shape forest ecosystems over time? The preceding section identified major uncertainties concerning the ways in which climate change, natural disturbance, and human activities have operated at local to regional scales through time. Of specific interest are details of the natural disturbance regimes, especially variations in wind, pathogens, and fire and the way in which these have interacted with prehistoric and historical human activity and environmental change.

2. What are the contrasting effects of natural, physical disturbance versus novel, anthropogenic stress on the function of forest ecosystems? Increasingly, forest ecosystems are exposed to chemical and climatic stresses that are qualitatively different from the types of impacts that forests have experienced for millennia. Recognizing that forest species evolved within a context of natural disturbance and environmental
Figure 3. Paths of major hurricanes that have affected New England and the Harvard Forest during the historical period.

Figure 4. Forests damaged by the 1938 Hurricane were also changed by the massive salvage effort that followed. Photograph from the Harvard Forest Archives.
Figure 5. Forest cover and population trends for New England.

Figure 6. Change in forest cover in Massachusetts from 1830 to 1999.
Figure 7. Hemlock woolly adelgid infestation and the range distribution of hemlock across the eastern United States (USDA 2002).

Figure 8. Geographic pattern of atmospheric nitrogen deposition across New England. Concentrations of nitrogen are strongly related to westerly air flow from major sources of human production of nitrogen elevation which controls precipitation that contains nitrogen compounds (Ollinger et al. 1995).

N Deposition (kg ha$^{-1}$ yr$^{-1}$)
change, it is important to assess whether forests retain the same degree of control over ecosystem processes (for example, nutrient cycling, hydrology, and forest growth) under these novel conditions as they do under historically important stresses. Specifically, we are interested in contrasting the relative effects of physical disturbance such as hurricane with important new stresses such as nitrogen additions and rapid climate change.

3. What changes in forest patterns and processes were generated by the history of intensive land use since European settlement, and how persistent are the physical and biological legacies of this historical disturbance in New England's reforested landscape? Large areas of northwestern Europe, Latin America, and eastern North America have experienced or are currently undergoing landscape transformations analogous to the forest-deforestation-reforestation history of New England, and thus lessons from our region should have general relevance. Major questions remain concerning the initial effects of colonial land-use activity, the ability of forest ecosystems to return to predisturbance conditions, and the legacy of historical changes on modern forest characteristics. For example, is the history of sites that were in agriculture 150 years ago reflected in the modern forest composition, soils and fertility, or the way that the forest will respond to the next hurricane or to acid rain?

4. What application do answers to these questions have for environmental policy issues such as (a) designing effective local and regional conservation strategies, (b) anticipating forest ecosystem response to modern stresses and disturbances, and (c) developing global strategies to mitigate future climate change? As we develop an improved understanding of modern forest ecosystems and their history of change, we can bring this information to bear on fundamental ecological questions concerning the patterns and processes of natural ecosystem organization and dynamics. We can also assist in the application of this information to education and the management of our natural environment and resources.

Design of the Harvard Forest Long-Term Ecological Research Program

In order to address the broad ecological questions raised above, our research effort has been organized to integrate studies across disciplines, scientific approaches, and a range of spatial and temporal scales. By augmenting the lengthy record of ecosystem change that had developed over nearly a century of study at the Harvard Forest, we have selected historically important and relevant processes for investigation. We have also expanded existing programs in order to make education and public outreach a major goal of our program.

We use a suite of scientific approaches in order to identify important ecological processes to create a long-term series of measurements and to assess ecosystem response and dynamics.

Ecological history provides information on the range of environmental conditions and types of natural and human disturbance processes that have been historically important in a landscape. This information identifies processes that are critical to study in order to understand ecosystem structure and function, and it contributes to our understanding of the relative role of historical factors versus environmental factors in controlling modern conditions. In addition, many key ecological processes, such as succession, ecosystem development, large disturbances, species invasion, and ecosystem response to environmental change, operate on decadal to millennia timescales or with such great temporal variability that they are difficult or impossible to measure through conventional studies. Historical techniques enable the evaluation of such processes and allow these observations to be placed within the context of long-term trends and cycles of environmental change.

Experimental field manipulations allow us to evaluate infrequent though historically important processes as well as to anticipate future ecosystem response to predicted changes in climate or chemical stresses. At the Harvard Forest, we have focused large experiments on a subset of important though contrasting disturbances and stresses, including simulation of windthrow from an intense hurricane, timber harvesting, chronic nitrogen amendments to
simulate enhanced deposition of nitrogen, soil warming as a component of climate change, and alteration of organic matter inputs to soils to examine basic soil processes linked to carbon and nitrogen dynamics. In the case of historically important processes such as hurricanes and forest logging, results from the experimental manipulations are compared directly with long-term studies of "natural experiments," such as the 1938 hurricane or historical logging that occurred throughout central New England. Many of the experiments are compared with parallel studies in different ecosystems. For example, the nitrogen saturation experiment has counterparts at the Bear Brooks watershed in Maine maintained by the U.S. Forest Service and in the enhanced deposition of nitrogen that is occurring at high elevations in New England and in central Europe; the soil warming experiment has been replicated in the subarctic region at the Abisko Research Station in northern Sweden; organic matter manipulation experiments have been undertaken at the University of Wisconsin and other sites within the U.S. LTER network; and results from the experimental hurricane have been compared with those from natural events in many temperate and tropical forests. In all cases, the integrated measurements of ecosystem structure and pattern enable comparison among these important manipulations.

Long-term measurements of ecosystem patterns and processes in a range of natural forests carry forward observations of current conditions and results from reconstructive studies. In particular, measurements continued over decades to assess seasonal and interannual variation, long-term trends and trajectories, and ecosystem function under highly varied sets of conditions.

Table 2. Spatial Scales and Research Approaches of Harvard Forest Studies.

<table>
<thead>
<tr>
<th>REGION</th>
<th>SUB-REGION</th>
<th>LANDSCAPE</th>
<th>SITE</th>
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<tbody>
<tr>
<td>Area Size</td>
<td>New England</td>
<td>C. Massachusetts</td>
<td>Petersham</td>
</tr>
<tr>
<td>Elevation 0 – 1870 m</td>
<td>1000 km</td>
<td>100 km</td>
<td>10 km</td>
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<tr>
<td>RECONSTRUCTION</td>
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<td>Paleoeocology</td>
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<td>Archaeology</td>
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<td>History</td>
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<td>Dendrochronology</td>
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<td>Hurricane Modeling</td>
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<td>Ecosystem Modeling</td>
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<td>MEASUREMENT</td>
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<td>Vegetation Surveys</td>
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<td>Soil Surveys</td>
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<td>Fauna/Flora</td>
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<td>Remote Sensing</td>
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<td>Atmosphere-Biosphere Exchange</td>
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<td>EXPERIMENTAL MANIPULATION</td>
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<td>Hurricane Pulldown</td>
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<td>Nitrogen Saturation</td>
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<td>Soil Warming</td>
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<td>Organic Matter</td>
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<td>Controlled Environment</td>
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<td>Hemlock Removal</td>
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<tr>
<td>APPLICATION</td>
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<td>Atmospheric Deposition</td>
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<td>Water Management</td>
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<td>Education</td>
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Many important processes, including natural and human disturbance, wildlife movement, and hydrologic flows, occur at a landscape scale where physiography, slope position, vegetation structure, and soil variation interact to form complex patterns. In central New England, the area of an individual town (often approximately 10 by 10 kilometers) captures substantial landscape variation of the characteristic hill and valley topography. Consequently, the town of Petersham, Massachusetts, serves as one focus for many landscape studies because it includes the main tracts of the Harvard Forest and represents a typical rural village in the New England uplands. Given the politically independent structure of New England town governments, much of the geographical, social, and environmental data relevant to ecological studies are collected or aggregated by public agencies at a town level, making this political unit a particularly convenient scale of study.

To place site- and landscape-level studies in a broader context and to examine variation in environmental, social, and biotic processes, we conduct a considerable amount of research at the subregional scale (for example, central Massachusetts, Cape Cod and the Islands, the White Mountains of New Hampshire, the Connecticut Valley), and the regional scale of New England, oftentimes including adjacent New York. Selection of these areas is based on ecological, cultural, and pragmatic considerations. For example, the central Massachusetts subregion (approximately 5,000 square kilometers) extends 100 kilometers east from the Connecticut Valley Lowland through the Central Uplands physiographic region to the Eastern Lowlands west of Boston, and 50 kilometers south from the New Hampshire border approximately halfway to the Connecticut border. Petersham and the Harvard Forest lie directly in the center of this diverse subregion, which encompasses a wide range of the physical and biological variation in central New England, as well as a substantial amount of the cultural variation that has occurred from Indian to modern times. The ability to place intensive studies within the context of these major cultural and environmental gradients is extremely useful for interpreting the generality of results and

Permanent plots and repeated sampling of forest stands at five- to ten-year intervals continue long-term experiments and observations that were initiated in the early 1900s by the first faculty and students at the Harvard Forest. Remote sensing, using modern and historical aerial photographs or satellite images, increases the coverage of many measurements across two or more of our spatial scales of observation (for example, from plots in a forest to the landscape or region) and over many decades. Control areas, which are the undisturbed but monitored parts of our experimental manipulations, provide baseline measurements that may be linked with other data sets, such as the studies of atmosphere-biosphere exchange at our Environmental Measurement Station. The coupling of retrospective historical studies and long-term measurements of intact and experimentally manipulated ecosystems provides an integrated assessment of ecosystem dynamics and function under a range of historical, modern, and simulated conditions.

Harvard Forest research operates at four primary spatial scales of investigation: site (approximately 1 kilometer), landscape (approximately 10 kilometers), subregion (approximately 100 kilometers), and region (approximately 1,000 kilometers) (Figure 1, Table 2). Intensive site studies at the scale of individual organisms, forests, or sample plots represent the heart of our long-term effort. Most of our studies at this scale occur on Harvard Forest land (approximately 1,200 hectares) in central Massachusetts where varied vegetation, site conditions, and history, along with nearly 100 years of study, provide an ideal setting for long-term measurements and experiments (Figure 9). Infrastructure improvements, such as access to electrical and telecommunications cables at major experiments, erection of a series of canopy access and environmental measurement towers, the use of mobile lifts to reach into the crowns of mature trees, and surveyed grid points, enable diverse studies. Geographic information system-based data management systems allow field sampling to be integrated with other sources of information such as low-elevation aerial photography, satellite imagery, radiotelemetry, historical surveys, and vegetation maps.
Figure 9. Major study sites at the Harvard Forest, Petersham, Massachusetts.
for understanding the broadscale controls over major ecological processes. On the practical side, this subregion consists of fifty townships in four counties of one state, which presents a manageable, though considerable, challenge for the collection and archiving of archaeological, historical, environmental, and biological data. Information for this region comes in three primary forms – continuous spatial coverage (for example, elevation, land-cover maps, and remote sensing imagery), township-level data (for example, population, agricultural, and forestry statistics), or networks of site-specific data (for example, sample plots, archaeological sites, and intensive measurement locations).

Considerably greater variation in environmental and cultural conditions occurs across the New England region, and the dynamics and effects of many of the broadscale disturbances and anthropogenic stresses can be understood only at this scale. In order to evaluate processes that are relevant at the regional scale, we conducted select studies utilizing diverse historical, modern, and modeling approaches. These studies yield data that may be continuous, aggregated at the county scale, or site specific. Importantly, these studies also enable us to see how well our approaches and results translate to other areas.

The research approach followed by the Harvard Forest LTER program is a continuation of the long-standing approach to understanding the New England landscape that Harvard Forest researchers have used for nearly a century. We use historical studies to understand the development of modern forests and to study infrequent and variable events and slow processes; we integrate our understanding of modern measurements and experiments with results from retrospective studies; we emphasize long-term experiments with an informative and secure data management structure; and we attempt to synthesize the results of all of these studies such that they address fundamental ecological questions and provide insights into societally relevant management issues.

Education Integrated with Research

Interdisciplinary ecological research programs based at established field institutions provide much more than insights into important scientific questions; they also afford the opportunity to train the next generation of scientists and to convey information to an interested public audience. Education thus forms an essential part of the HF LTER program, providing both a means for developing science and an outlet for disseminating it. Students are directly integrated into our ecological studies. A summer research program brings 25-35 undergraduates and recent graduates to the Forest to work on research projects, to undertake independent studies, and to learn how science is conducted by large research groups representing diverse institutions and composed of faculty, staff and technical scientists, post-doctoral associates, graduate students, and administrators. Graduate students from the MS and PhD programs of many northeastern universities pursue thesis studies as part of this effort and the Bullard Fellowship Program for Forest Research at Harvard Forest annually enables 4-8 mid-career faculty and professionals from around the world to interact with LTER researchers. Local K-12 classes also learn about ecological research through participation in the LTER Schoolyard program. Finally, permanent exhibits, scientific poster displays, and audio-visual programs at the Fisher Museum expand on research results and inform more than 5000 visitors annually about the natural history and management of New England forests.

National Institute for Global Environmental Change (NIGEC) Northeast Regional Center

The National Institute for Global Environmental Change is a funded activity of the U.S. Department of Energy. NIGEC focuses its attention at a regional level by dividing the U.S. into six separate regions in order to take into account geographical and geological diversity when researching the consequences of environmental change for the United States. Since the Institute's inception in 1990, its mission has been to assist the nation in its response to human-induced influence on the environment by pursuing
excellent research in the field of global climate change. The Northeast Region includes the states of Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island and Vermont.

The Northeast Regional Center (NERC) has pioneered multi-disciplinary, coordinated studies of representative forest ecosystems in the Northeast to quantify and understand the effects of forests on the atmosphere (especially greenhouse gases such as CO$_2$) and the effects of the atmosphere on forests (deposition of pollution and nutrients), both regionally and globally. The program emphasizes synthesis of long- and short-term observations, manipulations, ecological and historical studies, and modeling to address directly and quantitatively the main factors that regulate forest processes. The studies span time scales from transient changes in environmental conditions (hours) to climatic forcing and legacies of prior land use and disturbance (years, decades).

The strategic vision of the NERC emphasizes integrated research on ecological responses of forests to management, climatic change, and environmental stressors (air pollution, inputs of nutrients, heavy metals, and acids, invasive species such as the hemlock woolly adelgid). The main focus is on quantifying and understanding the structure, development, productivity and net uptake or release of CO$_2$ by forests of northeastern North America. An important supporting focus is on quantifying and understanding emissions and deposition of pollutants, greenhouse gases, and ozone-destroying chemicals in the region. NERC emphasizes interdisciplinary research with process studies and modeling integrated within a framework of unique, long-term quantitative observations and manipulations.

The goals of NERC are to (1) investigate carbon exchange of forest ecosystems, (2) study the effects of climate change, disturbance by pests, logging and severe weather, and air pollution on forest resources, (3) study of the effects of forests on regional air quality and climate, and (4) quantification of emission sources of greenhouse gases and ozone-destroying chemicals from the industrialized Northeast.

Long-term eddy flux observations at two sites, Harvard Forest (Petersham, MA) and Howland Forest (Howland, ME), provide the anchors for the program. These sites are the focus for a diverse set of manipulations (e.g., open-top chambers, logging, soil warming, and nutrient additions), ecological studies of forest development and invasive species, stable isotope measurements, analysis of meteorological and environmental observations, measurements of concentrations and deposition of air pollutants, modeling, and historical and palynological studies. They are the longest running of the continuous eddy flux measurements in the AmeriFlux network, and have served as testing grounds to resolve methodological issues in long-term flux measurements. These issues continue to be the subject of ongoing research.

NERC functions as a Science Team to bring these diverse disciplines together. Scientists supported by NERC communicate often and meet annually to review results and plan coordinated work. All data are required to be shared with NERC researchers soon after collection, at the annual meeting, and with the public through the NIGEC-NERC data archive (http://www-as.harvard.edu/data/data.html) and the AmeriFlux data archive (http://cdiac.esd.ornl.gov/programs/ameriflux/data2.htm). The policy of maximum data sharing is viewed as essential to success of the NERC strategic vision.

Site and Facilities

The 1200-hectare Harvard Forest in north-central Massachusetts (Figure 1) has been operated as a silvicultural and ecological research facility by Harvard University since 1907. The Forest lies in the New England Upland physiographic region, with moderate local relief ranging from 220 m to 410 m above sea level. A bedrock dominated by granite, gneiss, and schist is generally overlain by sandy-loam glacial till soils that are moderately to well drained, acidic, and average 3 meters in thickness. Local variations in parent materials, textures, alluvial and colluvial deposits, and slope produce poorly drained and excessively drained sites as well. The regional climate is cool temperate (July mean
20°C, January -7°C) and humid, with precipitation (annual mean 110 cm) distributed fairly evenly throughout the year.

The Forest lies in the Transition Hardwood-White Pine-Hemlock forest region. Dominant species include red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta*), white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*). On drier soils white oak (*Quercus alba*), black oak (*Q. velutina*), hickory (*Carya ovata*) and, formerly chestnut (*Castanea dentata*) increase. Cool, moist, but well-drained sites support a northern mixed forest of yellow birch (*Betula alleghaniensis*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), ash (*Fraxinus americana*), hemlock and white pine, whereas red spruce (*Picea rubens*), black spruce (*P. mariana*) and larch (*Larix laricina*) occupy oligotrophic peatlands. Approximately 7% of the Forest is occupied by plantations of diverse composition and age. Detailed stand records, including prior site history, and repeated growth measurements are available for each plantation and many natural stands. A well-developed network of woods roads provides good access to all areas in the Forest.

In addition to the three major tracts of land in Petersham (Prospect Hill, Tom Swamp and Slab City tracts), the Harvard Forest owns two smaller parcels in Petersham, the 28-ha Tall Timbers tract in Royalston, Massachusetts, the 40-ha Matthews tract in Hamilton, Massachusetts and the 10-ha Pisgah tract in Winchester, New Hampshire. The Pisgah tract, an old-growth stand blown down in the 1938 hurricane, is part of the 5000-ha Pisgah State Forest and is the site of much historical research and an active focus of LTER studies (Foster 1988a).

The Harvard Forest provides a complete base for research in forest, ecosystem and historical ecology and biosphere-atmosphere interactions. In the past decade, the Forest has overseen phenomenal growth in scientists, educators, students, collaborators, research and education programs, and laboratory, computing, archival, teaching and housing facilities.

Shaler Hall contains offices, seminar rooms, a 23,000 volume library, dining facilities for 40, laboratories for paleoecological, tree-ring, morphological, computational and GIS studies, and a complete herbarium of the local flora. The Torrey Laboratories include two research greenhouses, offices, and physiology and nutrient analysis laboratories with fume hoods, gas chromatograph, Lachat autoanalyzer, CN analyzer, nano pure water, balances, and drying ovens. The Archives (2200 sq ft) houses 100 years of data on the land and research, a sample archive with cold storage facilities, and air photo interpretation systems.

The woods crew and the forest manager are equipped for experimental manipulations, forestry operations, construction, and maintenance. Large equipment including a mobile canopy lift, back-hoe, bulldozer, tractor, crawler, dump truck, flat bed truck, pick-up and van, are stored in garages and in a 2400 sq ft pole shed. The staff operates a wood-working shop which serves as the center for building maintenance and a sawmill is operated seasonally.

The University owns five houses and eight apartments, which provide housing for staff, students and visiting scientists. The Fisher House provides accommodation for approximately 20 visiting scientists and students.

Fisher Museum houses the Harvard Forest Models, twenty-three dioramas portraying the history, ecology and management of central New England forests. The Gould Audio Visual Center and lecture hall with seating for one hundred persons is also on the first floor. On the second floor are exhibits related to forest ecology: root biology, soil science, plant/pathogen interactions, the effects of disturbance on vegetation, and the local history of land-use in Petersham.

**History of Research and Established Data Bases**

The Harvard Forest has a long and rich history in the study of forest ecosystems, vegetation history, and development (Whitney 1989; see "Publications of the Harvard Forest LTER," this volume). This research background provides baseline data for current studies at the Harvard Forest.

Beginning in 1907 studies at the Forest focussed on silviculture and forest production including mineral nutrition (Spaeth 1922, Mitchell and Chandler 1939) and early breeding experiments. By the 1930s research had expanded
to include studies of forest nitrogen economy (Gast 1936, 1937), forest dynamics and succession (Fisher 1928, 1933, Griffith et al. 1930), soil morphology, mycorrhizal fungi (Finn 1942) and microclimate (Rasche 1958). S. Spurr increased the local interest in remote sensing, catastrophic disturbance (Spurr 1956b), and micrometeorology (Spurr 1956a), whereas M. B. Davis (1958), H. Raup (1937, 1964) and others (Goodlett 1954, Stephens 1955, Hack and Goodlett 1960) created a strong background in historical ecology and disturbance processes (Stephens 1956, Henry and Swan 1974, Oliver and Stephens 1977, Hibbs 1979, 1982).

Within the past 25 years studies have focussed on organism-, community- and ecosystem- level research. Particular strengths have been in tree physiology (Zimmermann 1978, 1983, Holbrook and Zwieniecki 1999), plant development and architecture (Tomlinson 1983, 1987), forest microbiology (Torrey 1978, Tjepkema et al. 1981) and vegetation dynamics (Foster 1988a, 1988b). Research by investigators from the Marine Biological Laboratory Ecosystems Center (Melillo et al. 1983, Melillo and Aber 1984, Nadelhoffer et al. 1986, Steudler et al. 1986), the Woods Hole Research Center (Davidson et al. 2000), and University of New Hampshire (Aber et al. 1983, Aber et al. 1985) have provided a very strong ecosystem component. Integrated research among the many groups using the Forest has contributed to a strong interdisciplinary understanding of forest processes. Data from recent studies and further description of current research themes can be found at the Harvard Forest website: http://harvardforest.fas.harvard.edu/.
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Modeling the Impact of Hemlock Loss on New England Forests with the Ecosystem Demography Model

M. Albani and P. Moorcroft

The spread of the exotic hemlock woolly adelgid (Adelges tsugae, HWA) across the eastern United States is expected to have a substantial impact on New England's forests, due to both direct pathogen-induced mortality of hemlock and by associated pre-emptive and salvage logging operations. Since eastern hemlock is a dominant species in several forest ecosystems, it is expected to cause a cascade of biological, biogeochemical, and physical changes in the landscape. In this study, we use the Ecosystem Demography (ED) model, an individual-based vegetation model describing the growth, reproduction and mortality dynamics of a plant community coupled to biogeochemical models of the associated soil fluxes of carbon, water and nitrogen, to predict the impact of hemlock losses on the structure and function of New England forest ecosystems. The effects of HWA infestation are incorporated into ED as an additional mortality term on hemlock, which increases from 0 to 90% over a period of approximately ten years from the first arrival of the infestation. Simulations of the model at Harvard Forest show that, even in mixed forests where hemlock biomass represents around only 10% of the above ground biomass, the onset of hemlock mortality causes an immediate decline in Net Ecosystem Productivity (NEP Fig. 1). At the peak of infestation, NEP is reduced by 35% compared to non-infested stands, and is still 25% lower 20 years after initial infection. The long-term impact on the carbon cycle is due to the replacement of hemlock by hardwoods that have higher rates of biomass turnover. We are now modeling forest dynamics at 0.5-degree resolution for the whole of New England, to examine HWA impact on regional carbon fluxes. These regional simulations incorporate the historical expansion of the HWA as recorded at the county level by the US Forest Service, and its projected expansion in the next 50 years.

A Comparison of Methods for the Characterisation of the Edaphic Environments of Some CTFS-Asia Plots in Tropical Rain Forests

I.C. Baillie

Clarification of the relative contributions from the biotic processes, as encapsulated in the Neutral Theory, and abiotic niche constraints in explaining the complexity and diversity of tropical forests requires, amongst other things, the detailed characterization of the forests’ edaphic environments.

The Center for Tropical Forest Studies has coordinated the establishment of a network of large (up to 52 ha) plots at 17 sites throughout the tropical lowland forest biome. The data collection on all of these follows strict guidelines, in order to avoid the methodological variability that has complicated previous attempts at pantropical comparisons and syntheses.

Until recently there was a considerable mismatch in the data for the CTFS plot between the massive, detailed and dynamic characterization of the biotic components of the ecosystems and the generalized categorization of their physical environments. This will be remedied substantially by the recently developed protocol for the standardized sampling and analysis of the soils of CTFS plots. Because of the problems of inter-lab variation, the Protocol stipulates that the soils can be described and extracted in-country but that the extracts are all assayed in a single laboratory, at Cornell University.

This study examines two aspects of the Protocol’s choice of methods. Firstly, only the top 10 cm is sampled. This is the zone of highest nutrient uptake by root and mycorrhizal systems. However, it is also the zone of highest temporal and spatial variability in nutrient contents. The second is the choice of the Mehlich III solution as the extractant. This is a moderate extractant, and removes higher quantities of P, and probably also of the main nutrient cations, than the neutral salts or weak acid extractants used for conventional determinations of available P and exchangeable
The forthcoming data will facilitate the comparison of results obtained by different analytical techniques. In particular it will enable older data to be compared with those obtained under the new Protocol. The site characterizations obtained by the different analyses will be compared with the botanical zonations of the plots. It is anticipated that no single method will be wholly effective in elucidating edaphic effects on forest. Rather results indicating apparent effects will need to be integrated. The data from topsoils and the weaker extracts are better indicators of the pool of nutrients in circulation through the vegetation-litter-topsoil organic matter. Data from subsoils and stronger acid-based extractants better indicate the size of the nutrient reserves in the mineral components that may be available to top up the biotic cycle.

During the fieldwork on CTFS plots in Sarawak, Thailand and Sri Lanka, I am conducting a subsidiary study of the occurrence and importance of throughflow in different

Figure 1. ED simulation of the impact of hemlock woolly adelgid infestation on the annual Net Ecosystem Productivity (NEP) of a mixed hardwood forest (10% hemlock by aboveground biomass) on medium soils in central Massachusetts.

M. Albani and P. Moorcroft
tropical forest systems. At Lambir a preliminary attempt at measurement was destroyed by the intensity of the throughflow. Different methods of measurement are being considered. For the present qualitative observations continue.

Establishment of the Hemlock Removal Manipulation Study

A. Barker Plotkin, A. Ellison, J. Butler, D.R. Foster, and D.A. Orwig

Hemlock decline in New England is caused by direct and indirect effects of invasion of the hemlock woolly adelgid. Direct damage from the insect is causing gradual mortality of hemlock, and widespread harvesting of hemlock in advance of mortality creates a contrasting disturbance. Although both processes affect thousands of acres of forest annually we have only a limited understanding of their effects on forest ecosystem function and productivity and the nature of the subsequent forest community. We anticipate that harvesting will yield different consequences than gradual mortality from the insect. Therefore we have designed an experiment to simulate the impact of both in order to contrast them. To simulate some of the effects of the adelgid (e.g., progressive mortality, retention of the wood on the site) we are girdling all hemlocks in a hemlock-dominated stand. In the adjacent area we are conducting a commercial harvesting of hemlock. Results from both experimental treatments will be compared to the changes observed in forests that are being infested by the adelgid, and can also be included in integrated analyses of a suite of large experiments that form a core component of the Harvard Forest LTER program.

We established eight large (0.8 ha) experimental plots at the Simes Tract of the Harvard Forest (Fig. 1). There are two replicates of the following treatments: hemlock girdling (to simulate many of the effects of HWA), hemlock commercial logging (to simulate the preemptive logging that is occurring in hemlock forests in our region), hemlock control (no treatment), and hardwood control (representing a possible future composition of post-hemlock forest). In 2005, treatments will be implemented on the entire 90m by 90m plot. The interior 30m by 30m is the focus of intensive measurements, whereas the surrounding 30m will act as a buffer. We are currently working to measure diameters, tag and map all the trees greater than 5 cm diameter in the plots. Results from the core 30m by 30m area of each plot confirm that hemlock dominates basal area and stem numbers in all hemlock plots, and hardwoods dominate the two hardwood control plots (Table 1). Basal area and stem density are within the observed range for these forest types. Black birch is common in the two hardwood control plots, which dominates many sites after hemlock mortality (Orwig and Foster 1998).

Numerous collaborators in this study have already begun collection of data on the flora (understory vascular plants), fauna (ants and salamanders), and ecosystem processes (soil carbon and nitrogen dynamics) in these plots to establish strong baseline information before treatments are implemented.


Harvard Forest Hurricane Experiment: The Next Generation

A. Barker Plotkin, K. Wilson* and D.R. Foster

The hurricane experiment at Harvard Forest was designed to simulate the impacts of a catastrophic storm like the 1938 New England Hurricane to mature red oak – red maple forest. In October 1990, canopy trees were pulled over using a winch, resulting in direct and indirect damage to nearly 70% of the stand. Despite massive structural reorganization, the site maintained biogeochemical function and resisted major change in understory species composition. This contrasts with the more dramatic changes seen after the 1938 hurricane, where hurricane effects were conditioned by a landscape dominated by old-field white pine, and the region-wide salvage logging that
Figure 1. Map of the Simes Tract of Harvard Forest, showing locations of the hemlock manipulation plots (plots 1 – 6) and hardwood control plots (plots 7 and 8). Plots are 90m by 90m; treatments (girdling and logging) are planned for 2005.

Table 1. Percent basal area by species and total basal area (m²/ha) and stem density (number of trees/ha) for the core 30m by 30m area of the eight hemlock removal manipulation plots at the Simes Tract of Harvard Forest. Survey of overstory trees in the buffer area of these plots continues. Other species include yellow and paper birches, sugar maple, black oak, white ash, hickories, black cherry, and hophornbeam.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Hemlock</th>
<th>White pine</th>
<th>Red maple</th>
<th>Red oak</th>
<th>White oak</th>
<th>Black birch</th>
<th>Other</th>
<th>Total Basal Area</th>
<th>Total Stem Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>1: hemlock</td>
<td>82</td>
<td>13</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>49.6</td>
<td>889</td>
</tr>
<tr>
<td>2: hemlock</td>
<td>68</td>
<td>10</td>
<td>2</td>
<td>20</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>44.2</td>
<td>1011</td>
</tr>
<tr>
<td>3: hemlock</td>
<td>56</td>
<td>16</td>
<td>8</td>
<td>9</td>
<td>10</td>
<td>0</td>
<td>1</td>
<td>40.5</td>
<td>822</td>
</tr>
<tr>
<td>4: hemlock</td>
<td>77</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>19</td>
<td>0</td>
<td>51.4</td>
<td>1200</td>
</tr>
<tr>
<td>5: hemlock</td>
<td>78</td>
<td>0</td>
<td>8</td>
<td>6</td>
<td>1</td>
<td>6</td>
<td>1</td>
<td>52.2</td>
<td>856</td>
</tr>
<tr>
<td>6: hemlock</td>
<td>70</td>
<td>9</td>
<td>11</td>
<td>5</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>71.9</td>
<td>633</td>
</tr>
<tr>
<td>7: hardwood</td>
<td>6</td>
<td>36</td>
<td>9</td>
<td>13</td>
<td>0</td>
<td>24</td>
<td>12</td>
<td>44.8</td>
<td>1222</td>
</tr>
<tr>
<td>8: hardwood</td>
<td>0</td>
<td>0</td>
<td>14</td>
<td>33</td>
<td>0</td>
<td>45</td>
<td>8</td>
<td>26.4</td>
<td>1144</td>
</tr>
</tbody>
</table>

A. Barker Plotkin, A.M. Ellison, et al.
followed this hurricane (Foster et al. 2004).

One goal of the experiment is to study regeneration mechanisms and changes in tree species composition. In summers 2000 and 2003, we surveyed all stems that had grown above 5 cm dbh (diameter at breast height) across the experimental and control sites. These new recruits to the stand represent the most vigorous fraction of the total regeneration at the site, and suggest how the future composition of the forest will differ from the pre-manipulation stand.

Between 2000 and 2003, the number and basal area of new stems ≥5 cm dbh increased greatly in the experimental site (Table 1). These trends suggest that the stand is still in the stand initiation phase of development (Oliver and Larson 1996), although observed mortality of saplings in the site suggests that competitive thinning of the stand is occurring simultaneously. In the unmanipulated control site, stem density and basal area also increased between 2000 and 2003, but the total amount of recruitment remains very low.

After the hurricane manipulation, vigorous sprouting of damaged trees helped to stabilize the site (Cooper-Ellis et al. 1999). However, most of the stems that have grown above 5 cm dbh are saplings (mostly seedlings that were present in the understory before the manipulation, plus some trees that regenerated from seed following the manipulation), whereas sprouts comprise less than 20% of the recruits.

Species composition remained stable between 2000 and 2003. The new cohort in the manipulation is dominated by black birch (Betula lenta), followed by red maple (Acer rubrum) and yellow birch (Betula alleghaniensis) (Fig. 1). Early successional species such as paper birch (Betula papyrifera) and pin cherry (Prunus pensylvanica) form a relatively minor component of the new cohort, and are mostly found on localized areas of soil disturbance such as tip-up mounds. Red oak (Quercus rubra) was a dominant species in the pre-manipulation forest, but only three red oaks have grown into the 5 cm size class since 1990. We will continue to monitor this new cohort, and expect that species composition may change once stem numbers of the new cohort peak and competition begins to eliminate many of the trees.


Measurement of the O₂–CO₂ Stoichiometry of Terrestrial Ecosystems

M. Battle

We are presently constructing an instrument to simultaneously measure O₂ and CO₂ in situ in ambient air. The instrument (based on a design of Stephens et al. [2001]), will be installed at the Environmental Measurement Site at Harvard Forest. Air will be drawn from two heights: one near the ground and another near the top of the canopy. With active pressure and flow control, and appropriate standard tanks, we expect to achieve a precision of ~1.5 per meg (0.0015 permil) for O₂ and 0.08ppm for CO₂ for a 6-minute measurement. O₂ and CO₂ measurements will be tied to the Scripps and WMO scales through a suite of 4 high-pressure standard tanks. A schematic diagram of the equipment is shown in Fig. 1. We expect to install the instrument at the EMS in the summer of 2004.

Simultaneous measurements of O₂ and CO₂ in ambient air characterize the stoichiometry of carbon storage and release at the ecosystem scale. This stoichiometry (hereafter α) is of interest for two reasons:

1. α is essential for inferring carbon fluxes from measurements of atmospheric O₂
Table 1. Stem numbers and basal area of new stems ≥5 cm dbh in the Harvard Forest hurricane experiment and control plots ten and thirteen years after the manipulation.

<table>
<thead>
<tr>
<th>Year</th>
<th>Hurricane Experiment Plot</th>
<th>Control Plot</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Stems per hectare</td>
<td>Basal area (m²/ha)</td>
</tr>
<tr>
<td>2000</td>
<td>630</td>
<td>2.45</td>
</tr>
<tr>
<td>2003</td>
<td>902</td>
<td>4.05</td>
</tr>
</tbody>
</table>

Figure 1. Species composition of new stems (≥5 cm dbh) in the hurricane experiment. Overall numbers increased, but species composition remained stable between 2000 and 2003.

A. Barker Plotkin, et al.
M. Battle

(see e.g. Keeling and Shertz [1992]). This is because terrestrial photosynthesis stores carbon and releases O\textsubscript{2} in the molar ratio \(\alpha\). Thus, measurements of O\textsubscript{2} are useful for determining carbon fluxes only if \(\alpha\) is independently known. To date, \(\alpha\) has been directly measured for only one ecosystem [Stephens, 2001], yet we expect \(\alpha\) to vary from one ecosystem to the next. All global estimates of \(\alpha\) are indirect [Severinghaus, 1995].

2. The value of \(\alpha\), and its temporal behavior, will provide insight into the cycling of nutrients in the forest. This is the case because we expect \(\alpha\) to depend upon whether respiration is heterotrophic or autotrophic, the nitrogen content of the biomass being synthesized and respired, and the source of nitrogen in the system (ammonium vs. nitrate). [Severinghaus, 1995].


Hydrological Stations

E. Boose, E. Colburn and P. Barten

Plans to begin long-term hydrological measurements on two small headwater streams in the Prospect Hill Tract at the Harvard Forest were further developed over the past year through the following activities:

1. A survey of all Harvard Forest researchers was conducted to identify research questions that might be advanced by hydrological measurements, and to solicit recommendations on locations and methods for such measurements.

2. A draft plan was created for the deployment of weirs and wells in the Nelson and Bigelow Brook watersheds, based on the results of the survey and on field inspection of potential sites. This plan will be finalized in spring 2004, with deployment to begin in summer and fall 2004.

3. The Fisher Meteorological Station (http://harvardforest.fas.harvard.edu/hfmet) was upgraded with new sensors to measure photosynthetically active radiation (PAR) and net radiation (short and long wave). These measurements will complement planned hydrological measurements and provide essential data for hydrological modeling.

Information Management

E. Boose

The Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html) contains data and metadata (documentation) for research projects based at the Forest. Several improvements were implemented over the past year:

1. The number of datasets in the Archive was nearly doubled (from 63 to 105), primarily through the addition of recent datasets.

2. Discovery-level metadata for each dataset was updated using survey forms filled out by individual researchers. This information, which enables “discovery” of appropriate datasets from a catalog, includes project title, personnel (investigators and contact person), temporal coverage (start and end dates), geographical coverage (location description, latitude, longitude, elevation), taxonomic coverage (species, genera, etc. studied), keywords, abstract, methods, and related datasets.

3. The updated metadata was encoded into EML (Ecological Metadata Language), an application of XML (Extensible Markup Language) developed for use by ecologists and adopted by the LTER Network as its standard for scientific metadata (for details see http://ecoinformatics.org). EML provides a highly structured format that can be read and interpreted directly by computer (interested Windows users can view EML files in Internet Explorer). Implementation of EML across the LTER Network and beyond is expected to greatly enhance the ability to locate, interpret, and integrate scientific datasets.

4. The Data Archive was redesigned to include an Overview page, Data page, and link to EML file for each dataset. Overview pages contain discovery-level metadata and are produced directly from EML files using a translation program written in XSL (Extensible Stylesheet Language). Data pages contain entity-level metadata (information on individual tables and variables) and links to data files, and for the most part are still encoded in html by hand.

5. Entity-level EML files were completed for two datasets (HF000 and HF001). Data pages for these datasets were created directly from EML files using a second XSL translation program. Completion of entity-level EML for other datasets in the Data Archive is a goal for the coming year.

A Statistical Analysis of Tower-Based Estimates of Gross Primary Production

B.H. Braswell, S.C. Hagen, E. Linder, S.V. Ollinger and A. Richardson

Time series of gross ecosystem CO$_2$ uptake, with associated uncertainty estimates, is desirable for detailed evaluation of process and satellite-based models of canopy
photosynthesis. Furthermore, the models operate on a variety of time scales, so one needs a way to provide error accounting for the time integrated gross fluxes (e.g., daily, monthly, and annually). Gross photosynthesis \((P)\) is generally estimated as the difference between statistically modeled respiration \((R)\) and net ecosystem exchange \((F)\). The relatively large number of data gaps (>40%) also requires statistical predictions for gap filling during the day, so that

\[
P = \begin{cases} 
0 & \text{Night} \\
\hat{R} - \hat{F} & \text{Day, No Gap} \\
\hat{P} & \text{Day, Gap} 
\end{cases}, \quad (1)
\]

where \(\hat{R}\) and \(\hat{P}\) are estimates based on climate, time of year, time of day, and/or other covariates. Alternatively, \(F = \hat{R} + \hat{P}\) can be estimated using all the valid NEE data, based upon an ecosystem process oriented model that prescribes the functional forms, and thus the separate roles of \(P\) and \(R\), for example,

\[
F = R(T_{\text{air}}, T_{\text{soil}}) - P(T_{\text{air}}, PAR, VPD). \quad (2)
\]

This second formulation may be desirable because it does not assume respiration controls are the same in the day as they are at night, but it conversely does not easily allow for separation of errors in \(P\) and \(R\) during the day. Thus in this presentation we focus on the sequential approach (Equation 1). Unfortunately, ordinary multiple-linear or nonlinear regression is problematic using eddy flux data because of (1) strong heteroscedasticity (e.g., Fig. 1), which indicates that the uncertainty should be a function of temperature or other variables; and (2) autocorrelation of the prediction errors, which indicates that accumulated error for time-integrated fluxes will be inaccurate. Confidence intervals for time-integrated fluxes should not be estimated by Monte-Carlo simulation based upon 2-\(\sigma\) variations in fitted parameters, because the resulting distributions are associated with the mean response, not the variance of the observations, which is often much smaller. We combined weighted least

\[
\text{Figure 1. Nighttime NEE and modeled respiration as a regression fit based on temperature only. If temperature is used to model respiration, then the uncertainty (prediction standard deviation) for each daytime estimate should be a function of temperature. A weighted uncertainty transformation of the data results in confidence intervals that adequately represent this uncertainty.}
\]

B.H. Braswell, et al.
squares and ARIMA modeling to resolve these problems, resulting in estimates of gross ecosystem uptake of CO$_2$ and error estimates, at various time scales.

**Forest Harvesting in Massachusetts**

*J. Burk, J. Hall, B. Hall, D. Kittredge, D.R. Foster and G. Motzkin*

Since mid-2001 we have been mapping and recording data for timber harvesting throughout Massachusetts for the period 1984 to 2001. This is an expansion of the pilot North Quabbin study, based on Chapter 132 Forest Cutting Plan files maintained by the state Department of Conservation and Recreation (formerly Department of Environmental Management) foresters and filed at six regional offices.

Preliminary analysis, including data from the pilot study, indicates that over 470,000 acres were harvested during this time, with an average of 38 acres per operation; the largest individual cut was 900 acres. Totals of approximately 976,000 million board feet and 786,000 cords were reported harvested. Stand types, harvest objectives, and species data were also recorded for every plan.

Seventy-eight percent of the 12,200 harvests filed during this time were conducted by private landowners, while the state Metropolitan District Commission and Department of Environmental Management accounted for 7 and 3 percent respectively. The remaining 12 percent was divided among local public agencies, nonprofit organizations, sawmill operators, and the Army Corps of Engineers. Harvest density was generally consistent from the Berkshires to the I-495 region, with notably heavy activity in the Westfield River and North Quabbin areas; there was a significant decrease east of 495 with many towns not reporting any cutting during this time. Data was close to complete for the state for the time period, with the only missing information being several years from the North Shore region.

We are currently in the process of checking for errors and discrepancies in the maps and databases, based on a small sample (5 percent) of the plans entered to date. During the coming year plans from 2002 and 2003 will be added, which will give us 20 years of data. Information from the project has already been used as part of the hemlock woolly adelgid study, and will be used for a major study of invasive plant dynamics in Massachusetts.

**Northern Pitcher Plants a Sink for Red Spotted Newts**

*J.L. Butler, D. Atwater* and *A.M. Ellison*

The northern pitcher plant (*Sarracenia purpurea*) receives much of its nutrients from the decomposition of prey by the food web that inhabits its pitcher-shaped leaves. With the exception of a rare frog or lizard, the captured prey consists predominantly of ants, beetles, spiders, and slugs. In the summer of 2003, we recorded an unusual occurrence of 22 red-spotted newts (*Notophthalmus viridescens viridescens*) captured by northern pitcher plants during our nutrient manipulation experiment at Tom Swamp (Fig. 1). Newts were found among the larger of our experimental plants but were not associated with any particular nutrient-addition treatment. This observation suggests that capture of amphibian prey by northern pitcher plants might not be as rare an event as previously believed.

Our observations provide insights into both the behavior and population dynamics of red-spotted newts and the nutrient dynamics of northern pitcher plants. Newts were found during the months of August and September, a time when they are preparing to undergo metamorphosis into terrestrial red efts. The sequences of events that led newts to enter pitcher plants and subsequently die are not clear. However, it is possible that while in search of a place to undergo metamorphosis, newts were attracted to pitcher plants while also in search of food or a place to avoid predation. Once trapped within the pitchers, newt mortality might have been caused by
intolerance to the low pH of the pitcher water or a result of bacterial or autolytic enzyme attack. As a consequence, newts became a source of prey for the pitcher plant and its associated inquiline community.

Compared to prey typically caught by pitcher plants in Massachusetts, which is generally one to five ants each day, one newt represents a much more substantial source of nitrogen. In particular, the amount of nitrogen in the biomass of one larval newt (5 mg N) is over 100 times greater than the total nitrogen in a single ant (0.042 mg N). Furthermore, one newt contains (supplies) an amount of nitrogen equivalent to the total nitrogen found within an entire pitcher. Although the ecological implications of our observations require further study, these findings suggest that the capture of newts by northern pitcher plants may represent a significant source of nitrogen previously overlooked in pitcher plant nutrient dynamics.

Figure 1. A red-spotted newt (Notophthalmus viridescens viridescens) larva captured by and drowned in a pitcher plant (Sarracenia purpurea).

Seasonal Dynamics and Higher-Order Community Structures of Birds and Their Parasites at Harvard Forest

D. Causey

The emergence of West Nile Disease Virus (WNV) in North America in 1999 had an immediate and devastating impact on bird communities in the Northeastern US. Even though the area of active outbreaks has moved westward, general monitoring and surveillance activities on WNV prevalence indicates that the virus is still prevalent within the Northeast. This project is focused on understanding the ecological and evolutionary patterns of prevalence in avian viruses and parasites, including naturally occurring viruses like Newcastle Disease Virus (NDV) and Influenza A, and emergent diseases like WNV. In this initial phase of the work, I am studying the relative roles of migrant species, which may act as long-distance vectors, and resident species, which may act as amplifying hosts and reservoirs for disease organisms. To this end, it is particularly important to be able to quantify the seasonal dynamics and interactions among residents and migrants to provide a context for temporal and spatial variability of prevalence in viruses and other parasites.

We have been conducting a census of birds at three tracts at Harvard Forest (Symms, Tom Swamp, Prospect Hill) by sight, sound, and mist-netting at roughly two-week intervals since May, 2003. Mist-netted birds additionally are being sampled by cloacal swab for subsequent analysis designed to detect the presence of viral RNA and DNA; birds are released after capture. Laboratory work is ongoing, but intensive study has been delayed until the renovation and construction of lab space at the MCZ. The most complete results to date relate to observations of the seasonal dynamics and community structure within the avifauna.

Observational data includes presence and numbers of positively identified birds, habitats and site characteristics, exact localities (determined by GPS), and behavior. Sight, sound, and netting data were converted into absolute abundances using Distance 4.1, a software program designed to convert census data into densities and trajectories. From these data, community structure was visualized as social networks using UCINET and PAJEK, and modeled by log-linear multiway contingency analysis. An example is shown below, where the interactions among the 30 commonest species found in four contiguous habitats (disturbed, secondary growth, pine forest, and meadow) are indicated by a 3-D
multi-digraph of associations. In early summer, 21 species are closely associated by incidence spanning forest-meadow habitats; five species (e.g., Dark-eyed Junco [J hyem]alis) range widely but interact only with a few select species (e.g., Chipping Sparrow [S passerina]). These peripheral members of the community are hypothesized to act as bridging vectors of disease pathogens in migrant and casual visitors into the core community of residents.

Aquatic Macroinvertebrates as Indicators for Biomonitoring Long-Term Change in Lakes and Ponds in the Cape Cod National Seashore.

E. Colburn and H. Jensen-Herrin

Over the past year we continued to collect aquatic macroinvertebrates from flooded vernal pools and from deepwater and shoreline habitats in kettle ponds on Cape Cod. Processing of the samples is underway. Preliminary multivariate analysis of habitat variables for the lakes suggested no distinctive groupings based on size, depth, water chemistry, trophic status, or geological history. Instead, each water body appears to be unique. It remains to be seen whether aquatic macroinvertebrate assemblages suggest similarities among ponds not elucidated by common limnological data.

Salt-Tolerant Midges: Important Considerations for Restoration of a Coastal Wetland in the Cape Cod National Seashore.

E. Colburn

Attempts by the National Park Service to restore tidal flow to East Harbor, a tidally restricted lagoon in the Cape Cod National Seashore, Truro, MA, have been hampered by a variety of interacting physical, biological, and sociological variables. Among these is the presence in the lagoon of high densities of larval aquatic midges, Chironomus decorus. When the adult midges emerge, they form dense clouds of insects, clouding screens, darkening the sky, fouling paint on vehicles and buildings, and piling up in reeking windrows as they decay. Nuisance emergences occur only sporadically, and the most recent of these coincided with a number of actions taken by the Park Service to begin restoring tidal flow to the lagoon. To address concerns that tidal restoration might exacerbate the midge problem, we carried out laboratory studies of salinity tolerance in the midge larvae. Our results show that in cold water, larvae tolerate all but very high (35 ppt) or very low (0 ppt) salinities. At temperatures allowing larval growth, most larvae complete development at salinities up to 7 ppt, and some individuals can develop successfully at salinities as high as 17.5 ppt. If projected levels of tidal exchange are met in the lagoon, it seems probable that future nuisance emergences of C. decorus will be avoided.

Molecular and Isotopic Studies of Biogenic Aerosols and Source Vegetation at the Howland Forest Ameriflux Site

M.H. Conte and J.C. Weber

Changes in the concentration and carbon isotopic composition of atmospheric CO$_2$ can be used to partition the terrestrial and ocean carbon sinks because terrestrial photosynthesis strongly discriminates against $^{13}$C whereas discrimination during ocean uptake is negligible. This approach, though powerful,
depends upon the accurate knowledge of the temporal and large spatial scale variation in terrestrial photosynthesis discrimination ($\Delta$), yet quantifying $\Delta$ on these scales is a formidable task due to heterogeneity of terrestrial ecosystems. Recently, we have shown (Conte and Weber 2002, Nature 417, 639-641) that the isotopic composition of higher plant derived leaf wax aerosols can be used to derive direct estimates of isotopic discrimination of terrestrial photosynthesis ($\Delta$) on large regional space scales and at ~monthly resolution. The method exploits the specificity of plant biomarkers with the integrating properties of atmospheric mixing.

Our studies at Howland Forest have focused upon more closely examining the processes linking photosynthetic isotopic discrimination at the leaf and ecosystem level with the isotopic composition of the integrated plant wax inventory in the atmosphere. The specific objectives of our studies are (1) to better constrain the plant wax biosynthetic fractionation factor ($\varepsilon_f$) to more accurately convert the leaf wax $\delta^{13}C$ signal to an estimate of photosynthetic discrimination, (2) to test the assumption that the $d^{13}C$ of ablated waxes in boundary layer aerosols accurately tracks ecosystem $\Delta$, (3) to correlate temporal changes in waxes with environmental variables and climatic conditions, and (4) to compare the leaf wax estimates of $\Delta$ with estimates of ecosystem discrimination using [CO$_2$] and $\delta^{13}CO_2$ variations (Keeling plots).

We measured the molecular and isotopic composition of waxes in canopy foliage of the major species of the Howland ecosystem (hemlock, spruce, red maple, pine, cedar, white birch) and also continuously collected wax aerosols above the canopy over the 2001 and 2002 growing seasons (May-Oct). The composition of the wax aerosols indicate that the northern mixed hardwood ecosystem upwind of Howland also contributes to the boundary layer aerosols sampled at Howland, in addition to local conifer forests, and confirms that the “footprint” of the wax aerosols in boundary layer air masses is of a regional (or larger) scale. We also observed temporal and inter-annual variations in the wax aerosol molecular and isotopic composition, although no clear seasonal trends were apparent. In July 2002 we sampled a smoke plume from forest fires in Quebec. The plume contained greatly elevated concentrations of both organic carbon and waxes, and allowed an independent estimate of wax biosynthetic fractionation relative to fixed carbon in forest biomass (~6.3 per mil). Using this estimate, we estimated the mean $\Delta$ of the wax aerosol “footprint” as 17.7 per mil. Our estimate closely agrees with model-based estimates of ecosystem $\Delta$ (Lloyd and Farquhar) for northern mixed forest ecosystems, and provides additional evidence that the weighted isotopic composition of plant waxes in the atmosphere reflects the $\Delta$ of the ecosystem.

A Sampling Plan for Hemlock Woolly Adelgid

S. D. Costa, J. Brown*, D. A. Orwig and B. L. Parker

There is a need for a statistically based sampling plan for detecting and assessing forest populations of hemlock woolly adelgid (HWA), Adelges tsugae. We wanted to establish methodology that would allow us to: 1) determine a minimum detection threshold for HWA in hemlock dominated forests, 2) define the attributes, such as sample size and type, and the number of samples needed to assess the percentage of trees infested, and 3) characterize the relationship between the percentage of trees infested in a hemlock stand and the level of infestation on the trees. Observations were made in hemlock stands across the Connecticut River Valley and Quabbin Reservoir region of Massachusetts during late spring and early summer 2003. The presence/absence of HWA signs (white woolly masses and/or their remains) on 100 trees in each of 17 sites were made at the level of tree, 2 lower branches/tree and 5 branchlets/branch. Also, the number of white woolly masses on each branchlet was recorded so that their population levels could be related to the percentage of trees infested – no attempt was made to determine developmental stage, survival status or actual presence of an
We choose the white woolly mass criteria for its ease of determination, particularly with the naked eye, which facilitates sampling operations. However, their use restricts sampling activities to periods when obvious white woolly masses are present.

Our findings suggest that the most reliable method for sampling involves examining 2 lower branches per randomly selected tree for the presence or absence of white woolly HWA masses (contact S. Costa for details). The minimum detection threshold based on a 75% probability of detecting 1 or more infested trees within an 100 tree sample of a given site is slightly lower than a 2% infestation rate. A binomial model was used to relate observed population counts to predicted percent trees infested by applying Taylor’s Power Law. There was no significant (alpha=0.05) difference between observed and predicted infestation levels. Based on optimum sampling size analysis, a minimum of 25 and a maximum of 150 samples are recommended for characterizing HWA populations down to 10 % trees infested with precision=0.25, the standard level used for assessment and management initiatives. Greater precision, as might be required for research purposes, would increase the number of samples needed. Further research is necessary to accumulate additional datasets for validation of the current sampling statistics and planned approach to sample collection.

**High Frequency Measurements of CO₂ Efflux from Forest Soil**

*P. Crill and R. Varner*

We completed automatic chamber measurements of soil CO₂ exchange at the Harvard Forest Environmental Measurement Site (EMS). A fully-automated gas-exchange system that multiplexes 8 soil chambers developed for unattended operation at remote field sites was deployed on April 20th, 2003. The frequency (48 fluxes per 24 hours) of the autochamber measurements allow us to capture immediate responses to moisture changes in the soil, the diurnal variation across the season and over a moisture gradient and the interannual variability not captured with a manual style campaign. Automated chamber flux systems also provide an independent and simultaneous measurement of nocturnal CO₂ efflux, a means to quantitatively partition one component of the net efflux therefore providing a way to evaluate and constrain the eddy-flux measurements made at the EMS tower.

A total of 7299 measurements of soil CO₂ efflux were completed between April 20th and November 21st, 2003. The average flux over the moisture gradient for the sampling period was 2.7 µmoles CO₂ m⁻² s⁻¹. The magnitude of soil CO₂ efflux varied due to temperature and soil moisture content. Daily average fluxes correlated well with average litter later temperature (Fig. 1). Soil moisture content, measured with ECHO soil moisture probes, varied significantly over the sampling season but no strong correlations with flux were observed. Collar location along the moisture gradient was qualitatively indicative of soil CO₂ efflux (Fig. 2). Sampling season averages for the poorly drained, moderately drained and well drained collars were 2.7 ± 0.03, 3.0 ± 0.03, and 3.2 ± 0.05 µmoles CO₂ m⁻² s⁻¹, respectively.

![Figure 1. Daily average efflux of CO₂ of all chambers versus litter layer temperature](image-url)
The Structure and Composition of Old-Growth Forests in the Berkshire Hills of Western Massachusetts

A.W. D'Amato and D.A. Orwig

The recent discovery of 28 remnant, old-growth forests in the Berkshire Hills and Taconic Mountains of western Massachusetts has provided an unprecedented opportunity to document the composition, structure, dynamics, and ecosystem properties of these rare ecosystems. In particular, we are interested in quantifying structural attributes, such as canopy height, snags, and coarse woody debris (CWD), the composition of understory plant communities, ecosystem properties, including nitrogen retention and nutrient stores, and the stand and landscape-level dendroecological dynamics.

We recently documented the forest composition and structure of six old-growth stands within the Cold River Gorge in western Massachusetts. This site contains one of the highest concentrations of remaining old-growth forests in Massachusetts as well as some of the oldest documented trees in the state. All sites were characterized by extremely steep slopes (mean = 81.3 %) that ranged in elevation from 330 to 480 m a.s.l. Stands were located on northern or northwestern slopes and ranged in composition from mixed Tsuga canadensis/Picea rubens forests to northern hardwood forests containing mixtures of Acer saccharum, Fagus grandifolia, and Betula alleghaniensis. All sites were characterized by uneven-aged forests with a range of tree sizes and ages. In addition, the forests contained sapling thickets of Acer pensylvanicum, Tsuga canadensis, Fagus grandifolia, and Kalmia latifolia in areas with a recent history of canopy disturbance. Extensive dendroecological analyses of these sites revealed T. canadensis ranging from 36.4 to 54.7 cm dbh to be between 289 and 487 years old, while F. grandifolia trees were between 150 and 225 years old. Discrepancies in the distribution of age-classes between plots, stands, and topographic positions suggest that the disturbance history of these sites has been dominated by small-scale disturbances such as windthrow and may indicate a differential susceptibility to disturbance based on forest composition as well as topographic and physiographic setting. We will continue to pursue these investigations in additional sites in the Berkshire Hills and the northern and southern Taconic Mountains (Fig. 1).

The Ratio of Soil: Ecosystem Respiration Varies Seasonally at Howland and Harvard Forests

E. A. Davidson, K. Savage, D. Hollinger and A. Richardson

Partitioning of aboveground and belowground respiration is important for understanding their respective responses to environmental factors such as temperature, day length, drought, and frost. At the Howland Forest in Maine, aboveground respiration accelerates first in the early spring, presumably due to bud break and foliar expansion, which results in soil respiration being only 30-40% of total ecosystem respiration in the early spring (Fig. 1b). Soil respiration then gradually increases to about 60-70% of total ecosystem respiration during the summer.
and 90-100% in the autumn and winter. A similar pattern is observed at the Harvard forest, except that an apparent mismatch between footprints of chamber measurements of soil respiration and tower measurements of ecosystem respiration results in unusually low ratios in the winter and high ratios in the summer (Fig 2b). Nevertheless, the same pattern of increasing importance of soil respiration from spring to summer is apparent. The ratio also tends to drop during summer droughts in both forests, which is consistent with less CO₂ production in the litter layer during drought.

Seasonal hysteresis of Q₁₀s for total ecosystem respiration and soil respiration at the Howland Forest provides an example of multiple processes interacting to produce variable apparent temperature sensitivities. Soil respiration always exhibited a higher Q₁₀ in the spring than in the autumn (Table 1), perhaps because of springtime root growth. Soils warm from the top downward in the spring, and they cool from the top downward in the autumn, so hysteresis based on temperature measured as a fixed depth could also be influenced by varying soil depths of CO₂ production. During the spring, soil respiration Q₁₀ was always higher than total ecosystem respiration Q₁₀, but the reverse was observed in the autumn (Table 1). In the autumn, both nighttime respiration and daytime net ecosystem exchange of CO₂ drops sharply immediately after the first frost and remains low for the rest of the autumn and winter. If both photosynthesis and respiration drop sharply in response to the first autumn frost, the apparent temperature sensitivity of ecosystem respiration may be elevated in the autumn because of this physiological threshold effect that induces relatively abrupt dormancy.

This analysis demonstrates that components of total ecosystem respiration do not always respond to temperature, moisture, and phenology in synchrony.

Figure 1. Location of four old-growth focal areas in western Massachusetts, each containing 3 to 7 old-growth stands. Old-growth overlays are adopted from Leverett and Beluzo, unpublished data.

A.W. D’Amato and D.A. Orwig
Table 1. Ratio of respiration at 15°C/respiration at 5°C at the Howland forest, Maine, USA. Total ecosystem respiration data are from Hollinger et al. (1999) and Hollinger et al. (submitted). Soil respiration data are from Savage and Davidson (2001) and more recent unpublished data.

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Figure 1. (A) Total ecosystem respiration, soil respiration, and aboveground respiration (by difference) at the Howland Forest, Maine, USA. (B) The ratio of soil respiration:ecosystem respiration; note that the ratio falls below 0.4 every spring and increases to near 1.0 by the autumn. Data sources are the same as in Table 1.
Ant Diversity at the Harvard Forest: Preliminary Data from the Prospect Hill and Simes Tracts, with Additional Observations from the Chronic N Addition Plots.

A.M. Ellison, J. Chen*, and M. Lau*, and N.J. Gotelli

In terms of biomass and ecological dominance, ants are the most important invertebrate taxon in terrestrial ecosystems and they can alter significantly fundamental processes and dynamics of soil ecosystems. Over 40 years ago, Walter Lyford suggested (in Harvard Forest Paper No. 7, 1963) that “the entire A horizon of some, if not most, virgin Brown Podzolic soils in New England consists of material returned by ants to the surface from the B horizon” and that ants could generate an A horizon of 10-18 inches (25-37 cm) thick in as little as 3000 years. Other than Lyford’s detailed work, however, there have been few studies of ants at the Harvard Forest. In the summer of 2003, we began an inventory of ant species diversity at the Forest. This inventory has three complementary goals. First, we are documenting the taxonomic diversity of ants at the Forest and relating this diversity to vegetation composition, soil characteristics, and land-use history. Second, we focus intensively on sampling at the Simes Tract to assess changes in species composition after the large-scale hemlock removal experiment. Third, we use samples taken from the chronic N addition plots to test hypotheses that suggest that ant species richness is positively correlated with energy availability (e.g., insolation) or nutrient availability and primary productivity.
In 2003, we sampled all eight 0.8-ha experimental plots in the Simes Tract (see abstract by A. Barker Plotkin et al.); all eight chronic N plots; and eight sites scattered throughout the Prospect Hill Tract (in compartments II, III, VIII, and IX) that represented a range of successional stages and stand types. Each sample consisted of a grid or transect of 25 48-hr pitfall traps and 1-hr cookie baits, and 4 L of leaf litter. All sites were sampled twice between mid-June and early August. Stefan Cover at Harvard’s Museum of Comparative Zoology (MCZ) confirmed our identifications of the species.

The current list of 33 species for the Harvard Forest is given in Table 1. Our survey added 22 species to the list published by Mike Kaspari (American Naturalist 161: 459-477, 2003). Old fields and early successional stands have the highest number of species, whereas pine and hemlock stands are least diverse (Fig. 1). At the Simes Tract, there were no differences in species richness or composition within stand types, although within-plot species richness was lower in the hemlock plots (3 ± 1 species per 0.8-ha plot) than in hardwood plots (8 ± 1 species per 0.8 ha plot). In the chronic N plots, species richness was higher in the hardwood stands than in the red pine stands, but in contrast to predictions from the literature, ant species richness did not differ among treatments within stands or with difference in light availability (estimated from hemispherical canopy photographs).

Hardwood and conifer stands differed in species composition (Fig. 2). Non-metric multidimensional scaling (NMDS) separated the hardwood stands from the conifer stands, and the mixed stands were more similar to the conifer stands than to the hardwood stands. The principal reason for this separation is that no species in the genus Formica were found in the conifer or mixed stands. Note that this ordination excluded the old-field samples, as these samples were so different from the forest samples that an ordination that included the old-field samples could not separate any of the forest stands from each other.

This survey will be extended in 2004 to complete the sampling of compartments and stand types at Prospect Hill.

The Post-Glacial History of Hemlock in Massachusetts

E.K. Faison, D.R. Foster, W.W. Oswald, B.C.S. Hansen, and E. Doughty

Global climate change and exotic pathogens are two of the most important threats to eastern North American forests today, as well as to forests worldwide. Introduced pathogens have greatly reduced or eliminated canopy dominant trees such as elm, chestnut, and beech on decadal time scales or less (Castello et al. 1995). Rapid climate change in the past has caused shifts in vegetation composition over similar time frames (Post 2003). Today, eastern hemlock is suffering conspicuous declines in southern New England from the recently introduced hemlock woolly adelgid (HWA) (Orwig 2002). Several studies show that elevated CO₂ levels increase the abundance of phloem-feeding insects (Whittaker et al. 1999), suggesting that current atmospheric trends could exacerbate the damage of this pest on hemlock.

Long-term questions that arise in the face of HWA and global warming are: 1. how reduced will hemlock become in New England as a result of this pathogen outbreak; 2. how long will it take hemlock to recover from HWA; 3. how will the transition-hardwoods forest be altered by hemlock’s decline; and 4. how will climate change interact with the current hemlock decline. To address these questions, we place current conditions into a meaningful, long-term context by investigating the post-glacial record of hemlock in New England. A combination of paleoecological data -- fossil pollen, charcoal, and % organic content of sediment cores from lakes spanning a broad geographic and environmental gradient in Massachusetts -- historical records (maps, documents, and witness tree data), and modern vegetation data are employed in this retrospective.
Table 1. Preliminary checklist of ant species for the Harvard Forest.

<table>
<thead>
<tr>
<th>Ponerinae</th>
<th>Myrmicinae</th>
</tr>
</thead>
<tbody>
<tr>
<td>*Amblypone pallipes</td>
<td>Aphaenogaster rudis</td>
</tr>
<tr>
<td>*Cremaogaster lineolata</td>
<td></td>
</tr>
<tr>
<td>Formicinae</td>
<td>Leptothorax longispinosus</td>
</tr>
<tr>
<td>*Camponotus nearticus</td>
<td>Myrmecina americana</td>
</tr>
<tr>
<td>*Camponotus novaboracensis</td>
<td>*Myrmica americana</td>
</tr>
<tr>
<td>Camponotus pennsylvanicus</td>
<td>*Myrmica detritinodis</td>
</tr>
<tr>
<td>*Formica aserva</td>
<td>*Myrmica fracticornis</td>
</tr>
<tr>
<td>*Formica incerta</td>
<td>*Myrmica nearticcta</td>
</tr>
<tr>
<td>*Formica lasiodes</td>
<td>Myrmica punctiventris</td>
</tr>
<tr>
<td>Formica neogagates</td>
<td>*Myrmica sculptilis</td>
</tr>
<tr>
<td>Formica subaenescens</td>
<td>*Protomognathus americanus</td>
</tr>
<tr>
<td>*Formica subsericea</td>
<td>*Stenamma brevicorne</td>
</tr>
<tr>
<td>Lasius alienus</td>
<td>Stenamma dieckie</td>
</tr>
<tr>
<td>Lasius nearticctus</td>
<td>Stenamma impar</td>
</tr>
<tr>
<td>*Lasius neoniger</td>
<td>*Stenamma schmittii</td>
</tr>
<tr>
<td>Lasius pallitarsus</td>
<td>*Solenopsis molesta</td>
</tr>
<tr>
<td>Lasius umbratus</td>
<td>*Tetramorium caespitum</td>
</tr>
</tbody>
</table>

Dolichoderinae

*Tapinoma sessile

*New records from 2003 survey. Lyford (1963) listed Formica fusca, the name of which is now restricted to a European species. The North American “F. fusca” is F. subaenescens. Nomenclature of Myrmica follows the unpublished work of André Francoeur.

Figure 1. Ant species richness in different stands at the Harvard Forest. PH: Prospect Hill. All plots within stand types of the N-saturation experiment are pooled, as there were no differences in species richness or composition among treatments within stand types. Similarly, all plots within stand types at the Simes Tract are pooled, as there were no differences in species richness or composition within stand types.

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Figure 2. Ordination of the stand types based on ant community composition using non-metric multidimensional scaling. Old-field samples were excluded, as their inclusion led to no separation among the forest stand types. The principal difference between stands is that no species in the genus *Formica* were found in the conifer or mixed stands.

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Preliminary results show that hemlock was present in low numbers in Mass. ~12000 cal BP but became established in the region ~10,500 cal BP at the end of the Younger Dryas Cold period (Fig.1); the species appears to have colonized the region from southeast to northwest over the course of 500-1000 years. Once established, hemlock became more abundant in central and western Mass., as is true today. After increasing rapidly, hemlock suffered its first major decline, presumably in response to a region-wide dry period from 10000-8000 cal BP (Newby et al. 2000) that was accompanied by higher fire in the eastern half of Mass. Pine declined with hemlock, and oak and ragweed increased. After ~ 8000 cal BP, moisture levels increased significantly (Newby et al. 2000), and hemlock percentages increased. Beech arrived at this time and increased along with hemlock, while oak declined, and pine fell to its lowest levels in the Holocene.

The dramatic, region-wide hemlock decline at ~5300 cal BP (Fig. 1) was likely caused by a pathogen outbreak, although a concurrent shift to drier conditions may have exacerbated the decline (Newby et al. 2000). Influx of hemlock pollen decreased by as much as 95% during this time and did not return to comparable pre-decline levels for 1000+ years; in most cases, hemlock never regained its former abundance. Oak increased during the hemlock decline except in southeastern, Mass., where beech increased dramatically.

About 500-1000 years ago, hemlock began a gradual decline, presumably in response to the cooler climate of the Little Ice Age (LIA), while spruce returned in low numbers. Hemlock’s decline was later exacerbated by the processes of European settlement: land clearance, increased fire,
logging for the tanning industry, and intensive animal browsing following these disturbances (Rogers 1978). Today, hemlock and other late successional species remain less abundant than they were at the time of European settlement, and in most cases far less abundant than they were at 6000 cal BP. Early and mid-successional species such as birch and red maple are more abundant today (Hall et al. 2002).

Hemlock levels have experienced rapid changes in response to climate change and pathogen disturbances in the past. Recovery from major declines has often been lengthy – as long as 2000 years. Today’s pathogen-climatic situation may be similar to conditions of the mid-Holocene hemlock decline and if true, hemlock’s return to pre-HWA numbers may be centuries in the making.


**Blood Pond, Dudley, MA**

![Pollen diagram from south-central Massachusetts depicting 12,000+ years of hemlock dynamics along with coincident changes of other major taxa.](image)

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**Figure 1.** Pollen diagram from south-central Massachusetts depicting 12,000+ years of hemlock dynamics along with coincident changes of other major taxa.


We continue our studies of mass and energy exchanges between the forest and the atmosphere. We place particular emphasis on a) understanding how turbulent flux convergence affects microclimate and b) how local site characteristics may introduce local bias into flux observation. In separate climatological studies, we treat spring leaf emergence as a land use “experiment”, to study what changes occur in the environment accompany leaf emergence.

During this period, we pooled some resources from NIGEC with funding from the NSF to augment CO$_2$ observations during the Hudson Valley Ambient Meteorology Study (HVAMS), whose intensive observation period occurred during September and October 2003, though ongoing measurements continue. The EMS tower at Harvard Forest served as a reference site for HVAMS, since the project surface measuring stations were not located in forested areas. A research aircraft operated during HVAMS and was used to make a series of comparison passes by the EMS tower in October 2003. At the Symposium, we will briefly discuss our ongoing radiative and turbulent flux observations but concentrate on some interesting details of the fly-by and from the CO$_2$ observation component of HVAMS.

- Climatology studies: Our previous studies have showed that leaf emergence along the East Coast can be detected not only by analyzing maximum and minimum temperatures (Fitzjarrald et al. 2001), but also through analysis of runoff properties in the same region (Czikowsky and Fitzjarrald 2004). During this period we acquired data for the rest of the continental U. S. and also from Mexico. We are now extending these studies to cover these regions.

Flux measurements:

- EMS site at Harvard Forest: We continue to operate observations of the radiation suite at tower top at EMS, as well as the subcanopy sonic anemometer at 8 m, in addition to recording the tower top turbulent variables as a backup to the Harvard system. We are in the midst of a large ‘turbulence climatology’ project, whose aim is to determine the frequency and intensity of nocturnal mixing events. This effort is using data from the decade-long time series now available.

During this period, the first results from the subcanopy drainage flow project at EMS was published (Staebler and Fitzjarrald, 2004).

- Related measurements during the Hudson Valley Ambient Meteorology Study (HVAMS): Several efforts were made during HVAMS to link NIGEC work at HF with the project. This includes the King-Air overflight at EMS tower on October 28, 2003. (Fig. 1, Fig. 2) and a series of aircraft profiles (Figs. 3, 4). A second effort was the establishment of a flux tower in the Hudson Valley near Red Hook NY, whose measurements will be continuing for another year at least. A third effort was the addition of CO$_2$ measurements to a number of flux-capable weather stations that were operated during intensive operations from September-October, 2003. This latter effort is aimed to test the viability of operating a large-scale network of CO$_2$-observing weather stations across the country (see example, Fig. 5).


**Figure 1**: Trajectory of the King Air flight legs passing over the Harvard Forest EMS tower, October 28, 2003.

**Figure 2**: King Air time series of Theta and q for the Harvard Forest EMS tower flight legs. Light green vertical lines indicate passage times over the Harvard Forest EMS tower.

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Figure 3: (Left): Profiles of theta and q for the King Air missed approach (descending portion) at Orange, MA Airport, October 28, 2003, 17:42 GMT. (Right): Profiles of O₃ and CO₂ for the same missed approach, illustrating how the forest was exhibiting little net uptake in the late autumn.

Figure 4: (Left): Profile of potential temperature and q taken in the Hudson Valley (42.60 N, 73.9 W) on October 8, 2003, 14:16:51 GMT. (Right): Profile of CO₂ and O₃.
We examined how chronic nitrogen (N) enrichment of pine and hardwood forest stands has affected the relative abundance, functional capacity, and activity of soil bacteria and fungi. During Fall 2002 we collected one soil core (5.6 cm diam; organic horizon plus 10 cm of mineral soil) from each of four 5 x 5 m subplots within the control, low N (5 g N m⁻² y⁻¹), and high N (15 g N m⁻² y⁻¹) plots in both the hardwood and pine stands at the Chronic Nitrogen Amendment Study at Harvard Forest. The samples were analyzed for total and active bacterial and fungal biomass, microbial catabolic response profiles, the activities of cellulolytic and ligninolytic enzymes, and total, labile and microbially-derived organic carbon (C). Live, fine roots were also collected from the control and low N pine plots and analyzed for ectomycorrhizal fungal community composition and diversity. Active fungal biomass was 27-61% and 42-69% lower in the fertilized compared to control plots in the hardwood and pine stands, respectively (Table
1). Active bacterial biomass was not greatly affected by N additions, resulting in significantly lower fungal:bacterial biomass ratios in the N-treated plots. This shift in microbial community composition was accompanied by a significant reduction in the activity of phenol oxidase, a lignin-degrading enzyme produced by white-rot fungi (Fig. 2). In the pine stand, ectomycorrhizal fungal community diversity was lower in the low N treated plot than in the control plot (Table 2). Differences in ectomycorrhizal community structure were also detected between control and fertilized pine plots, including a reduction in those species with the highest relative frequencies in the control community (Fig. 1). Finally, N enrichment altered the pattern of microbial substrate use, with the relative response to the addition of carboxylic acids and carbohydrates being significantly lower in the N treated plots, even after the data were normalized to account for differences in microbial biomass (Fig. 3). These patterns are consistent with lower decomposition rates and altered N cycling observed previously at this site.


A Nitrogen Experiment in a Maine Spruce- Hemlock Forest: Results From a Wet NH₄NO₃ Canopy Fertilization.

In response to unanswered questions about impacts to the carbon (C) cycle by increasing anthropogenic nitrogen (N) inputs to ecosystems, we fertilized a 21 ha spruce-hemlock forest canopy in Howland, ME. A 21 ha plot is receiving 18 kg N ha⁻¹ growing season⁻¹ above ambient N input. Liquid NH₄NO₃ additions occur 5 times per growing season by helicopter, in order to more closely mimic naturally occurring atmospheric N deposition. Within the treatment area, three sub plots were intensively sampled to determine the fate of the experimental N. In two sub plots a 1% ¹⁵N label was used to trace ammonium and nitrate respectively, in foliage, throughfall, soils and soil water. After three seasons of fertilization, we determined that approximately 40-50% of the experimental N is retained in the canopy with 10% reaching the forest floor on the day of fertilization, approximately 10% lost through canopy volatilization and 20-30% washed from the canopy by precipitation events. Ambient precipitation nitrate constitutes 50-70% of atmospheric N inputs and approximately 82% of this is retained in the canopy (compared to only 50% retention of ambient NH₄⁺). However, the experimental nitrate appears to have saturated canopy assimilation as NO₃⁻ concentrations in throughfall exceed those for NH₄⁺. Green foliage ¹⁵N contents also show a trend of nitrate preference in the canopy but this may be tempered by transport of NH₄⁺ and NO₃⁻ to other tissues.

Factors Affecting Saturability of Nitrate Immobilization in Northern Forest Soils
M. Glessner, B. Dail, E. Davidson, J. Chorover

Anthropogenic activities have resulted in increased levels of nitrogen deposition to northern temperate forests in recent decades. These inputs, primarily in the form of atmospherically derived ammonium (NH₄⁺) and nitrate (NO₃⁻), have been the result of increased fertilizer use and reliance on fossil fuel. Research has shown that the major sink for these inorganic nitrogen inputs have been forest soils, which was somewhat
Chronic Nitrogen Enrichment Affects the Structure and Function of the Soil Microbial Community

Table 1. Total and active microbial biomass, active fungal:bacterial biomass ratio (F:B) and catabolic evenness for soil collected from hardwood and pine stands at the Chronic Nitrogen Amendment Study at Harvard Forest

<table>
<thead>
<tr>
<th>Stand/Plot</th>
<th>Total microbial biomass</th>
<th>Active microbial biomass</th>
<th>Catabolic Evenness&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fungi</td>
<td>Bacteria</td>
<td>Fungi</td>
</tr>
<tr>
<td><strong>Hardwood</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>501 (41)</td>
<td>33 (4.0)</td>
<td>7.5 (0.9)</td>
</tr>
<tr>
<td>Low N</td>
<td>365 (71)</td>
<td>28 (2.8)</td>
<td>5.5 (0.6)</td>
</tr>
<tr>
<td>High N</td>
<td>637 (53)</td>
<td>34 (1.7)</td>
<td>2.9 (0.6)</td>
</tr>
<tr>
<td><strong>Pine</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>407 (60)</td>
<td>24 (0.1)</td>
<td>6.2 (1.5)</td>
</tr>
<tr>
<td>Low N</td>
<td>406 (50)</td>
<td>24 (1.3)</td>
<td>3.6 (0.5)</td>
</tr>
<tr>
<td>High N</td>
<td>433 (48)</td>
<td>36 (1.5)</td>
<td>1.9 (0.9)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Total fungal and bacterial biomass were determined by direct epifluorescent microscopy. Active microbial biomass was estimated by substrate-induced respiration with selective inhibitors. Values represent the mean of four replicates ± one standard error.

<sup>b</sup>Catabolic evenness (E) = 1/Σp<sub>i</sub> where p<sub>i</sub> is summed for all substrates and p<sub>i</sub> = r<sub>i</sub>/Σr<sub>i</sub> defined as the respiration response of each substrate (r<sub>i</sub>) as a proportion of total respiration responses summed over all substrates (Σr<sub>i</sub>). The maximum achievable evenness value is 25, the point at which all substrates are used equally. The lower the evenness value, the more variable (i.e., less even) is the respiratory response among the 25 substrates.

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Table 2. Ectomycorrhizal fungal community diversity for control and low N pine stands. Confidence intervals (CI) for Simpson’s and Shannon’s diversity indices were generated from 1000 bootstrap replicates for each plot. Richness is the total number of observed species per plot.

<table>
<thead>
<tr>
<th></th>
<th>Samples</th>
<th>Richness</th>
<th>Simpson’s D</th>
<th>95% bootstrap CI</th>
<th>Shannon’s H’</th>
<th>95% bootstrap CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>119</td>
<td>19</td>
<td>0.90</td>
<td>0.86 – 0.91</td>
<td>2.51</td>
<td>2.26 – 2.57</td>
</tr>
<tr>
<td>Low N</td>
<td>33</td>
<td>10</td>
<td>0.75</td>
<td>0.57 – 0.83</td>
<td>1.71</td>
<td>1.25 – 1.98</td>
</tr>
</tbody>
</table>

Figure 1. Ectomycorrhizal fungal community structure in the pine stand. Solid bars are relative frequencies of EMF species in the control plot; hatched bars are relative frequencies of EMF species in the low N plot.

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Figure 2. Activity of the cellulolytic enzyme, β-1,4-glucosidase (A), and the lignin-degrading enzyme, phenol oxidase (B), for soil collected from control, low N, and high N plots in the hardwood and pine stands at the Chronic Nitrogen Amendment Study at Harvard Forest. Each bar represents the mean of four replicates and the error bars are one standard error.

Figure 3. Principal components analysis of the catabolic response profiles for soil collected from control (C), low N (L), and high N (H) plots in the hardwood (H) and pine (P) stands.

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surprising in the case of NO3- owing to its tendency to be easily leached from soil profiles. NO3- rarely accumulates external to living organisms in a terrestrial ecosystem because soil particles are similarly charged and favor adsorption of cations (like NH4+) but repulsion of anions (such as NO3-). NO3- entering a system as wet or dry deposition should be either (a) quickly assimilated by plants and microbes, (b) microbially converted to an N-containing gas (N2O, N2), or (c) leached from the soil. Theoretically, it should be easy to determine the fate of increased NO3-deposition by measuring inputs, biotic demand and hydrologic N outflows (in most forest ecosystems, gaseous losses are thought to be minimal). Eventually, increased inputs may exceed microbial and plant demand and be leached from the system without being utilized; this ecosystem would be said to have reached a state of “N saturation”. Recent studies have shown, however, that NO3-additions to forest ecosystems are immobilized rapidly and abiotically in some forest soils. Observation that labeled NO3- is reduced within minutes of addition to sterilized organic horizon soils has led to new questions about NO3-reactivity and speculation about possible physico-chemical fates for NO3- in soil. Furthermore, both physico-chemical and biological N retention need to be understood in order to explain the resilience of forests to additional N deposition.

At Harvard Forest in Petersham, Massachusetts, experimental manipulations have been performed to determine the fate of additional N (as NH4+ and NO3-) in forest ecosystems. In order to experimentally push forest ecosystems toward nitrogen saturation, inputs of NH4+ and NO3- have been applied to control, low N, and high N (receiving 0, 50, and 150 Kg N/ha/yr) plots within both pine and hardwood stands. We took soil cores from each of these plots, divided into mineral and organic layers and exposed them to 15NO3-. Composite samples were used to determine initial soil characteristics (dry mass equivalence, water holding capacity, initial inorganic nitrogen quantities, etc.). Following the addition of labeled 15NO3 to soil, we took subsamples at initiation and after 24 hour incubation. These subsamples were analyzed to determine soluble and insoluble N fractions using a series of extractions and isotope diffusions coupled with solid state isotope ratio mass spectroscopy. We present results for 15NO3- additions to mineral soil horizons under mixed hardwood and red pine plantation sites undergoing the experimental N additions.

Ecosystem Carbon Exchange on Little Prospect Hill

J. Hadley and P. Kuzeja

In October 2003 we completed the second growing season of carbon exchange measurements using the eddy covariance procedure at a site on Little Prospect Hill (Fig. 1). Due to surface topography, valid carbon exchange measurements at the site are possible only with SW, W or NW winds, because winds blowing from the east over the top of Little Prospect Hill create turbulence patterns incompatible with valid C flux measurements. During data analysis in 2003 and early 2004, including reanalysis of 2002 data, we furthermore observed that anomalously large carbon effluxes appeared to occur with SSW winds, specifically between 180 and 215° compass direction from the tower. These apparent carbon releases may have also been a result of turbulence created as air passed over slightly higher terrain before reaching the eddy covariance tower from the SSW. Fossil fuel combustion and agricultural activity near Shaler Hall and the Fisher House (which are situated at a compass bearing of about 200° from the eddy covariance tower) could also have contributed to the large carbon releases observed in data from this wind direction. In either case, we concluded that flux measurements with wind from between 180 and 215° could not be used in estimates of forest CO2 exchange.

With this correction to our data analysis procedure, the estimate of carbon storage at the Little Prospect Hill site in 2002 increased substantially over our previous estimate. Total carbon storage at this site for May through August 2002 was very close to average C storage measured at the EMS site (Fig. 2),
although this was followed by lower C storage in September and greater C loss in October at the Little Prospect Hill site relative to EMS. Relative values at the two sites reversed again during November and December 2002, and we do not yet have data from the EMS site for 2003. Through the last 8 months of 2002, estimated cumulative net ecosystem exchange (NEE) of carbon was nearly equal for Little Prospect Hill and for EMS (Fig. 3). Comparing estimated carbon storage at Little Prospect Hill for the growing seasons of 2002 and 2003, we found that C storage for the first half of the season was lower in 2003, especially in May and June (Fig. 4), leading to about 1 Mg/ha less carbon stored over the 2003 growing season compared to 2002. The primary factor in this difference was heavy cloud cover in late May and early June 2003, which delayed leaf development and reduced early-season photosynthesis.


Massachusetts’ Woodlands in the Mid-19th Century: Where Were They, What Did They Look Like, and What Are Their Long-Term Legacies.

B. Hall, G. Motzkin, and D.R. Foster

The 1830 map of Massachusetts’ woodlands has been an important tool in numerous research projects conducted at the Harvard Forest. This map provides valuable insight into the histories of individual study locations and for the Massachusetts landscape as a whole. Since 1830 was near the peak of agriculture in New England, we have hypothesized that many of the sites that were wooded at that time probably remained wooded until the present, resulting in contrasting vegetation structure and composition, and ecosystem processes than nearby formerly-cleared sites. This year we have begun an in-depth analysis of this map in an attempt to describe more fully what was depicted in 1830 and what those woodlands look like today. In particular, we are seeking to identify the environmental and cultural characteristics that best predict the presence of 1830 woodlands for the different physiographic characteristics of the state. These results will allow us to model forest locations in towns without 1830 maps and to evaluate the reliability of the map in specific areas. Mid-19th century manuscripts including farmers’ diaries and agricultural journals will be examined to get an overall impression of what the 1830 woodlands may have looked like in terms of structure and composition and how they were used for wood products, pasturage, and how they may have been managed. In a related project on recent forest cutting in central and western Massachusetts, we will conduct field surveys comparing the forest vegetation and soil characteristics between sites that were shown as wooded versus open on the 1830 map; this will allow us to estimate the percentage of stands mapped as woodlands in 1830 that were subsequently cleared for agriculture and enable us to determine the long-term legacies of 19th century land-use on modern forests.
Figure 1. Carbon exchange measurement sites at Harvard Forest. EMS is the location of measurements since 1992 (Barford et al. 2001, Goulden et al. 1996, Wofsy et al. 1993) and is surrounded by a 65-100 deciduous forest in a lowland area, dominated by red oak and red maple. Data for the EMS site were obtained via the Internet at ftp://ftp.as.harvard.edu/pub/nigec/HU_Wofsy/hf_data, and are currently posted only through December 2002. H indicates an eddy covariance tower in a hemlock forest. LPH (Little Prospect Hill site) is like EMS a deciduous forest dominated by red oak and red maple, but on an upper hill slope and with trees ages of 45 years or less within 200 m of the eddy covariance tower and older trees at greater distances. Arrows in the figure indicate direction and probable magnitude of nocturnal cold air drainage, which can influence C exchange measurements at night. RP indicates planted red pine stands, RS and BG indicate red spruce and black gum growing in a swamp, and HK and WP indicate eastern hemlock and white pine.

J. Hadley and P. Kuzeja
Figure 2. Estimated monthly ecosystem carbon storage for two sites at Harvard Forest from May 2002 through October 2003. Carbon storage estimates for the Little Prospect Hill site have been revised upward in the past year after eliminating data for SSW winds that appeared to show anomalously large carbon releases, possibly generated by human activity and fuel combustion in the headquarters area of Harvard Forest.

Figure 3. Estimated cumulative net ecosystem carbon exchange (NEE) for two sites at Harvard Forest from May 2002 through October 2003. In this figure carbon uptake is plotted as a negative number, and carbon release is positive. Each point indicates cumulative NEE at the end of the month indicated on the x-axis. For site descriptions and explanation of the shorter record for EMS, see Figures 1 and 2.

J. Hadley and P. Kuzeja
Assessing N Availability Through Multiple Resin Extractions Following the Onset of the Hemlock Woolly Adelgid

S.S. Jefts and D.A. Orwig

Introduced exotic pests can pose serious perturbations to ecosystem function, particularly to nutrient cycling and nutrient availability. Using the context of a natural experiment, the elimination of eastern hemlock (Tsuga canadensis) by the introduced pest the hemlock woolly adelgid (HWA), we are able to obtain unique insights into the effects this pest has on N availability. This study examined N availability via ion exchange resins over the period of 1 year as well as over the growing season only and the efficacy of multiple resin extractions in a set of hemlock stands ranging in HWA damage severity. Overall, heavily infested stands demonstrated higher available NO3-N concentrations (Figs. 1 and 2). This suggests higher nitrification rates as well as higher NO3-N availability, possibly leading to increased NO3-N leaching and denitrification. Uninfested and recently infested stands exhibited similar or greater NH4-N availability when compared with heavily infested stands indicating that the majority of NH4-N in heavily infested stands has been nitrified to NO3-N. Interestingly, two sites that no longer have a hemlock component, exhibited different responses. One previously infested site that was logged now exhibits extremely high NH4-N and NO3-N availability (21.21 and 22.35 mg N/L, respectively) indicating lack of plant uptake as well the possibility for high NO3-N leaching and denitrification. Another site which lost all hemlocks due to HWA 10 years ago and which previously had high N availability, has been replaced by black birch (Betula lenta) and now exhibits low N.
availability (1.77 and 1.47mg N/L for NH4-N and NO3-N) indicating increased plant uptake as black birch continues dominance of the site. The recovery efficiency of using one resin extraction was lower in sites with high N availability. This was most pronounced for NO3-N indicating that more than one extraction may be needed for sites with expected or known high N availability (Figs. 3 and 4). We are currently analyzing corresponding soils data, which will be compared with the resin data as well as the variability in microclimate.

Scaling Forest Canopy Carbon Flux from Sites to Landscapes Using Airborne Remote Sensing and Canopy Nitrogen Chemistry.


Combining light use efficiency (LUE) estimates with satellite-derived FPAR represents the current state of the art in remote estimation of vegetation carbon uptake in terrestrial systems. A critical component of this approach involves understanding sources of variation in LUE and deriving methods for estimating LUE values both within and between biomes. In one recent study, a simple index created from leaf N concentration, specific leaf weight and LAI was able to explain 85% of the observed variance in LUE across all species and biome types with foliar N being the most influential term. This suggests that improving our understanding of variability in canopy N concentration variability and exploring new methods for scaling canopy N to the resolution of the modern suite of global remote sensors will improve our ability to make broad scale estimates of carbon uptake and productivity.

Here, we report on progress in a research effort aimed at using remotely-sensed canopy nitrogen as a spatial scaling tool for integrating carbon flux estimates between eddy covariance towers and broad-scale remote sensing. The sites involved are all part of the AmeriFlux network and are located along a latitude gradient in eastern U.S. forests (Maine to Florida). The specific goals of the project are: 1) to explore spatial patterns in foliar N within the landscapes surrounding each site using hyperspectral remote sensing; 2) to link spatial data for canopy N to tower-based C flux measurements using an ecosystem simulation model; and 3) to scale landscape-level carbon fluxes and canopy traits to broad scale multi-spectral and multi-angle remote sensing data through use of a coupled ecosystem and canopy radiative transfer model.

Salamanders and Benthic Invertebrates in the Headwaters of Bolton Brook, Mount Wachusett, Massachusetts

H. Jensen-Herrin, D. Williams and E.A. Colburn

Headwater streams are at risk in Massachusetts from land development and pollution, and in some cases are not protected by environmental laws. Little attention has been given to what role these streams serve in supporting biodiversity on the landscape, or to their function as habitat or refugia for aquatic or terrestrial species. Gregory et al. (2002) demonstrated that close to 85% of upland areas in some parts of the Piedmont of North Carolina are drained by headwater streams, making them an important physical interface between upland and higher order streams and rivers. The streams central to our study are identified as “intermittent streams” that carry water after storm events or during seasonal runoff, but have only subsurface or interstitial flow at other times of the year. The salamanders, aquatic insects and fish using these intermittent streams as habitat often extend their range and influence beyond the stream banks into the surrounding terrestrial habitat, yet the species assemblages for intermittent streams have not been well studied in New England.

Between July 2002 and February 2003 we mapped both intermittent and perennial
Figure 1. Nitrate and ammonium values of yearlong deployment of resins by varying infestation levels.

Figure 2. Nitrate and ammonium values of resins deployed for the growing season by varying infestation levels.

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Figure 3. Percent of nitrate and ammonium captured by the first, second and third extractions of resins deployed for one year grouped by varying infestation levels.

Figure 4. Percentage of nitrate and ammonium captured by the first, second and third extractions of resins deployed for the growing season (approximately 6 months) by varying infestation levels.

S.S. Jefts and D. A. Orwig
sections of the headwaters of Bolton Brook, a small mountain stream on the Wachusett Mountain State Reservation, Worcester County, town of Westminster, Massachusetts. Our goal was to examine the distribution of stream salamanders and macroinvertebrates, and identify species assemblages in intermittent and perennial sections of the stream system. We examined the effects of physical characteristics including flow periodicity and substrate/habitat types on the species assemblages. We also hoped to identify key organisms that might be useful indicators of stream class in central Massachusetts.

On each 50 meter stream reach we established random transects of 4M x half stream width (in meters) with a minimum of 4 x 1 meters and searched them thoroughly for salamanders. We recorded habitat variables including substrate characteristics, gradient, flow, temperature, and presence of brook trout, \textit{(Salvelinus fontinalis)} for each transect. Visual surveys for salamanders were also conducted throughout the study area. We sampled macroinvertebrates in a single, random, square-meter quadrat in each 50-meter stream reach by vigorously dipnetting in the surficial substrate, live-picking all animals in the field, and preserving them in 70 percent ethanol for later identification in the laboratory. Physical habitat variables were recorded as above for each quadrat.

Three species of stream salamanders, the northern dusky salamander, \textit{Desmognathus fuscus}, the two-lined salamander, \textit{Eurycea bislineata}, and the spring salamander, \textit{Gyrinophilus porphyriticus}, as well as the terrestrial Redbacked salamander, \textit{Plethodon cinereus}, were identified in the stream. All three stream salamander species routinely co-occured with \textit{S. fontinalis} in parts of the stream where the fish are present. The Redbacked salamander, \textit{Plethodon cinereus}, appears to be using the damp organic debris in dry and intermittent portions of the stream channel as refugia during dry periods. Macroinvertebrate numbers and species richness declined with increasing stream intermittency and gradient. A key indicator species, \textit{Pseudostenophylax uniformis}, a caddisfly restricted to intermittent streams, was identified in this system. Chi square analysis demonstrated significant differences in both salamander and macroinvertebrate populations between intermittent and perennial stream reaches. Salamander distributions differed significantly between perennial and intermittent stream reaches (\(\chi^2 = 98.07, \ df = 3, \ p< 0.05\)) Fig. 2. Chi square analyses of frequencies of occurrence of all 4 species of salamanders encountered by transect or quadrat in the stream system based on the intermittent or perennial nature of the stream channel returned significant Chi \(^2\) value (\(\chi^2=98.79, \ df=3, \ p=0.05\)). Spearman Rank Correlation showed an inverse relationship between Red-backed salamanders and stream width. Spearman Rank Correlation showed an inverse relationship between Red-backed salamanders and stream width. Chi \(^2\) distribution calculated on the frequency of occurrence of Trichoptera taxa between intermittent and perennial stream types, demonstrated a significant Chi \(^2\) value (\(\chi^2= 402.10, \ df=11, \ p=0.05\)) Fig. 1. Multivariate analyses of habitat and substrate characteristics were used to identify specific habitat requirements or preferences for salamanders and selected macroinvertebrate species with less significant results.

**Timber Harvest in a Fragmenting Landscape Dominated by a Diversity of Ownerships**

\textit{D.B. Kittredge}

Earlier work with timber harvesting regulatory data has documented its extent across a sample landscape in Massachusetts, and shown its random occurrence with respect to biological, physical, or cultural features (Kittredge et al. 2003). Subsequently, data have been collected for the entire state for 1997 – 2001, and are in the process of being collected and reviewed for 1984 – 2001. In addition to their value of documenting an important form of anthropogenic disturbance, these data are also useful to explore the extent to which harvest as a management and economic activity continues to occur in a fragmenting forested landscape. Wear \textit{et al.}
Trichoptera Species Assemblages by Flow Regime

Salamander Species Assemblages by Flow Regime

Figure 1.

Figure 2.

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(1999), for example, estimate that the probability of harvesting approaches zero in a Virginia landscape where population density exceeds 388 km$^{-2}$. Barlow et al. (1998) showed that distance from urban centers (>50,000 inhabitants) in Mississippi and Alabama was positively and significantly related to the probability of harvest (estimated by FIA plots). If forested landscapes dominated by thousands of small family, NGO, and municipal ownerships are to remain productive sources of wood products (e.g., Berlik et al. 2002), it is important to understand the influences of parcelization and fragmentation.

Massachusetts forest cutting data for 1997 – 2001, and timber tax data from New Hampshire for 2001 (provided by M. Tansey, NH Division of Forests and Lands) were used to describe the extent of harvest on a town-by-town basis, in terms of the number of operations km$^{-2}$ and harvest volume (m$^3$/hectare forest). Fragmentation of a town’s overall forest area was estimated by its average Mean Shape Index (MSI: an expression of perimeter: area ratio of a patch of forest, weighted by its size). Parcelization of a subset of towns in MA and NH (stratified by population density, n=55) was estimated using actual tabular tax assessor data, which provides the number and size of parcels. A number of metrics of parcelization were developed (e.g., percent of a town’s land in parcels > 10 hectares; number of parcels/ hectare of land). Parcel data are not spatially explicit, so they cannot be related to actual forest ownership, but can only serve as a relative indication of the degree of parcelization in a community.

Preliminary results indicate:

- As the percent of a town’s land in parcels > 10 hectares declines towards 40, the likelihood of harvest operations km$^{-2}$ approaches zero;
- Likelihood of harvest operation km$^2$ forest area in NH approaches zero with a MSI > 1.8
- Likelihood of harvest operation km$^2$ forest area in MA approaches zero with a MSI > 2.2, implying harvest occurs in more fragmented forest

More data on parcelization and harvest activity are needed for more rigorous analysis and to draw stronger conclusions, but preliminary results suggest there are distinct fragmentation and parcelization thresholds beyond which harvest ceases to be viable in these otherwise forested landscapes.


**Environmental History of Two New England Ponds: Natural Dynamics Versus Human Impacts**

*D. Köster and R. Pienitz*

Analyses of sedimentary diatoms and stable isotopes in two New England ponds indicate limnological changes during the past 2500 years related to climate change, anthropogenic activities and natural disturbance. Deforestation during the 18th and 19th centuries temporally affected diatom assemblages with subsequent recovery, but algal communities did not return to pre-settlement conditions due to natural disturbances, delayed recovery from acidification and continued climatic change. In both lakes, short-term rises in diatom-inferred DOC was related to partial removal of vegetation by logging or a hurricane in 1937 at North Round Pond. At Levi Pond, increasing diatom-inferred DOC concentrations during the
past ca. 2000 years seem to reflect a long-term increase of allochtonous organic matter loading and probably peat development in the watershed related to moister conditions, which is supported by coincident patterns in stable isotope and vegetation composition. These results correspond to moisture patterns in adjacent areas inferred by pollen and sediment analyses, suggesting that diatoms in Levi Pond recorded a larger regional trend in increasing moisture. Our results showed that long-term trends in climate change and small-scale natural disturbance patterns still contribute to dynamics of man-altered ecosystems. Furthermore, this study suggests that fossil diatoms may be a promising proxy for future paleohydrological studies in temperate regions.

Photosynthetic $^{13}$C Discrimination in North American Temperate Forest Biomes


The $\delta^{13}$C values of atmospheric CO$_2$ can be used to partition global patterns of CO$_2$ source/sink relationships among terrestrial and oceanic ecosystems using the inversion technique. This approach is very sensitive to estimates of photosynthetic $^{13}$C discrimination by terrestrial vegetation ($\Delta_A$), and depends on $\delta^{13}$C values of respired CO$_2$ fluxes ($\delta^{13}$C$_R$). Here we show that by combining two independent data streams - the stable isotope ratios of atmospheric CO$_2$ and eddy-covariance CO$_2$ flux measurements - regional estimates of $\Delta_A$ can be successfully derived in terrestrial ecosystems. Annual mean, flux-weighted $\delta^{13}$C values of net ecosystem CO$_2$ exchange (NEE) were estimated for 3 forest ecosystems (Wind River Canopy Crane, Harvard Forest and Howland Forest) by analyzing daytime flask measurements collected at the top of canopies. Our approach was based on the assumption that variations in CO$_2$ mole fraction observed in terrestrial ecosystems were dominated by biological activities during the growing season (May – early October). Harvard Forest, however, was found to experience significant fossil fuel impacts toward the end of the growing season. By constraining measurements to those collected between May-August, we were able to successfully derive the NEE-$\delta^{13}$C value for the Harvard Forest. We also present the first weekly dataset of seasonal variations in $\delta^{13}$C$_R$ from these 3 forests. Combining $\delta^{13}$C values associated with respiratory and net fluxes, we demonstrate a method for estimating whole-canopy $\Delta_A$ in terrestrial ecosystems directly from field measurements. The $\delta^{13}$C associated with NEE fluxes ($\delta^{13}$C$_{bio}$) at these forests range between $-26.0 \pm 2.8$ and $-27.8 \pm 2.4 \%$. These estimates differ from a previous study, when $\delta^{13}$C$_{bio}$ values of these ecosystems were compared to forests at comparable latitudes. Our observations indicate large variations in the value of $\delta^{13}$C$_R$ across 3 temperate forests (-24.9 ± 0.4 to -31.3 ± 0.6 \%). Despite that no significant correlations were found between $\delta^{13}$C$_R$ and water status at the Harvard Forest, monthly-mean $\delta^{13}$C$_R$ values were significantly correlated with growing-season soil water availability for the two coniferous forests. We suggest that shifts in the $\delta^{13}$C values of terrestrial CO$_2$ fluxes are driven by region-wide drought patterns that could be of sufficient magnitude globally to impact partitioning calculations of CO$_2$ sinks between oceanic and terrestrial compartments.

Does Evolutionary Change in Resource Allocation by Alliaria petiolata Drive Invasiveness?

K.C. Lewis and F.A. Bazzaz

It has been hypothesized that evolutionary change in species introduced to a new location can enable the species to become invasive. This hypothesis has been supported by the observation of lag time between introduction and invasion, and by observed alteration in size of plants introduced outside of their home ranges. Reduced herbivory is one consistent change in selection pressure which may result in evolution in the new location. Reduced herbivory could result in altered allocation of resources to anti-herbivore
defenses, affecting growth and reproduction. The expected patterns of change in defenses after introduction depend strongly on the assumptions made about herbivore load change, herbivore identity, and resource availability.

Our previous work analyzed the differences in sinigrin content in young leaves of *Alliaria petiolata* in native and invasive populations and found significantly higher concentrations of sinigrin in leaves from the invasive populations in some cases. However, these differences in sinigrin content were strongly correlated with plant size, which is dependent on resource availability. In this study, we investigated life-stage variation in sinigrin concentrations in *Alliaria petiolata* populations in its native Europe and in its new range in the US. We utilized herbivore exclusion treatments to investigate the role of inducibility in geographic patterns of defenses. Plants in European (native) populations experienced significantly greater herbivore damage than plants in North American (invasive) populations. Contrary to anecdotal evidence suggesting invasive species are larger in their introduced ranges, we found that plants in the native populations were consistently larger than those in the invasive locations. We found no consistent difference between native and invasive populations in sinigrin concentration in either first- or second-year plants. There does not appear to be a pattern of induced production of sinigrin in response to herbivory, nor does herbivory seem to be dependent on sinigrin concentration of target plants. The negative correlation of sinigrin content to leaf size and plant size was significant in the first-year plants, but was weaker in the second year, presumably due to reallocation of resources from defenses to reproduction at flowering. Our data suggest that life stage and interannual variation in resource availability are the main determinants of allocation to defense and growth, and suggest that there has been little evolutionary change in production of sinigrin in *A. petiolata* since introduction into North America.

The Rise and Fall (and Rise And Fall) of Spruce in Massachusetts

*M. Lindbladh, E. Faison, D.R. Foster, and W.W. Oswald*

Due to difficulties in separating pollen from the three spruce species occurring in eastern North America, little is known about their history. However, a method for the separation has recently been developed (Lindbladh et al. 2002). The first application of the method to eight sites in Maine showed a shift from a forest of white spruce (*Picea glauca*) and black spruce (*P. mariana*) in the late glacial to a forest of red (*P. rubens*) and black spruce in the late Holocene (Lindbladh et al. 2003). The small number of red spruce grains identified from the late glacial samples (<5%) suggested that that species was either absent or rare at most of the sites. However, the study included only one level from each site from the late glacial and late Holocene, respectively.

In an ongoing study from several pollen sites in Massachusetts we have for the first time applied the method to consecutive levels. One of the sites investigated is Blood Pond in south-central Massachusetts. This site showed high amounts of spruce pollen (as most ca 45%) from ca 16,000 to 11,000 cal BP but recorded almost no spruce pollen from there after. The preliminary results show that white spruce probably was the only spruce species at Blood Pond in the beginning of the record (Fig. 1). Starting at ca 14,500 cal BP black spruce started to increase, and it had almost entirely replaced white spruce by ca 13,500. Very few grains were identified as red spruce. The pollen record shows two peaks of spruce during the late glacial, a pattern that has been observed at other nearby sites: the first ca 14,500 cal BP and the second at the beginning the Younger Dryas chronozone (12,900 – 11,600 cal BP). Our data show that the first peak was dominated by white spruce and the second peak consisted almost entirely of black spruce. The pattern with an initial dominance of white spruce and gradual replacement by black spruce is also present in the pollen record from
Berry Pond in northeastern Massachusetts, although the record is not yet dated.

Our results suggest that the fluctuation in spruce pollen percentages before and during the Younger Dryas should not be interpreted as a range shift of a single species related to climate change (Shuman et al. 2002), but rather as a change in species composition during the period.

Following the interval of black spruce dominance, spruce pollen percentages dropped dramatically and remained low for the next ca 7000 years. Then, starting around 4000 cal BP, spruce percentages began to increase at sites across the region, presumably in response to increasing effective moisture. We are currently mapping the pattern of spruce pollen percentages across New England (Fig. 2), to better understand the spatial and temporal variability of this late Holocene increase in spruce abundance. In general, it appears that the spruce increase occurred first (ca 4000-2000 cal BP) in the northern and western portion of this region, including the Adirondacks, western Massachusetts, and the northern parts of Vermont, New Hampshire, and Maine. At sites in coastal Maine and eastern Massachusetts, the increase in spruce pollen percentages occurred later (after 2000 cal BP).


**Soil Warming at Barre Woods: Megaplot Responses After One Year of Warming**


Will the increase in available nitrogen resulting from soil warming lead to an increase in carbon storage in vegetation? And if yes, how much? To answer these questions we initiated a “mega-plot” soil warming study in 2001, in the Barre Woods site in Harvard Forest’s Slab City Tract. The study area is a mixed deciduous temperate forest less than 100 years old. During the summer and fall of 2001 we buried 5.7 km (3.4 miles) of heating cable at a 10cm depth in a 30 x 30m plot. We delineated a second 30 x 30m area to serve as the control plot. Results from the original soil warming experiment confirmed that the soil disturbance associated with the installation of heating cables has had no effect on soil temperatures and only minor and variable impacts on soil moisture, as well as producing no significant effect on soil carbon and nitrogen dynamics.

In April of 2002 we began a one-year period of baseline measurements before turning on the heat in the new megaplot. We saw no significant pre-treatment differences in CO$_2$ release, N$_2$O flux or CH$_4$ uptake from the soil between the two plots. Nitrogen mineralization measurements revealed higher rates in the turnover of soil N in the plot to be heated, as well as differences in the foliar chemistry of some species. We will account for these baseline differences to isolate ecosystem responses due to heating.

We turned on power in May of 2003 (Fig. 1), and the "manipulation phase" has begun. After one year of heating, monthly CO$_2$ flux (Fig. 2) increased an average of 30.8% and nitrogen mineralization (Fig. 3) increased an average of 38.4%, total understory biomass increased 45%, and foliar nitrogen increased, significantly in birch (22%) and ash (9%) species. Minimal nitrogen left the system through leaching (measured using lysimetry) or gaseous (N$_2$O) emissions. Monthly dendrometer band measurements on all trees in
Figure 1. Pollen diagram from Blood Pond, MA. Undiff. denotes spruce pollen with intermediate characters that can not be differentiated to species. Thirty grains per level are analysed.

Figure 2. Map showing the locations of selected pollen records in the northeastern United States. Symbol size indicates the timing of the initial increase of spruce pollen percentages during the late Holocene

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Figure 1. Continuous thermister data from the Barre Woods soil warming plots, demonstrating system control of temperature differential. X-axis is day of the year. Data is from September, 2003.

Figure 2. Monthly total soil respiration at the Barre Woods Megaplot Experiment, pre-treatment and with heating. Error bars indicate standard error of the mean.

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Figure 3. Monthly net Nitrogen mineralization at the Barre Woods Megaplot Experiment. Error bars indicate standard error of the mean.

Figure 4. Monthly oak, maple, birch and ash biomass additions at the Barre Woods Megaplot Experiment. Allometric equations are used with monthly woody increment measurements to estimate biomass additions.

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the plots clearly reveal seasonal growth patterns, as well as the dominance of the site by red oak (*Quercus rubra* L.) (Fig. 4). We detected no significant differences in growth due to heating after six months of heating. The story of the changes taking place at this site will continue to unfold this summer.

**Ecosystem Response to 15 Years of Chronic Nitrogen Additions.**


Anthropogenic nitrogen deposition has the potential to alter nitrogen cycling patterns and processes in ecosystems. The long-term impact of elevated nitrogen inputs was studied in two temperate forest stands at the Harvard Forest LTER site. Key indicators of nitrogen saturation, including forest productivity, foliar chemistry, and soil solution chemistry, were measured in red pine and mixed hardwood stands receiving six NH$_4$NO$_3$ additions over each growing season from 1988 to 2002. Four treatment plots were located in each stand with the following application rates: 0 (control), 5 (low N) and 15 (high N) g N m$^{-2}$ yr$^{-1}$. Aboveground biomass was severely impacted with red pine mortality reaching 56% by 2002 in the pine high N plot. (See photo cover). The hardwood high N plot showed increased ANPP, but a severe drought in 1995 contributed to mortality of 72% of red maple trees by 2002. Species importance and litterfall patterns were altered in several plots after 1995. Foliar and fine root N concentrations in treated plots increased 25 – 80% over control plot values. Inorganic N leaching below the rooting zone (60 cm) were elevated in both high N addition plots starting as early as 1990 (pines) and 1995 (hardwoods). Roots, foliage, and wood have diminished as net sinks for added N, emphasizing the role of soils in N retention. Two mechanisms for large net retention of added N are proposed: abiotic N immobilization and assimilation and re-exudation by mycorrhizae.
intensive searches: correlation = -0.390 P < 0.10).

*P. cinereus* are nocturnal and only one individual was encountered on visual surveys of transects. No evidence was found that *P. cinereus* was more abundant in hardwood stands from cover board monitoring (P = 0.98) as abundance was higher in all five sites in eastern hemlock stands. However, *P. cinereus* abundance as measured by intensive searches of 1 m² quadrats was significantly greater (P < 0.05) in hardwood stands than in eastern hemlock stands (Fig. 2; Table 1). *P. cinereus* abundance was unrelated to soil pH (P > 0.25).

Our research suggests that eastern hemlock mortality caused by HWA and the conversion of eastern hemlock stands to hardwood stands may cause decreases in juvenile *N. v. viridescens* abundance in these stands during the late summer and fall as both methods yielding data regarding this species found evidence of a higher abundance in eastern hemlock stands. It is unclear how *P. cinereus* abundance would be affected within these stands as the methods used to measure this species abundance produced contradictory results. Future research should test the hypothesis that the results from the intensive searches in this study are accurate in suggesting that *P. cinereus* abundance is higher in hardwood stands, and that this species’ abundance appears higher in eastern hemlock stands when monitoring ACOs because cover is limiting in these stands. This could be tested by intensively searching areas surrounding ACOs before and after removing them to determine if there is a greater increase in *P. cinereus* abundance after ACOs are removed in eastern hemlock stands. A similar technique was used, and found that cover was not limiting in a red oak – white pine forest (Monti et al. 2000).


Sugar Biomarkers as Source Indicators of Biogenic Organic Carbon in Aerosols Collected at the Howland Experimental Forest, Maine

*P. Medeiros, M.H. Conte, J.C. Weber and B.R T. Simoneit*

Bulk aerosols (>1 µm) were collected continuously above the Howland forest canopy from May – October 2002. Each sample integrated approximately a two week period. Soluble mono- and disaccharide sugars were extracted using a direct microscale extraction method and were analyzed as their TMS derivatives by GC-MS.

Concentrations of total aerosol sugars ranged from 10 to 160 ng m⁻³. Glucose (α and β) was the most abundant sugar (30-60% of total sugars). The monosaccharides arabinose, fructose, galactose, xylitol and sorbitol, and the disaccharides sucrose, maltose and mycose (aka trehalose) were also present in lower concentrations. The sugar composition in the aerosols varied seasonally. Fructose and sucrose were more prevalent in early spring and decreased in relative abundance as the growing season progressed. Reduced sugars (xylitol and sorbitol) and the disaccharides maltose, a microbial degradation product of starch, and mycose, a fungal metabolite, were more prevalent in autumn. The changes in the sugar
Figure 1. *Notophthalmus viridescens viridescens* abundance as measured by visual surveys of transects and time constrained (2-minute) intensive searches of 1-m² quadrats (TS – hemlock stand; HW – hardwood stand).

* significant difference between stand types as measured by transect walks at P < 0.01

Figure 2. *Plethodon cinereus* abundance as measured by monitoring of ACOs and time constrained (2-minute) intensive searches of 1-m² quadrats (TS – hemlock stand; HW – hardwood stand).

* significant difference between stands as measured by intensive searches at P < 0.05

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Table 1. Summary of the abundance of juvenile eastern red-spotted newts, or red efts (*Notophthalmus viridescens viridescens*) and adult and juvenile eastern redback salamanders (*Plethodon cinereus*) in eastern hemlock stands and hardwood stands.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>N</th>
<th>Mean (per m²)</th>
<th>Std Dev</th>
<th>SE Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. cinereus</em> abundance as measured by ACO monitoring in hemlock stands (N = number of ACOs)</td>
<td>363</td>
<td>1.456</td>
<td>0.63</td>
<td>0.03</td>
</tr>
<tr>
<td><em>P. cinereus</em> abundance as measured by ACO monitoring in hardwood stands (N = number of ACOs)</td>
<td>180</td>
<td>1.044</td>
<td>0.50</td>
<td>0.03</td>
</tr>
<tr>
<td>Two-sample t-test Tot HW = Tot TS (vs &gt;): T = -2.06  P = 0.98  DF = 438</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. cinereus</em> abundance as measured by time-constrained intensive searches in hemlock stands (N = number of 1-m² quadrats searched)</td>
<td>100</td>
<td>0.080</td>
<td>0.27</td>
<td>0.02</td>
</tr>
<tr>
<td><em>P. cinereus</em> abundance as measured by time-constrained intensive searches in hardwood stands (N = number of 1-m² quadrats searched)</td>
<td>100</td>
<td>0.180</td>
<td>0.41</td>
<td>0.04</td>
</tr>
<tr>
<td>Two-sample t-test Tot HW = Tot TS (vs &gt;): T = -2.03 P = 0.022  DF = 171</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>N. v. viridescens</em> abundance as measured by transect walks in hemlock stands (N = number of 90-m² transects searched)</td>
<td>119</td>
<td>0.0271</td>
<td>0.04</td>
<td>0.00</td>
</tr>
<tr>
<td><em>N. v. viridescens</em> abundance as measured by transect walks in hardwood stands (N = number of 90-m² transects searched)</td>
<td>65</td>
<td>0.0083</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td>Two-sample t-test Tot TS = Tot HW (vs not =): T = 4.06 P = 0.001  DF = 180</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>N. v. viridescens</em> abundance as measured by intensive searches in hemlock stands (N = number of 1-m² quadrats searched)</td>
<td>100</td>
<td>0.11</td>
<td>0.37</td>
<td>0.03</td>
</tr>
<tr>
<td><em>N. v. viridescens</em> abundance as measured by intensive searches in hardwood stands (N = number of 1-m² quadrats searched)</td>
<td>100</td>
<td>0.04</td>
<td>0.19</td>
<td>0.02</td>
</tr>
<tr>
<td>Two-sample t-test Tot TS = Tot HW (vs not =): T = 1.66 P = 0.099  DF = 150</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Composition in the aerosols reflected seasonality in the relative production of sugars in the ecosystem, with greatest synthesis of simple sugars at the beginning of the growing season, and greater contributions of metabolites from microbial degradation of primary compounds during the early autumn period of leaf senescence and decay. Smoke plumes from Quebec forest fires passed over the Howland site in late June and early July 2002. Levoglucosan, a degradation product of cellulose combustion and a biomarker of biomass burning, increased by an order of magnitude in the aerosol samples collected during this time. Glucose, galactose, and to a lesser extent arabinose also increased in concentration by factors of 2-5 in the smoke-impacted samples, indicating the fires may have also enhanced atmospheric emissions of uncombusted organic materials. In contrast, concentrations of arabinose, fructose, reduced sugars and the fungal metabolite mycose were not significantly higher in the smoke-impacted samples and indicated that biomass burning was not a significant source of these compounds in aerosols.


In the first decade of the Prospect Hill soil warming experiment at the Harvard Forest, we documented changes in soil carbon and nitrogen cycling. We showed that while soil warming accelerates soil organic matter decay and CO$_2$ fluxes to the atmosphere, this response is small and short-lived for a mid-latitude forest because of the limited size of a microbially-accessible soil carbon pool. We also showed that warming increases the availability of mineral nitrogen to plants. Since plant growth in many mid-latitude forests is nitrogen limited, warming has the potential to indirectly stimulate enough carbon storage in plants to at least compensate for the carbon losses from soils.

In years 11, 12 and 13 of the study, the effect of warming on soil carbon losses has remained small (Fig. 1). The large increase in available nitrogen created early on in response to warming has begun to diminish somewhat (Fig. 2), although nitrogen leaving the system in soil water or N$_2$O has not increased. We still do not know where the "excess" available nitrogen has gone, but speculate that over time, it is becoming tied up in nitrogen pools with long storage times such as refractory soil organic matter and the woody tissue of the trees (Fig. 3). We are testing these ideas in a large-plot soil warming experiment at Barre Woods.

Additional findings from the soil warming study at Prospect Hill include the following:

Methane uptake - Between 1991 and 2003, the average net uptake rate of CH$_4$ by the soil system in the heated plots was about 17% higher than in the disturbance control plots (Fig. 4).

Microbes and labile carbon in 2003 (see Smith et al. this volume).
- Active microbial biomass is 26% lower in the organic horizon of the heated plots than in the organic horizon of the controls, and 44% lower in the mineral horizon.
- The cohort of microbes that were present in the heated plots demonstrated different respiratory responses to a variety of added substrates than those in the control plots.
- Soil analyses revealed less labile C in the heated plots relative to the controls.

Understory vegetation (study done by Elizabeth Farnsworth, New England Wild Flower Society)
- Measurements made in the early years of soil warming (1992-1993) showed: 1) acceleration of herbaceous plant emergence in the spring in heated plots; 2) decreased species richness in heated plots; and 3) increased relative diameter growth of woody vegetation.
- The same measurements were made in 2003, and the effects of soil warming had changed over the course of 13 years. For example, relative diameter growth of woody vegetation was significantly lower in heated plots, and species composition had diverged among the three treatment types.

Impacts of Aerosols and Clouds on Forest-Atmosphere Exchange

Q. Min

The impact of aerosols and clouds on CO$_2$ uptake and water use efficiency at Harvard Forest has been studied by using collocated turbulent flux and radiation measurements. We developed a fast retrieval algorithm for synthesizing the visible spectrum from multi-narrowband instruments (MFRSR) and applied it to predict the Action PAR (CA_PAR) by convolving with a normalized action spectrum of plants. Taking advantage of simultaneous measurements of direct and diffuse spectral irradiances from a MFRSR, we quantitatively studied issues of “diffuse use efficiency”, CO$_2$ uptake efficiency and water use efficiency and cataloged the impact of aerosols and clouds through photosynthesis on CO$_2$ uptake.
Figure 1. Percent changes in carbon release in response to soil warming. Data are presented as three-year running means.

Figure 2. Percent changes in nitrogen mineralization in response to soil warming. Data are presented as three-year running means.

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Figure 3. Nitrogen availability conceptual model. Year 0: Soil temperature is increased by 5°C. Year 4: N mineralization rates more than double. Increases in available carbon and nitrogen greatly increase potential for carbon storage by trees. Year 8: With time, increases in N mineralization rates begin to decline, but woody storage continues to increase as nitrogen moves through the system. Year 12: Nitrogen mineralization rates head towards a new equilibrium as nitrogen sources mobilized by a 5°C increase in temperature are depleted and the pulse of nitrogen continues to move through the system.

Figure 4. Annual CH$_4$ uptake at the Harvard Forest soil warming experiment. Measurements were made April – November.

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Optical properties of aerosols and clouds have significant impacts on photosynthesis not only through changes of the total amount of PAR, but also through changes of its spectral distributions (or light quality) and its partitioning between direct and diffuse components. Fig. 1 shows scatterplots of direct and diffuse CA_PARs against optical depths of aerosols and clouds in three atmospheric categories: aerosols, thin clouds, and thick clouds. For a given optical depth, the atmosphere loaded with aerosols has higher direct CA_PAR and lower diffuse CA_PAR than with thin clouds. Clouds enhance diffuse irradiance at longer wavelengths much more effectively than aerosols. The averaged values of direct and diffuse CA_PARs for optical depths between 0.44 and 0.46 are 0.295 and 0.187 mmol m\(^{-2}\)s\(^{-1}\) under aerosol conditions, and 0.234 and 0.272 mmol m\(^{-2}\)s\(^{-1}\) under thin cloud conditions, respectively. The ratio of direct CA_PAR to diffuse CA_PAR dramatically changes from 1.57 under aerosol conditions to 0.86 under thin cloud conditions, i.e. the diffuse CA_PAR is substantially enhanced under thin cloud conditions. The total CA_PAR (direct + diffuse) under thin cloud conditions is about 5% more than under aerosol conditions.

To illustrate the importance of spectral variation of PAR, we compare the reconstructed PARs by convolving with the normalized action spectrum (CA_PAR) and the response function of LICOR sensors (LICOR_PAR). Fig. 2 shows ratios of CA_PAR and LICOR_PAR under three categories of atmospheric conditions for solar zenith angles between 55 and 60 degrees. This ratio indicates the portion of LICOR_PAR that directly involves in the photosynthesis process. Under aerosol conditions, the ratio slightly decreases with increasing of aerosol optical depth. Under thin and thick cloud conditions, the ratio increases from 0.55 to 0.75 as cloud optical depth increases. It indicates that spectral distributions of PAR under cloudy conditions are more favorable to plant photosynthesis than under aerosol conditions. It demonstrates the importance of light quality (spectral distribution) on photosynthesis due to variations of aerosols and clouds in the atmosphere.

Fig. 3 shows scattergrams of measured CO\(_2\) uptake flux against effective CA_PAR under different sky conditions for the growing season of 1998 at the Harvard Forest site. The “diffuse use efficient” coefficients under aerosol and patch/thin cloud conditions are 1.95 and 3.40 with maximum correlation coefficients of \(R^2\), 0.62 and 0.71, respectively. This means that under patch/thin cloud conditions the enhanced diffuse irradiance due to clouds is more efficiently intercepted by the forest and thus increases carbon assimilation. Furthermore, the efficiency of carbon uptake increases from aerosols, patch/thin clouds, to thick clouds, as summarized in Table 1. Under thick cloud condition the CO\(_2\) uptake efficiency is about 57% and 13% higher than under aerosol and patch/thin cloud conditions, respectively.

The WUE, shown in Fig. 4, also shows significant enhancement as atmospheric conditions change from aerosol to thick clouds. The WUE under thick cloud condition is almost 5 and 3 times greater than under aerosol and patch/thin cloud conditions, respectively. The primary reasons are that moisture in the forest is enhanced due to the presence of clouds, and transpiration is enhanced due to the enhanced CO\(_2\) uptake efficiency. In addition to changes in moisture, the presence of clouds can both cause and be the consequence of changes in many atmospheric factors such as temperature, latent heating, VPD, and stomatal dynamics. We may conclude that an increase of radiation level might not be the only factor responsible for the enhance carbon assimilation. Changes in many other factors, such as temperature, moisture, latent heating, and precipitation, in the presence of clouds may have direct and indirect influences on carbon assimilation and water use efficiency.
Satellite Observations of Forest-Atmosphere Exchanges

Q. Min and B. Lin

Developing remote sensing techniques to observe biosphere processes is extremely useful for studies of regional and larger scale variations as the land surface types change induced by natural and anthropogenic influences. Satellite remote sensing is potentially a unique tool for this purpose. In this paper we use an integrated approach that combines multiple-platform/multi-spectrum visible, infrared, and microwave observations from surface and satellites to estimate microwave land surface emissivity (MLSE). By linking MLSE with collocated surface turbulent and radiative fluxes over dense forest area, Harvard Forest, we demonstrate the utility of satellite remote sensing to monitor surface land-atmosphere exchanges. More importantly, MLSE can be derived from satellite measurements during both day and night times with minimum influences from the atmosphere.

When a vegetation layer is present over the soil surface, it attenuates soil microwave emission and adds its own contribution to the optical depth of vegetation at microwave wavelength relates to vegetation water content (VWC) and canopy structure and varies systematically with frequency. This characteristic prompts us to define a new index based on emissivity difference between two frequencies to understand vegetation dynamics, i.e., the microwave emissivity difference index (MEDI) as

\[
MEDI_p = \frac{MLSE_p - MLSE_b}{0.5(MLSE_A + MLSE_B)}.
\]

We will apply MEDI data derived from 19.4 Ghz, and 37.0 Ghz channels of Special Sensor Microwave/Imager (SSM/I) measurements to investigate their potential for detecting vegetation physiology changes and estimating surface land-atmosphere exchanges.

Fig. 1 shows scatterplots of the derived evapotranspiration (ET) fraction (EF), \( EF = ET / Q \), at the Harvard Forest site against the satellite retrieved MEDI for years 1999 and 2000. The solid dots represent cases under cloud conditions when the averaged SW radiation was less than 250 W/m². The straight line represents a least squares fitting between the EF and the MEDI. The correlation coefficient \((R^2)\) between the EF and the MEDI is 0.51 for vertical polarization and is greater than 0.40 for horizontal polarization. In the following study, we will mainly use the MEDI_V. During transition periods of early growing season and leaf senescence (MEDI<0.014), there was no sign of water stress in both years, and thus water availability was not a limiting factor in ET. The transpiration determined by the stomatal resistance changes with the leaf physiology of the forest. The transpiration process plays dominant role in regulating ET during the early spring and later summer. However, during the growing season when the canopy resistance was low, the EF increased with MEDI_V but showed much less correlation. Evaporation process of intercepted water on leaves could have a significant impact on the ET process in these cases.

The ET process also strongly depends on the availability of energy to the canopy. Fig. 2 shows a scattergram of observed ET and newly defined an ET index: \( ETI = MEDI * SW \). The solid line represents a linear least squared fitting, indicating a good correlation between the MEDI_V and the ET, The correlation coefficient of \( R^2 \) is 0.89, much better than that of the EF vs. MEDI because ET is essentially decided by SW energy inputs and vegetation states. It further demonstrates an intrinsic linkage of the MEDI to biophysical parameters of canopy. It is worth to notice that the ET index is fully defined by remote sensed parameters from satellite measurements. The high correlation between the ET and the ETI demonstrates that we can solely use remotely sensed data from a combination of measurements from optical, infrared, and microwave sensors to accurately estimate ET.

Quantification of carbon stocks and fluxes is a key objective for ecosystem and carbon cycle studies. The CO₂ uptake fluxes are strongly related to vegetation characteristics and PAR fluxes. As demonstrated previously, the MEDI has an intrinsic linkage to
biophysical parameters of canopy. We further exploit the feasibility of utilizing remotely sensed MEDI to estimate \( \text{CO}_2 \) uptake flux. As ET flux cases, the products of the MEDI and observed surface PAR are well correlated \((R^2 > 0.6)\) with the \( \text{CO}_2 \) uptake observations at Harvard Forest (Fig. 3). Again, the surface PAR can be estimated accurately from satellite measurements in optical wavelength domain. Therefore, remotely observing land surface-atmosphere exchange of moisture and \( \text{CO}_2 \) from satellite is possible, which provides a vital means in studies of regional- and global-scale ecosystems and climate changes.

**Soil Warming Hastens Successional Dynamics in a Temperate Forest Ecosystem**

J.E. Mohan, F.A. Bazzaz, E. Burrows, H. Lux and J.M. Melillo

Extratropical forests of the Northern Hemisphere are currently important sinks for atmospheric carbon dioxide \((\text{CO}_2)\), largely due to forest regrowth on abandoned agricultural land. At the Barre Woods site in Harvard Forest, we tested the hypotheses that soil warming could affect forest regeneration dynamics by preferentially benefiting either highly-productive or slow-growing understory tree species - potentially altering rates of forest succession with accompanying implications for future net ecosystem productivity (NEP). Using data on pre-treatment and post-treatment growth of 11 tree species, we found that a 5 °C increase in soil temperature caused a 50% enhancement in understory productivity \((p<0.0001, \text{Fig. 1})\). The magnitude of the heating effect was negatively correlated with intrinsic growth rate, so that warming preferentially benefited slower-growing taxa (Figs. 2 and 3). Of the six species that exhibited significant growth enhancements from warming, five were the slowest growing taxa under control conditions: *Fraxinus americana* \((p=0.01)\), *Tsuga canadensis* \((p=0.005)\), *Quercus velutina* \((p=0.01)\), *Acer saccharum* \((p=0.001)\), and *Prunus serotina* \((p=0.07)\). The sixth species, *Acer rubrum*, had intrinsically rapid growth under control conditions but additionally grew faster with soil warming \((p=0.003)\). In contrast, fast-growing species like *Betula alleghaniensis*, *B. lenta*, and *Acer pensylvanicum* exhibited negligible responses to warming. These results may partially explain the large contemporary increase in *A. rubrum* abundance, and suggest that future forests may cycle more rapidly through successional development. Long-term carbon uptake by forests may be less than suggested by current estimates based on highly-productive aggrading stands, and projections of biotic feedbacks to the global carbon cycle may require revision.

**Table 1.** Diffuse-use-efficiency, \( \text{CO}_2 \) uptake efficiency, and water use efficiency under three categories: aerosol, thin and/or patchy clouds, and thick clouds.

<table>
<thead>
<tr>
<th></th>
<th>Diffuse use efficiency</th>
<th>Carbon uptake efficiency</th>
<th>Water use efficiency</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>(umol/mmol)</td>
<td>Correlation Coefficient ((R^2))</td>
<td></td>
</tr>
<tr>
<td>Aerosols</td>
<td>1.95</td>
<td>20.6</td>
<td>0.62</td>
</tr>
<tr>
<td>Patch/Thin clouds</td>
<td>3.40</td>
<td>28.7</td>
<td>0.71</td>
</tr>
<tr>
<td>Thick clouds</td>
<td>NA</td>
<td>32.3</td>
<td>0.71</td>
</tr>
</tbody>
</table>

Q. Min
Figure 1. The direct and diffuse CA_PAR vs. optical depths of aerosols and clouds under three categories: aerosols, thin clouds, and thick clouds.

Figure 2. Ratios of CA_PAR to LICOR_PAR under three sky conditions for solar zenith angles between 55 and 60 degrees during the growing season of 1998 at the Harvard Forest site.

Q. Min
Figure 3. Scattergrams of direct, diffuse, and effective CA_PAR vs. measured CO₂ uptake under aerosol, patch/thin cloud, and thick cloud conditions.

Q. Min
Figure 4. Scattergrams of total effective CA_PAR vs. measured WUE under aerosol, patch/thin cloud, and thick cloud conditions.

Q. Min
Figure 1. EF as a function of MEDI_V and MEDI_H for years 1999 and 2000.

Q. Min and B. Lin
Figure 2. ET as a function of MEDI_V for years 1999 and 2000.

Figure 3. CO₂ uptake fluxes as a function of MEDI*PAR for years 1999 and 2000.

Q. Min & B. Lin
Figure 1  Heated plants grow on average 50% faster after soil warming begins.

**5 of 6 responders are slowest growing taxa**

*Increasing Growth in Control Plot →*

*J.E. Mohan, et al.*
Twenty Years of Forest Harvesting Across Massachusetts: Influences on Stand Composition and Invasive Plant Species

G. Motzkin, D.R. Foster, D. Kittredge, J. Burk, B. Hall and J. Hall

Harvesting is widespread across the western two-thirds of Massachusetts and is expected to continue into the future. However, in part because selective logging is typical in the region and is difficult to document with remote sensing, comprehensive spatial data on harvesting activities are generally lacking, particularly for the non-industrial private forest (NIPF) lands that comprise ~80% of forests in the state. Massachusetts Executive Office of Environmental Affairs (EOEA) has a unique, spatially-explicit data set developed for regulatory purposes that can be analyzed to provide important information for management and conservation planning. Analysis of a subset of these data from 19 towns in north-central Massachusetts suggests a surprisingly high frequency of harvesting; approximately 1.5% of the forest area is logged annually in a spatially random pattern that has left few large forest blocks undisturbed over the past 20 years (Kittredge et al., 2003). Mean harvest intensity is 44.7 m³ ha⁻¹, or 26.7% of average stand volume, with the highest intensity logging (69.3 m³ ha⁻¹) conducted by the agency responsible for overseeing the largest conservation property in southern New England. The impact of such widespread, moderate intensity disturbance on forest management and conservation values and threats, including forest regeneration, distribution and spread of invasive species, and the integrity of forest, wildlife, and aquatic habitats, is almost completely unknown. We have initiated a study to document forest harvesting patterns across Massachusetts from 1984-2003 and to evaluate the influence of harvesting on residual forest composition, tree regeneration, and invasive species distribution.

This summer we will begin extensive field work across central and western Massachusetts which, in combination with the
20-year, spatially-explicit, forest harvesting data set, will enable us to: (1) document forest cutting patterns; (2) describe their spatial and quantitative characteristics with regards to important forest resource values and physical, cultural, and environmental factors; and (3) evaluate the influence of harvesting activity on residual stand composition, forest regeneration, invasive species distribution, and vegetation structure and composition. This study is a collaborative effort with The Nature Conservancy and results from this study will help inform regional conservation efforts. In addition, information that we gather will allow MA Department of Conservation and Recreation (DCR) staff to assess regional forest management concerns (i.e., high grading and invasive species) and will directly aid statewide Forest Certification and Ecoregional planning efforts.


G. Motzkin, D A. Orwig, and D.R. Foster

Over the past decade, we have conducted a series of investigations of the disturbance histories and dynamics of a wide range of barrens vegetation on sand plains in the Connecticut Valley and in the coastal region from Cape Cod to Long Island. In the current study, we extend these investigations to rocky ridgetops that support pitch pine or native red pine in southern New England. Despite strong similarities in vegetation between ridgetops and sand plains, it is likely that ridgetops differ substantially from sand plains with respect to disturbance history and vegetation dynamics. During this past year, we sampled ridgetop pitch pine vegetation on summits in the Taconic Mountains, where preliminary data suggest that stands are uneven-aged, similar to our previous results from Mt. Everett. The oldest individual ridgetop pitch pine that we have sampled to date exceeds 225 years of age, although most stems are substantially younger.

We are currently analyzing data from several ridgetop sites supporting native red pine. Although red pine has been planted widely in New England, very few sites are known in Massachusetts where the species is thought to be native. One site investigated supports numerous individuals that are ~180-220 years old, with a few older stems. Whereas some stands are apparently uneven-aged and have relatively abundant saplings or seedlings, others lack any recent red pine regeneration. Charcoal or scarring is evident in each of the red pine sites visited thus far, suggesting that fire has strongly influenced the occurrence and dynamics of these sites.

Woody Species Phenology, Prospect Hill Tract, Harvard Forest - 2003

J. O'Keefe

2003 was the fourteenth year in our ongoing investigation of the timing of woody vegetation development during the growing season. However in 2002 the scope of the study was changed significantly. For the first twelve years we observed bud break, leaf development, flowering, and fruit development on three or more individuals of 33 woody species at 3-7 day intervals from April through June. These observations documented substantial (up to three weeks difference) interannual variation in the timing of spring development, but good relative consistency among species and among individuals within species during these twelve years. Therefore, starting in 2002 we maintained the same observation schedule, but reduced the number of species observed to eight, including red maple (Acer rubrum), sugar maple (A. saccharum), striped maple (A. pensylvanicum), yellow birch (Betula alleghaniensis), white ash (Fraxinus americana), witch hazel (Hamamelis virginiana), red oak (Quercus rubra), and white oak (Q. alba). This subset of important, representative species should allow us to continue to characterize leaf development each spring, and document interannual variability while reducing the resources required for the study significantly. Weekly observations of leaf coloration and leaf fall began in September and continued through leaf fall. All individuals
are located within 1.5 km of the Harvard Forest headquarters at elevations between 335 and 365 m, in habitats ranging from closed forest, through forest-swamp margins, to dry, open fields.

The winter of 2002-2003 was much colder than normal with near normal precipitation, which resulted in snow cover well into April. Cool weather continued through the spring. By summer the pattern changed to warm and moist, which continued into the fall. The first frost at Harvard Forest didn’t occur until October 3rd, seven days later than the mean first frost date since 1990, but still eleven days earlier than the first frost in the anomalous fall of 2002.

For most species initial bud break in 2003 was extremely late (Table 1/Fig. 1), putting 2003 in a group with 1992 and 1997 as the years with the latest leaf emergence during the fourteen years of observation. Leaf development then progressed rather steadily with 75% leaf development also occurring among the group of very late years.

Fall coloration and leaf fall in 2003 were quite late, but still nearly a week ahead of the extremely late timing of these events in 2002. Averaging the four species in Fig. 1, 50% leaf fall occurred on October 20th, five days earlier than in 2002, but still five days later than the prior ten-year mean and even with the prior latest year (1999). The extreme lateness observed in 2002 expanded the variability observed in leaf senescence significantly, so that it more closely resembled the variability observed in leaf emergence over the course of this study, and began to call into question our previous assumption of considerably less variability in the timing of fall events. These observations again point out the need for long-term data sets and emphasize the importance of temperature in regulating these events.

Scaling Forest Productivity Through Space and Time Using Hyperspectral Remote Sensing and Ecosystem Modeling

S. Ollinger, M-L. Smith, J. Jenkins, L. Plourde, M. Martin, D. Hollinger and J. Aber

Understanding patterns of productivity and carbon cycling in temperate forests is important for a number of scientific and policy issues. Locally, estimates are needed to address land management issues ranging from timber harvesting to preservation of ecosystem diversity. Globally, forests play an important role in the earth’s carbon cycle and are believed to represent an important sink for atmospheric CO₂. The importance of understanding variation through space and time stems from the need to scale site-level measurements to their broader surrounding regions and to identify underlying mechanisms responsible for observed ecosystem behavior. We have been examining the degree to which canopy nitrogen chemistry can serve as an integrator of C flux patterns in northern temperate forests. The functional basis for using foliar N as a scalar of C uptake lies in the fact that the proteins responsible for CO₂ capture by leaves (e.g. rubisco) account for the majority of nitrogen in plant canopies. This and other linkages between terrestrial C and N cycles has motivated several new advancements in the ability to detect canopy nitrogen using hyperspectral remote sensing.

At several sites across New England, including the Howland Forest in Maine, The Bartlett Experimental Forest in New Hampshire and the Harvard Forest in Massachusetts, efforts to map canopy N using spectral data from NASA’s AVIRIS and Hyperion instruments have been coordinated with plot level measurements of stand and canopy properties. At Bartlett, mapped estimates of canopy N concentrations were used to drive the PnET ecosystem model, resulting in prediction accuracy that was considerably improved over previously-available methods and revealing environmental controls related to climate, land
Table 1. Estimated mean leaf development dates (month-day) for individuals of six representative species over twelve years (IBB = initial bud break, 75% = 75% leaf development).

<table>
<thead>
<tr>
<th></th>
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</table>

J. O’Keefe
50% BUD BREAK (bottom), 75% LEAF SIZE (middle), 50% LEAF FALL (top)

Figure 1
J. Okeefe
use and topography (Fig. 1). Model predictions and plot-level measurements both indicated strong relationships between whole-canopy N concentrations and measured aboveground productivity (ANPP; Fig. 2).

Much of our present understanding of temporal patterns in forest C dynamics derives from data collected using the eddy covariance method. At the Harvard Forest EMS tower, temporal trends in gross primary productivity include an upward trend over the period from 1992-2001, interrupted by a decline in 1998 (S. Urbansky and S. Wofsy; Fig. 3a, solid black line). This pattern is of interest for a variety of reasons, but few explanations have been brought forward. Running the PnET-Day canopy photosynthesis model over this time period using measured daily climate inputs and a constant foliar nitrogen value produced a roughly 10% underestimate and did not track these observed temporal trends (Fig. 3a, dashed gray line).

In a second set of model runs, interannual variation in canopy N was included using data from the control plots of the nearby chronic N study (data courtesy of A. Magill and J. Aber). Interestingly, data for the dominant deciduous species—black oak and red oak—showed a mild upward trend in foliar N over time, similar to that in GPP, and produced model predictions that agreed more strongly with measured flux data (Fig. 3b, gray line). The underlying causes of these patterns are still unclear, but these results suggest that temporal variation foliar N may help to explain the observed trends in carbon uptake.

Hemlock Woolly Adelgid at the Arnold Arboretum: Threats and Opportunities

D.A. Orwig, P. Del Tredici, H. Lux, R. Schulhof and D.R. Foster

Hemlock Hill at Harvard University’s Arnold Arboretum is located in Jamaica Plain and has long been considered a remnant of the forest primeval in the heart of Boston. Eastern hemlocks have dominated the flanks and crest of this hill for centuries, despite experiencing many past disturbances including cutting in the late 1700s and early 1800s, fire in 1932, hurricane damage in 1938, and heavy snow damage in 1997. Following this snowstorm, a new threat was discovered on the downed branches, the introduced insect pest, the hemlock woolly adelgid (HWA). Since the discovery of HWA at the Arboretum, an action committee was formed to develop plans for managing Hemlock Hill to meet the new threat. Over 1800 hemlock trees were tagged, measured for diameter, assigned a crown health rating, and mapped with GPS coordinates. Various chemical and biological control treatments were attempted to control the spread of HWA at the arboretum, with mixed success. From 1998 to 2002, 263 trees have died or were removed due to poor health. Of the remaining 1600+ trees, 70% are rated as being in poor condition. Since this is a heavily used portion of the Arboretum, which is part of the Boston Parks Department, the decision has been made to remove many of the dead and dying trees to reduce risks posed to the general public by falling limbs. This unfortunate turn of events provides us with an unusual opportunity to examine the environmental impacts of hemlock death and hemlock removal in an urban environment, including soil nutrient cycling, microclimate changes, and vegetation succession, especially the spread of invasive species. During 2004, we will collect baseline soils and vegetation information in 6 plots on the hill. Hemlocks will be removed from 4 plots in winter of 2005, and 2 will remain as control plots. Slash in the cut plots will either be chipped and left on site or removed to see what impact it has on ecosystem and vegetation trajectories. Data from this project will provide a nice comparison to the rural cutting and girdling that will take place at HF next year (see Barker Plotkin, Ellison et al., this volume). Simultaneously, we will be investigating the resistance of Chinese hemlock (Tsuga chinensis) to HWA. This species, which was planted on Hemlock Hill in 1999, appears to be extremely resistant to HWA and may be useful in reforesting portions of the hill.
Figure 1. Predicted net primary production for the Bartlett Experimental Forest in New Hampshire, generated by combining remotely-sensed estimates of canopy nitrogen with the PnET ecosystem model.

Figure 2. Predicted and observed wood growth in relation to canopy N concentrations at the Bartlett Experimental Forest. Wood growth measurements are from multiple-year biomass increments. Foliar N data are from plot measurements and spectral calibration of image data from the Airborne Visible and InfraRed imaging Spectrometer (AVIRIS).

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Figure 3. Predicted and observed daily gross primary productivity (GPP) at the Harvard Forest flux tower (data courtesy of S. Urbansky and S. Wofsy). Predictions were generated with PnET-Day using daily meteorological inputs. Figure 3a shows model predictions using a constant foliar N value. Figure 3b shows model predictions using variable foliar N data from the HF chronic N addition control plots.

S. Ollinger, et al.
Landscape Level Analyses of Hemlock Woolly Adelgid Outbreaks in Massachusetts

D. Orwig and N. Povak*

Over the last 18 years, hemlock woolly adelgid (HWA) (*Adelges tsugae*), an introduced aphid-like insect from Asia, has expanded its range from southern Connecticut to northern Massachusetts, causing widespread mortality and decline of *Tsuga canadensis* (eastern hemlock). Building on similar analyses in Connecticut, we have mapped the distribution of all *T. canadensis* stands (> 3 ha) prior to HWA infestation in a 4000 km² transect through Massachusetts to characterize the temporal and spatial patterns of damage generated by HWA since the time of its arrival into the area in 1989. To date, over 5000 stands with > 10% hemlock have been mapped, representing over 86,000 ha, or 21% of the study area (Fig. 1). We began sampling in the NW corner of the region in the summer of 2002 and have since sampled 79 stands to obtain information on forest structure, composition, and crown vigor, site and edaphic characteristics, potential replacement species, and the spatial pattern of HWA and associated canopy damage. Overstory *T. canadensis* importance ranged from 24 – 92% and total stand densities varied from 225 - 2025 ha⁻¹. Most stands were found on northern and western aspects with slopes of 20 - 30%. HWA was found in close proximity (a few km) to VT, suggesting it is continuing to migrate unimpeded at the northern extent of its current range.

HWA was present in almost 50% of the sampled stands, although overstory hemlock mortality levels are still very low in most stands. Only 5 stands had greater than 20% overstory hemlock mortality and 2 forests located along the southern border had overstory losses > 50%. Over half of the stands visited had experienced some level of hemlock logging in the last 10 years. This information has been incorporated into a GIS analysis of the landscape-level, biological, edaphic, and historical factors associated with the patterns of HWA-induced hemlock damage. Potential replacement species already present in the canopy of many *T. canadensis* forests include *Quercus rubra* (red oak), *Pinus strobus* (white pine), *Betula lenta* (black birch), and several *Acer* (maple) species.

We will continue to sample stands throughout this region in 2004 to examine the relationship between site and stand characteristics and intensity of infestation and extent of mortality that occurs.

![Figure 1. Distribution of all mapped hemlock stands in central Massachusetts, with location of sampled forests.](image-url)
Community and Ecosystem Effects of HWA-Induced Logging.

D. Orwig, L. Pustell, S. Jefts and D.R. Foster

The recent unimpeded infestation of the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) across the northeastern U.S. has created a situation in which large-scale hemlock decline and mortality is occurring. HWA has already infested over 40% of the towns in Massachusetts and, as a result, many landowners are choosing to pre-emptively harvest their hemlock stands. Information from timber harvesters, state agencies, and studies of landscape patterns of hemlock decline in southern New England indicate that the recent broad scale increase in logging associated with HWA is occurring with little ecological assessment and in the absence of scientific background for conservationists, land managers, or policy makers.

We are beginning a study that builds on previous work on hemlock logging (Kizlinski et al. 2002) and compares HWA impacts with those of hemlock harvest on the magnitude and trajectory of community and ecosystem dynamics. Twelve sites have been selected for intensive study throughout central Massachusetts on public and private lands where hemlocks have been recently harvested at varying intensities. At each site we will monitor: available soil nitrogen using semi-annual resin bags, soil mineralization and nitrification using *in situ* incubated soil cores, and soil temperature with dataloggers throughout the growing season. In addition, we will sample herb, shrub, and understory woody vegetation dynamics. We will contrast the rate, magnitude, and quality of community and ecosystem response to logging versus HWA and relate these to differences in site conditions, microenvironmental change, and disturbance intensity. We hope to be able to make recommendations to landowners about the most ecologically appropriate management practices for their hemlock stands.


Ecosystem Analyses of Hemlock Woolly Adelgid Outbreaks in Southern New England

D. Orwig, S. Jefts, L. Pustell and D.R. Foster

In 1998 we began examining the response of ecosystem processes to the stress and mortality caused by the introduced hemlock woolly adelgid (HWA) in 8 sites in southern New England varying in HWA infestation level. Over the last 5 years, chronic HWA infestations at most of these sites have led to deteriorating crowns and increases in forest floor light levels. In addition, these structural changes have led to lower soil surface moisture levels, higher soil temperatures, and higher sub-surface moisture levels. These microenvironmental changes, in combination with reduced uptake as trees deteriorate, have lead to attendant changes in N availability and cycling over time. Infested stands have consistently exhibited higher net nitrogen mineralization and nitrification rates, as well as higher nitrogen availability than uninfested or recently infested stands. Results indicate that introduced pests and selective tree decline can rapidly and dramatically alter ecosystem processes, even prior to the onset of extensive tree mortality. In 2001, we began examining 2 additional stands that contain high overstory hemlock mortality and a dense black birch understory (see Jefts and Orwig this volume). We will continue to sample these stands and select a few additional sites (e.g., uninfested controls and heavily infested stands with birch understories) as they deteriorate to determine the extent to which changes in overstory composition, microenvironment, and soil conditions produce fundamental changes in the cycling of nitrogen.
Late Holocene Vegetation Patterns of the Coastal Region of Southern New England and New York

W W. Oswald, D. R. Foster, and G. Motzkin

Plant communities of the coastal region of the northeastern United States, including grasslands, shrublands, and pitch pine-oak forests, are of great conservation interest because they provide habitats for numerous uncommon and rare species and assemblages of plants and animals. To inform management and conservation efforts, various approaches have been used to determine which factors influence the composition and distribution of coastal ecosystems. In general, three factors are thought to be responsible for the primary variations in vegetation: substrate, disturbance (e.g. wind, fire), and land-use history. To better understand how these and other factors affect modern ecosystems, we examine paleoecological records from sites along the coast and on nearby islands from Cape Cod, Massachusetts, to Long Island, New York (Fig. 1), and thus provide the first summary of late Holocene vegetation change across this region.

Pollen records are available from many coastal sites, including Cape Cod, Nantucket, Martha’s Vineyard, Block Island, and Long Island. These sites represent a range of modern plant communities, geographic settings, disturbance histories, and substrate types. We compared a subset of the records to explore regional patterns of vegetation for the time periods before and after European settlement, restricting the pre-settlement interval to 2500 years before present. Multivariate analysis of the 14-site dataset using detrended correspondence analysis (Figs. 2 and 3) reveals two general patterns: (1) compositional variations in pre-settlement forests, and (2) varying impact of settlement-era forest clearance.

For the pre-settlement interval, sites generally can be assigned to either pine- or hardwood-dominated forest types. Sites with high pine pollen percentages (20-60%) are located on Cape Cod (Round, Eagle, Fresh MA, and Duck) and Long Island (Wildwood). The Cape Cod sites are located on coarse-textured glacial outwash, a substrate that favors pitch pine. Wildwood Lake is located on a moraine within Long Island’s pine barrens region (Fig 1). Hardwood-dominated forest sites are characterized by high pollen percentages for oak (30-50%), beech (5-15%), hickory (5-10%), and/or maple (3-8%). Several of these sites are located on moraines (e.g. Deep, Sandy Hill, Fresh RI, and Harlock), but others occur on better-drained substrates (e.g. Jemima), indicating that the composition of pre-settlement forests was not determined by edaphic conditions alone. The pollen records from several of the hardwood-dominated sites exhibit a strong response to settlement, with large increases in the percentages of weedy and agricultural pollen types. In particular, Fresh RI, Ice House, Jemima, Duarte, and No Bottom Pond have large compositional differences between pre- and post-settlement samples, suggesting that these sites may have experienced the greatest degree of forest clearance. This interpretation is generally consistent with maps of mid-19th century forest cover, as several of these sites have little nearby forest cover at that time (Fig. 1).

This comparison of late Holocene pollen records from across the coastal region of southern New England and New York reinforces the conclusion that plant community patterns are strongly influenced by substrate and land-use history. Future analyses will incorporate sedimentary charcoal records to further explore spatial and temporal variations in fire across this region.

Contribution of Red Maple to Carbon Uptake in the Eddy-flux Tower Plot Forest

N. Pederson, E. Hammond Pyle, A. Barker Plotkin, G. Jacoby and S. Wofsy

Northern red oak (Quercus rubra L.) (NRO) and red maple (Acer rubrum L.) are the primary contributors to annual carbon uptake of the forest surrounding the eddy-flux tower at the Harvard Forest (HF). Both species were sampled to compare tree-ring and eddy-flux estimates of carbon uptake. NRO results were presented at last year’s symposium. (Pederson
Figure 1. Map of southern New England and New York showing study sites and surficial geology (top panel) and mid-19th century forest cover (bottom panel).

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Figure 2. Detrended correspondence analysis of pollen records from southern New England and New York. Closed and open symbols are centroids of pre- and post-settlement samples, respectively. Thick black lines = Cape Cod; thin black lines = islands; gray line = Long Island. Squares indicate sites located on glacial outwash deposits; circles indicate moraines and other substrates.

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Figure 3. Detrended correspondence analysis taxon scores for pollen records from southern New England and New York.

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et al., 14th Annual Harvard Forest Ecology Symposium Abstracts, 2003). We focus on red maple this year. Thirty-five previously tagged red maple were randomly selected and cored in the eddy-flux tower footprint (TP) and the Lyford Plot (LP) in July 2003. Three cores/tree were collected. The radii were cored approximately 120° from each other around the stem. Crossdating, a fundamental dendrochronological technique, was used to develop a precisely dated annual time series of growth. Crossdating is the process of identifying unique sequences of ring patterns and characteristics among all core samples to assign calendar dates to each ring. When done correctly this process creates a time series with a dating error of +/- zero years. After crossdating, annual ring widths were measured to the nearest 0.001 mm.

Red maple chronology development revealed that some trees were capable of great radial growth plasticity. For example, radius \( a \) of tree E4_822 in the TP experienced a significant growth reduction from 1956-1971 while the other radii grew fairly normally (Fig. 1A). Radius \( a \) of tree 4309 in the LP experienced a significant growth increase starting in the late-1980s while radius \( b \) continued to decline in radial increment (Fig. 1B). The plasticity suggests a survival strategy for red maple saplings that allows it to persist through years of poor growing conditions.

Six of the 35 cored trees had very little radial growth around their lower stem over the last 10-15 years (Figs. 1A, 2). Mensuration data supports these results. The largest growth declines occurred after gypsy moth defoliation in 1981, which appears in the form of a white colored, narrow 1981 ring. The declines also coincided with 6 years of August drought and two cold winters during the early 1980s. From 1930-1994 red maple growth was strongly correlated to increased August precipitation and prior-October through January temperatures. The combination of these abiotic and biotic events reduced red maple growth.

Canopy position and climatic sensitivity may explain differences in recent growth rates between NRO and red maple (Fig. 2). From 1930-1994 NRO was only weakly correlated to August precipitation and prior October temperatures and significantly, but negatively correlated to February temperatures. Since NRO growth was also negatively impacted by gypsy moth defoliation, it seems its dominant canopy position and relative insensitivity to winter temperatures versus red maple gives it a competitive advantage.

Comparison of NRO and red maple basal area increment curves, a proxy for biomass and carbon uptake, indicate that at the tree scale, the contribution of red maple to forest carbon uptake is declining (Fig. 2). Because of their large numbers (264 stems/ha vs. 124 stems/ha for NRO), however, red maple still contributes significantly to stand level carbon uptake. In contrast, NRO contributes a significant amount of carbon uptake primarily through higher growth rates.

This experimental research comparing tree-ring and eddy-flux estimates of carbon uptake is in its final stages. NRO and red maple chronologies from the Lyford Pots will be used to determine if the TP trees are a good representation of growth at the HF. Chronologies of eighteen NRO populations covering central New England and New York State will be used to place the HF NRO in a long-term and regional perspective.

Vegetation Control of Ecohydrologic Processes

N. Phillips, M. Daley, M. Friedl and G. Salvucci

The dynamics of water storage and depletion in trees occurs on timescales similar to that of the characteristic response times of small watersheds.

Our work at Harvard Forest seeks to understand how vegetation modulates ecohydrologic function, such as stream hydrographs. In our first summer of research we quantified hydraulic resistance to water flow and storage capacity in boles and branches of Paper Birch, Red Oak and Red Maple. We applied step changes in light and vapor pressure deficit to examine the time lags of water flux in these tree species. These data provide a diagnostic means of determining whole tree
Carbon Dynamics at Harvard Forest: Results From the EMS Tower and Ecological Plots


We use two approaches to characterize carbon dynamics at Harvard Forest – continuous eddy-flux measurements and ground based ecological plots. Eddy-flux measurements provide integrated whole system measurement of the interaction between forest and atmosphere. The ecological measurements provide context for eddy-flux measurements, allowing us to partition carbon fluxes among major forest carbon pools. Additional ecological measurements in an adjacent actively managed stand monitor the long and short-term changes in the carbon cycle following a typical New England harvest.

Since the tower was established in 1991, continuous eddy-flux measurements of carbon dioxide at Harvard Forest indicate annual uptake varies year to year, with annual carbon sequestration ranging from 0.8 to 4.2 MgC ha-1 (mean ~ 2.2 MgC ha-1 yr-1) from 1991 to 2002 (Table 1). The banner year of 2001 (see Urbanski et al. abstract from 2003 symposium) was followed by a return to long-term mean in 2002, with measured NEE (Net Ecosystem Exchange) of -2.7. With 11+ years of eddy-covariance carbon exchange measurements, an unambiguous secular trend of increasing GEE (Gross Ecosystem Exchange) and R (respiration) has emerged. The long-term trend of GEE and R is about +2%/yr, which is roughly twice the rate of live biomass accumulation.

In 1993, ecological plots (n=34, 10m radius) were established within the fetch of the EMS tower. In 1998, all trees greater than 10cm in diameter were outfitted with dendrometer bands for repeated measures of tree growth, and litter collections were established. In 2000 and 2003, coarse woody debris (CWD, all pieces of dead wood >7.5 cm diameter, 1m length) were measured in a subset of plots. In 1999, the active forest management study was created by combining three of the original study plots with five additional plots. Trees > 5cm dbh were banded, litter collection established, and CWD surveys were implemented in 1999 (pre-harvest), 2001 and 2003 (post-harvest.) The site was selectively harvested in 2001, with immediate results reported at the 2003 symposium (Hutyra et al.).

For analysis of ecological data, we treat major pools separately, looking first at flux in live biomass (live trees), then in dead biomass (CWD). Accrual of carbon in the pool of live biomass remains roughly consistent, year to year, ranging from 1.03 to 1.6 MgC ha-1 (Fig. 1a), and comprising 60-70% of NEE in most years. The episodic nature of mortality (Fig. 1a), however, leads to great variation in annual storage of carbon in the live biomass pool alone (Fig. 1b). Movement of carbon in the pool of dead biomass is examined by comparing repeated CWD surveys. In the undisturbed tower plots, carbon storage in CWD increased slightly (adding <1 MgC/ha/yr) between 2000 and 2003 (Fig. 2), as would be expected for an aggrading forest. For the logged plots, however, we found a loss of CWD between 2001 and 2003 (Fig. 2), reflecting the decomposition of heavy inputs during the logging (~ 10 MgC/ha/year added between 1999 and 2001).

In 2004, we plan to examine the spatial context of our ecological measurements by re-surveying plots implemented in 2000 by the Big Foot project. A preliminary comparison of tree growth in the Big Foot plots and our plot reveals consistent discrepancy: Big Foot plots show lower standing biomass, but similar annual increments (Fig. 3). This discrepancy might result from different human bias in sampling methods – fixed radius versus variable radius. We plan to address this by performing both methods on the same plots, and developing a relationship between the two data sets.
Figure 1 - Annual increment of 3 radii per tree for a tree in the A) Tower Plot tree E4_822 and B) Lyford Plot tree 4309 showing temporal variations in growth around the lower stem.

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**Figure 2** – Average basal area increment curves for northern red oak (solid line) and red maple (dashed line) in the forest surrounding the eddy-flux tower plot at the HF.

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**Table 1**: Net Ecosystem Exchange (NEE), Respiration (R), and Gross Ecosystem Exchange (GEE) for 11 years of study.

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*E. Hammond Pyle, et. al.*
Figure 1: (a) Gross fluxes in live biomass at Harvard Forest. Above-ground woody increment (AGWI) remains relatively consistent, while mortality appears to be episodic. (b) Net fluxes in live biomass. Episodic nature of mortality leads to greater variation in net storage in live biomass.

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Figure 2: Gross and net fluxes in coarse woody debris (CWD) in undisturbed (“Old 40”) and selectively logged (“Cut site”) plots, as estimated by repeated CWD surveys. “Additions” reflect pieces added between repeated surveys. “Decomposition” reflects pieces that disappeared between surveys. “Fragmentation” reflects reduction of size of remaining pieces.

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Figure 3: Comparison of our tower plots and big foot plots in years 2000 and 2001. Mean standing biomass for tower plots = 108 MgC/ha. Mean standing biomass for Big Foot plots = 71 MgC/ha.

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Red Maple Re-Visited

F. E. Rockwell

The invasion of the understories of oak stands by red maple (Acer rubrum) over the last half century has received considerable attention from forest ecologists. However, the significance of red maple's understory dominance for future canopy composition, or whether in the absence of a stand-replacing disturbance red maple will replace red oak (Quercus rubra) in the canopy as a late successional dominant, remains a subject of debate. Previous research has interpreted individual tree records from permanent plots at the Harvard Forest in Petersham, Massachusetts, and Black Rock Forest in Nyack, New York, as supporting a hypothesis of eventual red maple dominance of these stands. In this study, an additional 30 years of growth and mortality in these plots was analyzed to evaluate an alternative hypothesis, specifically that understory dominance by red maple need not translate into overstory dominance. Analysis of overstory and understory transition rates, growth, and mortality showed that red maple has successfully occupied canopy space released by the declines of Betula papyrifera, and Fraxinus americana. However, such gains in canopy representation have been offset by high rates of mortality, or overtopping associated with continued crown expansion by red oak. In addition, the increasing representation of late successional species such as Fagus grandifolia, as well as the increasing importance of Betula alleghaniensis and B. lenta, suggests that, in natural stands, by the time oak crown stop reiterating these species may be in a position to replace much of the individual oak mortality that occurs. Ecophysiological mechanisms that might explain red maples ubiquity in the understory, but apparent inability to compete with red oak once in the canopy, are discussed.

This study was based on research conducted at TS-1 (as well as data from the Harvard Forest Archives) with Audrey Barker Plotkin’s guidance in the spring and fall of 2003.

A Cross-site Study on the Effects of Experimental N Additions on Fine Root Biomass, N Concentration and Total Soil Respiration

L.E. Rustad, I.J. Fernandez, S. McNulty, A. Magill, J.D. Aber and the NERC N Network

Elevated atmospheric N deposition continues to be an environmental concern in many parts of the industrialized world. Considerable research has addressed the potential consequences of elevated N deposition for forested ecosystems, with significant advances in our understanding of the response of the aboveground plant community, soils, and surface waters to this non-point source pollutant. In contrast, much less is known about the response of the belowground ecosystem, particularly fine roots, to elevated N deposition. In order to address this information gap, we initiated a cross-site study on the response of fine roots to experimentally elevated N deposition. The specific goals of this study are to (1) conduct a meta-analysis of existing data on fine root response to elevated N deposition from experimental sites in the northeastern US, eastern Canada, and northern Europe, and (2) use common protocols to directly measure the effect of N additions on the production, metabolism, and turnover of fine roots at three internationally recognized forest ecosystem study sites in the northeastern U.S.: the Harvard Forest in MA, the Bear Brook Watershed in Maine (BBWM), and Mount Ascutney in VT.

Data from 17 experiments at 15 sites across North America and Europe were used in the meta-analysis. Results showed that, across all sites, N additions:

1. significantly decreased O horizon and upper mineral soil fine root biomass by a mean of 43% and 17%, respectively,
2. increased O horizon and upper mineral soil fine root N concentrations by a mean of 6% and 17%, respectively, and
3. decreased total soil respiration rates by a mean of 11%.
Preliminary data from the field study showed similar trends at the three experimental sites in the northeastern US, with a general decline in O horizon fine root biomass, an increase in O horizon fine root N concentration, and either no change or decrease in total soil respiration (Fig. 1).

Results from both the meta-analysis and initial year of the field study suggest that elevated N inputs decrease fine root biomass, increase fine root N concentrations, and decrease soil respiration. These results are consistent with the hypothesis that elevated N deposition decreases C allocation to fine roots. Other components of this research will evaluate the effects of N deposition on fine root life span and chemistry, and will attempt to separate the effects of elevated N inputs on root versus microbial respiration.

Coherence Analysis of High Frequency Soil Respiration, Temperature and Moisture Measurements

K. Savage, E.A. Davidson and D. Hollinger

Temporal variation of soil respiration is largely controlled by soil temperature and moisture. Temperature predominately influences the diurnal and seasonal trends in soil respiration, whereas soil moisture plays a significant role in seasonal and interannual variations. Our previous studies have also shown that soil respiration responds rapidly to precipitation events and that the magnitude and duration of response is dependent on many factors, such as length of dry period preceding precipitation, and the magnitude and duration of the precipitation event. In order to tease out these frequency relationships, high temporal frequency soil respiration measurements with corresponding temperature and moisture measurements are necessary. We installed an automated system for measuring soil respiration at a well-drained upland site approximately 150m SW of the EMS tower. Six automated chambers made half–hourly measurements between April 30th through November 28th, 2003. Soil temperature at 10cm depth and water contents in the leaf litter layer, F horizon and mineral soil horizons were logged at the same half-hourly temporal frequency as soil respiration measurements.

The daily and seasonal trends and effects of synoptic weather patterns are evident in the soil respiration measurements (Fig. 1a). Diurnal variations were observed most days (Fig. 1e). The seasonal trend is a general increasing rate of respiration over the course of the summer as soil temperatures warm (Fig. 1c) and then decline into the fall with declining soil temperatures. The effects of synoptic weather patterns appear immediately following precipitation and persist for several days, depending on the amount of precipitation. Periods of several days without rain cause drying of the O horizon and significant decreases in soil respiration.

Coherence analysis was preformed to investigate the relationship between soil respiration and soil temperature and water content at differing temporal frequencies from the spring through fall period of 2003 (Fig. 2). A strong coherence of soil respiration and soil temperature occurs at a one-day interval, representing the diurnal trend. Coherence with temperature is also important for synoptic weather patterns at 11-14 days and seasonal patterns at >90 days. Soil respiration shows a strong coherence with the litter layer and mineral soil water content at about 4 days and at 7-14 days, which corresponds with common intervals between precipitation events and wetting and drying cycles of the O horizon and mineral soil. By understanding sources of variation at diurnal, synoptic, and seasonal temporal scales, we can improve our empirical models and our conceptual understanding of the factors controlling variation in soil respiration.
Figure 1. Mean (a) O horizon live fine root (<1mm) biomass, (b) O horizon live fine root (<1mm) N concentration, and (c) total soil respiration at the BBWM Softwood and Hardwood (BBWM_SW and BBWM_HW) stands, the Mt. Ascutney (ASC) plots, and the Harvard Forest Hardwood (HAR_HW) and Pine (HAR_P) plots. Bars with different letters indicate significant differences between the treatment means within a site at the 0.05 level. Bars with ‘*’ indicate an overall difference between the treatment means within a site at the 0.05 level, without specific pairwise differences.

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Figure 1  a) mean (n=6) soil respiration rate, b) mean gravimetric water content in the litter layer and F horizon, c) volumetric water content in the mineral horizon, d) soil temperature at 10cm depth and hourly precipitation (Harvard Forest), e) soil respiration for jd 122-126 showing the diurnal trend.

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Figure 2: Coherence analysis of mean flux and soil temperature (Soil T), leaf litter water content (Oi WC) and mineral soil water content at 4.5cm depth (4.5cm VSM).

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Changes in Carbon Storage and Net Carbon Exchange After a Shelterwood Harvest at Howland Forest, Maine


While many forests in the northeastern US are actively sequestering carbon, little research has examined the direct effects of forest management practices in this region on carbon sequestration. This is a critical issue for the region, where a large proportion of forests are undergoing some form of management. Will forest management prolong the capacity of forests to accumulate carbon, or perhaps reduce maximum potential carbon storage? At Howland Forest in Maine, in collaboration with International Paper, we are using eddy covariance, biometric techniques and modeling to evaluate changes in carbon storage following a shelterwood cut that removed just under 30% of aboveground biomass. Shelterwood cuts have become increasingly popular in Maine, accounting for just over 25% of the harvest activity (in terms of land area) in 1999 (about 60,000 ha).

Prior to harvest, the stand contained about 76 Mg C ha⁻¹ (30 m² ha⁻¹ basal area) in above- and below-ground live biomass. Harvesting removed about 15 Mg C ha⁻¹ (SEM=2.1), and created about 5.3 Mg C ha⁻¹ (SEM=1.1) of aboveground and 5.2 Mg C ha⁻¹ (SEM=0.7) of root/stump detritus. Leaf-area index and litterfall declined by about 40% with harvest. When compared to a nearby unharvested stand (with average net annual uptake of 1.7 Mg C ha⁻¹ yr⁻¹), net ecosystem exchange (NEE) declined following the harvest by about 18% (Fig. 1), which is less than expected based on reductions in basal area and LAI and (expected) increased heterotrophic respiration resulting from slash decay. Both daily uptake and nocturnal respiration declined after harvest. Soil respiration declined slightly but non-significantly with harvest; harvesting had little effect on soil moisture and temperature.

Of the harvested wood, approximately half went into paper products and half for longer-lived wood products (half-life of 3.5 and 45 yr, respectively). Based on these assumptions, and estimates of slash decomposition (20, 7, 2, and 3.5 year half-lives for stumps/coarse roots, branches, foliage, and fine roots, respectively), we predict a much larger reduction in NEE (Fig. 2) than suggested by our initial comparison of NEE in the control and harvested stands. This could result from under-estimating carbon uptake by the trees after harvest, or over-estimating dead-wood decay. To better quantify carbon fluxes from dead-wood decay, we examined the relationship between dead-wood respiration rates, temperature, and moisture content. Both temperature and moisture content correlated positively with respiration rates, but temperature was important only when water content was >50% (Fig. 3). Below 50%, respiration from dead wood averaged 1.7 µgC g⁻¹ dw hr⁻¹. Above 50% water content, dead-wood respiration was estimated using the relationship between temperature and respiration rate (Fig. 3b). In conjunction with annual temperature data, these results can be used to estimate CO₂ production from dead-wood decay. Better estimates of tree growth are being obtained using a combination of forest inventory plots and dendrometer bands.

Temporal and Spatial Variation of Nearground Atmospheric CO₂ in a Permanent Woodlot Site in Prospect Hill

T. Sipe, J. Clowers*, A. Sanchez Sierra* and J. Vuong*

We measured ambient CO₂ concentrations in the herbaceous stratum during the first phase of a three-year study on the combined effects of nearground enriched CO₂ (NEC) and sunflecks on photosynthesis by herbaceous and woody species. CO₂ was sampled simultaneously every 30 minutes at two heights (10, 30 cm) each in 23 locations spaced regularly across a 30 x 50 m permanent plot in a mixed hardwood-hemlock forest. Fresh
samples were queued for analysis and stored in the sample tubes over a 3.5-minute period. Samples were then transferred sequentially to an infrared gas analyzer (LI-7000, Li-Cor, Inc.) through multiport switching valves and measured in differential mode against CO₂-free nitrogen gas bled through the reference cell. An entire measurement sequence required 11 minutes. Soil temperature (5 cm, thermistors) was measured at 8 of the 23 locations and windspeed (40 cm, cup anemometers) was measured at 3 of these 8 to provide data on the primary factors controlling soil CO₂ flux and nearground mixing. Soil respiration rates were estimated by applying empirical relationships for similar soils in Prospect Hill to the soil temperature data.

We tested the CO₂ measurement system by repeatedly sampling one intake tube 16 times over a 2.2-min period during each 30-min event across several 24-hour cycles. The 16 samples showed no trends across the 2.2 minutes, suggesting that the pumping did not induce significant vertical mixing at the tube inlets. The first sample showed a very high correlation to the mean for all 16 samples (R² = 0.96, N = 106), and was thus a reliable measure of ambient CO₂ at the time pumping was initiated. The sampling error, calculated across the 16 successive samples as the coefficient of variation, averaged 0.75% (range 0.2 to 2.0%, N = 106) over a 405-706 ppm range of ambient CO₂.

Ambient CO₂ averaged 475 ppm (range 356-1024) across the two heights, the 23 sample locations, and all sampling events during five successive 24-hour cycles (July 1-5). Daytime (6 am-8 pm) values were considerably lower (mean 447, range 356-829) than nighttime (8 pm-6 am) values (mean 511, range 394-1024). The diurnal cycle was pronounced, with peaks near midnight and troughs near solar noon on most days (Fig. 1). The cycle was phase-shifted with soil temperature by about 7 hours, so ambient CO₂ correlated poorly (R² = 0.12) with estimated soil respiration. The correlation was improved only marginally when samples were divided between daytime (R² = 0.29) and nighttime hours (R² = 0.39). Windspeeds ranged as high as 3.0 m/s, peaked in early afternoon, and were not measurable on most nights. Falling soil temperatures reduced soil respiration and eventually caused declines in ambient CO₂ during the early morning hours (1-6 am). Although soil temperature rose throughout the day, ambient CO₂ did not track temperature in midday and early afternoon due to increased wind and probably to photosynthesis in the herbaceous stratum. CO₂ began to build in the early evening and increased for several hours after soil temperatures peaked. Though we were not able to measure it, the subsidence of cooled air with comparatively low CO₂ concentrations from the canopy toward the forest floor probably contributed to the decline in ambient CO₂ in the early morning hours.

The difference in CO₂ between 10 and 30 cm averaged 20 ppm (range 4-70) across the 23 sample locations, and showed a modest exponential relationship to overall CO₂ concentration (R² = 0.74, N = 106). CO₂ concentrations at the two heights were strongly correlated across the 5-day run (R² = 0.98, N = 106). Global spatial variation expressed as the standard deviation across the 23 sampling locations averaged 23 ppm and showed an exponential relationship to ambient CO₂ for both 10 cm (R² = 0.68, N = 106) and 30 cm (R² = 0.62, N = 106). The two most divergent sample locations differed by an average of 94 ppm (range 21-306 ppm) at 30 cm. Horizontal variation expressed as the range across the 23 sample locations showed a fairly strong linear relationship to the maximum vertical difference between 10 and 30 cm (R² = 0.59, N = 106). These results, plus prior work on photosynthesis by several species, suggest there is marked variation both horizontally and vertically in nearground CO₂ environments and that the enrichment is of sufficient magnitude to substantially affect diurnal carbon gain by plants in the herbaceous stratum.
Figure 1. Comparison of net CO$_2$ uptake between eddy covariance towers in the control and harvested stands both pre-harvest and post-harvest. Differences in the slopes of these relationships suggest an 18% reduction in NEE following harvest.

Figure 2. Predicted changes in net carbon storage for 30 years after shelterwood harvest. Net C storage including slash and wood product decay. Net C storage including slash only. Net C storage not including either slash or wood products. Negative sign indicates net C loss.

N. Scott, et al.
Figure 3. Effects of temperature on dead-wood respiration rates when water content is <50% (a) and >50% (b).

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Figure 1. Diurnal patterns of nearground atmospheric CO₂, windspeed, and soil respiration estimated from soil temperature measurements over July 1-5, 2003 in a mixed hardwood-hemlock site in Prospect Hill. CO₂ was sampled simultaneously every 30 minutes at 10 and 30 cm above ground at 23 locations regularly spaced across a 30 m x 50 m grid. Soil temperature and windspeeds were measured continuously at 8 and 3 of the locations, respectively. CO₂ and windspeed data are smoothed (n = 7).

T. Sipe, et al.
Microbial Responses to Soil Warming

H. Smith, S.D. Frey, M. Knorr, H. Lux, and J. Melillo

During fall 2003 we collected soil cores (2.5 cm diam) from the control, disturbance control, and heated plots (n = 6) at the Prospect Hill soil warming experiment to examine the effects of soil warming on the active biomass and functional capacity of the soil microbial community. Each core was divided into O-horizon material (depth varied) and the top 10 cm of mineral soil. Total physiologically active microbial biomass was determined by substrate-induced respiration. Catabolic response profiles were obtained by measuring the short-term respiration responses to 25 substrates. This approach provides a fingerprint of the functional potential of the microbial community. The substrates consisted of two carbohydrates (glucose, mannose), two amines (D-glucosamine, L-glutamine), six amino acids (L-arginine, L-asparagine, L-glutamic acid, L-histidine, L-lysine, L-serine), and 15 carboxylic acids (L-ascorbic acid, citric acid, fumaric acid, gluconic acid, α-ketoglutaric acid, α-ketobutyric acid, α-ketovaleric acid, DL-malic acid, malonic acid, pantothenic acid, quinic acid, succinic acid, tartaric acid, uric acid, urocanic acid). We also measured several soil organic matter fractions in the mineral soil, including total C and N, particulate organic matter C and N, and labile C. We found no differences between the control and disturbance control plots for any of our measured parameters thus only show the data for the control and heated plots here.

Active microbial biomass was 26% and 44% lower in the heated compared to control plots for the O-horizon and mineral soil, respectively. Lower biomass in the mineral soil of heated plots was concomitant with significantly less labile C and a trend, though not significant, toward lower total and particulate organic matter C contents (Table 1). We observed a significant effect of warming on the overall respiratory response following addition to soil of 25 organic substrates. The microbial communities in the heated plots exhibited a reduced response in comparison to the control for a majority of the substrates; however, this could be largely attributed to lower microbial biomass with heating. To normalize the data for differences in microbial biomass, the response for each substrate was divided by the average response for each treatment-replicate. Principal components analysis indicated that normalized patterns of substrate utilization were significantly different between treatments for the mineral soil, but not the O-horizon material (Fig. 1). The mineral soil data separated along the first principal component which explained 66% of the variation in the data. For the majority of substrates, the heated soils exhibited lower relative utilization compared to the control. However, six substrates were utilized to a relatively greater degree in the heated plots. Taken as a whole, the catabolic response profile data indicate that there was differential use of specific substrates in heated soils. Microbial community composition and soil conditions interact to determine substrate use patterns, making it difficult to discern whether changes in catabolic response profiles are indicative of a change in species composition or a change in microbial function in response to altered soil conditions.

Forecasting Stream Ecosystem Responses to a Regional Landscape Disturbance: Indirect Ecological Consequences of the Removal of Eastern Hemlock from New England Forests

W. Sobczak and B. Colburn

The question of how organic matter moves from terrestrial to aquatic ecosystems and within aquatic food webs is of fundamental importance to ecology. Knowledge of mechanisms that control magnitudes and paths of organic matter flux translates directly into better ways to manage and restore aquatic food webs and ecosystem health. Such knowledge is of basic importance because it helps ecologists understand how seemingly diverse ecosystems are closely connected and how perturbation within one ecosystem or habitat can alter ecological functions and communities in adjacent or distant ecosystems or habitats.
Table 1. Carbon pools isolated from mineral soil collected from control, disturbance control, and heated plots at Harvard Forest Soil Warming Study.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Total soil C</th>
<th>POM-C&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Labile C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4840 (710)</td>
<td>1140 (87)</td>
<td>537 (48)</td>
</tr>
<tr>
<td>Heated</td>
<td>4490 (117)</td>
<td>963 (75)</td>
<td>365 (38)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Values represent the mean of six replicates ± one standard error.

<sup>b</sup>POM = Particulate organic matter

Figure 2. Principal components analysis of the catabolic response profiles for soil collected from control and heated plots.

H. Smith, et al

Eastern hemlock dominates many New England forests and stream-side riparian areas, thus influencing the supply of detritus and availability of light to many regional streams. Regional declines of hemlock have been documented following the invasion of the hemlock woolly adelgid, an exotic forest pest. The continued expansion of the adelgid's range into New England and subsequent loss of eastern hemlock from New England forests will result in an array of ecological consequences. Terrestrial ecosystem responses are just now being documented, yet aquatic ecosystem responses to regional changes in riparian forest composition are less certain. The proposed research aims to understand how the ecology...
and biogeochemistry of the region's stream ecosystems will be altered as riparian forests change. We plan to examine (with colleagues) changes in 1) stream hydrologic and thermal regimes, 2) stream light regimes and primary production, 3) quantity and quality of organic matter inputs, 4) microbial metabolism and downstream organic matter fluxes, and 5) macroinvertebrate biomass and functional feeding groups. Study areas will be streams dominated by hemlock or hardwood, including former hemlock streams where hemlock has been killed by the hemlock woolly adelgid.

Heartwood Formation in Forest Trees: Parenchyma Cell Death as a Driver of Sapwood Senescence

R. Spicer and N.M. Holbrook

The amount of sapwood maintained by a tree affects carbon balance at a range of scales, from the individual tree to the stand and ecosystem. Sapwood functions in both water transport and carbohydrate storage in tree stems, and is ultimately converted to heartwood through the death of xylem parenchyma cells. Heartwood then ceases to be physiologically active - it no longer conducts water, and does not contribute to any respiratory gas exchange because it contains no living cells. But what actually causes the death of xylem parenchyma cells is not known. Recent work demonstrating the role of transpiration in the supply of oxygen to internal stem tissue has raised the possibility that anoxia may be responsible for cell death, whereas others have proposed that a build-up of respiratory carbon dioxide may be involved. Instead, we have found that parenchyma cell respiration is only slightly inhibited at the reduced oxygen levels found within stems, and is also surprisingly robust to high levels of carbon dioxide. Species studied this summer at Harvard Forest, with the help of REU student Teresa Abbott, included two conifers (Tsuga canadensis, Pinus strobus), two ring-porous angiosperms (Quercus rubra, Fraxinus americana) and one diffuse-porous angiosperm (Acer rubrum). Respiration rates were measured for fresh xylem tissue from the outermost (youngest) and innermost (oldest) sapwood following equilibration to four combinations of O₂ and CO₂ (shown respectively, with mole fraction represented as a percent): 10% + 0%, 10% + 10%, 5% + 0%, 5% + 10%. In general, inhibition by reduced O₂ was far greater than inhibition by elevated CO₂. All species showed reduced respiration at low O₂ (average inhibition across species was just 25%), whereas only two species showed inhibition by high CO₂. In these cases, there was a significant interaction between the gases such that inhibition by CO₂ was reduced at low O₂. The effect of gas treatment was the same for both old and young sapwood. Our results suggest that gas concentrations within stems are unlikely to play a role in the transition from sapwood to heartwood. Instead, our work on the diversity of patterns of parenchyma cell death, as well as changes in nuclear morphology and cellular ultrastructure during this transition, suggest that this is a form of programmed cell death and should be viewed as an active stage in development.

Long-Term Trends in Soil CH₄ Consumption at the Harvard Forest Chronic Nitrogen Addition Experiment: Implications for the Future Growth in Atmospheric CH₄

P.A. Steudler, A.K. Chan, J.D. Aber, J. Gulledge, C. Cavanaugh and J.M. Melillo

For the past 15 years we have been conducting a field experiment designed to examine the short- and long-term effects of chronic N additions to temperate forests on a number of biogeochemical processes including soil CH₄ consumption. The N additions were begun in 1988 in a 50+ year-old mixed hardwood stand and a 70+ year-old red pine plantation. Nitrogen was applied as NH₄NO₃ at annual rates of 0, 50 and 150 kg N/ha over the six- month growing season. Forests in this region receive about 8 kg N/ha/yr from dry and wet deposition. During the first year of treatment we observed an immediate decrease in the rate of soil consumption of atmospheric CH₄ of about 23% in all of the amended plots compared to the controls. Over the next four...
years the overall decrease in consumption stabilized at about 36% and 62% in the hardwood and pine high N plots, respectively. We re-measured the consumption rates at these sites in 2003, after 15 years N addition. Results indicate that consumption rates have not remained constant at the levels measured in 1993, but have continued to decrease dramatically in all treatments. The greatest change was in the high N pine plot where the consumption rate was reduced by 83%, while the rate in the low N plot was reduced by 56%. The hardwood plots showed a similar pattern with a reduction in the rates in the high and low N plots by 66% and 40%, respectively.

Our findings on the long-term effect of N amendments on the rate of CH$_4$ consumption by temperate forest soils are consistent with measurements in other forests in the United States and Europe that have received moderate to high N deposition rates for decades. These results have important long-term implications for the CH$_4$ consumption capacity of temperate forest soils. It appears that even moderate levels of chronic N deposition may diminish the potential for these soils to slow the future growth in atmospheric CH$_4$.

**Elevated CO$_2$ Allows Smaller Plants to “Catch Up” to Dominants in Competing Stands of Common Ragweed (Ambrosia artemisiifolia)**

*K. A. Stinson and F. A. Bazzaz*

The predicted doubling of atmospheric carbon dioxide over the next century is likely to affect population, community and ecosystem processes by altering competition for resources within and among plant species. Asymmetric competition for light can arise when larger plants progressively pre-empt greater quantities of light per unit size than smaller ones, thereby further suppressing subordinate individuals and leading to greater size inequalities. Growth stimulation by elevated atmospheric CO$_2$ may either mitigate or exacerbate light competition, depending upon the developmental and architectural responses of small and large plants.

Because the effects of global change on weedy and invasive species raise ecological and socioeconomic concerns, we investigated how CO$_2$-enriched environments would influence light competition in the allergenic species, common ragweed (Ambrosia artemisiifolia). We grew competing stands at either ambient (360 ppm) or twice ambient (720 ppm) levels of atmospheric CO$_2$ in an open-top chamber experiment (Fig. 1). We measured variance in size, architecture, and photosynthetic rates between subordinate and dominant (small and big) individuals, and generated vertical light profiles for each competing stand in the two treatments.

The coefficient of variation (CV) was used to measure size inequalities among competing plants. We found that elevated CO$_2$ reduced the CV in plant size (Fig. 2). Thus there were smaller proportional differences between dominants and subordinate plants at high levels of CO$_2$. We also found more positive relationships between total biomass and shoot biomass inequalities at ambient levels compared to enriched CO$_2$ levels. In other words, larger plants showed proportionally less advantage relative to small plants in enriched CO$_2$ stands. Plants grown at high CO$_2$ also grew taller and had proportionally greater upper stem biomass than those in ambient conditions, which corresponded to decreasing light levels in the enriched treatments (Figs. 3 and 4). Finally, photosynthetic gains by larger plants were less pronounced in elevated- compared to ambient-grown plants, but only in the upper canopy leaves (Fig. 5).

We conclude that physiological and developmental stimulation in the growth of subordinate plants allows smaller individuals to "catch up" to larger individuals in high CO$_2$ environments, leading to a reduction in dominant-subordinate size structures. This is the first study to provide a comprehensive analysis of CO$_2$-induced effects on biomass allocation and photosynthesis in competing plant populations. Both architectural and physiological mechanisms lead to the reduced size asymmetry in competing stands of this allergenic pest species. Hence, these mechanisms are likely to affect the outcome of
competition, population densities, and human health in an enriched CO\textsubscript{2} world.

**The Impact of Garlic Mustard (*Alliaria petiolata*) on Native New England Forest Communities and the Importance of Habitat for Controlling its Spread.**

*K. A. Stinson*

*Alliaria petiolata*, or garlic mustard, threatens the native New England flora, including spring ephemerals and regenerating tree seedlings (Fig. 1). Garlic mustard establishes in two contrasting habitat types: open sites such as roadsides, trails and forest edges receiving high light levels (sunny habitat); and adjacent forest understory where light availability is much lower (shaded habitat). We are conducting studies aimed at understanding 1) the impact of garlic mustard on the native community structure of forests in New England, and 2) the influence of different habitats on the control and spread of this exotic plant.

We experimentally removed garlic mustard from forested sites in western Massachusetts in 2003. The Shannon Diversity Index was higher and native species were more evenly distributed in experimental removal plots compared to the control plots (Fig. 2). Thus, garlic mustard reduces native plant diversity by dominating the herbaceous component of forest understory vegetation in these sites.

Ongoing demographic observations and physiological experiments have further suggested that populations in high light sites contribute to invasion into the forest understory in central Massachusetts. Despite its successful invasion into forested habitat elsewhere in the region, Harvard Forest populations demonstrate lower reproductive output and population growth in forested compared to sunny sites (Fig. 3a). In addition, seedlings originating from parental plants in both habitats demonstrate higher photosynthetic rates, water use efficiency, and seed production when experimentally planted into sunny conditions versus shade treatments. Plants originating in sunny habitat also outperform those from shaded habitat, but have equally poor reproductive success when grown together in the shade (Fig. 3b). Thus, the invasion process appears to be driven by net influx of superior seeds from high light habitats into shaded ones at our study sites. It is possible that this process leads to an evolutionary “lag phase” which slows the successful invasion of forested sites by shade-adapted genotypes.

This study also includes a mapping project of garlic mustard populations in and around Harvard Forest (Fig. 4). Using these maps, we are estimating dispersal into target areas from local and more distant source populations and investigating relationships between land use history, habitat quality, and invasion success. This work will help explain how population dynamics and anthropogenic disturbance facilitate habitat expansion in this species.

Our results to date demonstrate that small scale removals of garlic mustard from the forest understory can result in the restoration of native plant diversity within one growing season. However, these removals are not likely to sufficiently control future invasions if high light populations are present. Roadside, forest edge, and other high light populations are probably important targets of eradication, even when management efforts seek to control invasion in forested sites.

**Historic and Current Influences on Habitat Invasibility in a Mosaic Landscape: Cape Cod National Seashore**

*B. Von Holle, D.R. Foster and G. Motzkin*

Effects of non-native species are a hazard to global biodiversity, second only to habitat destruction. For informed management decisions, we must determine factors that contribute to ecological resistance to biological invasion. Habitat invasibility to plant invaders was investigated in the highly resistant Cape Cod ecosystem through a spatially-explicit study of historical disturbances and current environmental and biotic properties of 20 x 20m field plots, randomly located across the
Atmospheric CO$_2$ was maintained at either ambient (350 µL L$^{-1}$) or elevated (720 µL L$^{-1}$) levels using 16 open top chambers. Experimental stands were created by planting seedlings into evenly spaced positions on a grid. This design achieved natural field densities of approximately 102 plants/m$^2$. Two replicate stands were grown in each chamber.

Figure 2. Average stand-level coefficient of variation (CV) for ragweed plants based on total branch length, showing decline in variation among small and large plants at elevated CO$_2$ and increased variation at ambient CO$_2$. Light and dark colored bars represent elevated (720 µL L$^{-1}$) and ambient (360 µL L$^{-1}$) CO$_2$ concentrations, respectively. Error bars represent ±1 standard error.
Figure 3. Light attenuation curves showing light availability through the canopy vertical profile for stands of ragweed. Open and closed symbols represent ambient (360 µL L⁻¹) and elevated (720 µL L⁻¹) CO₂ concentrations, respectively. Data points symbolize mean PAR values for each treatment for three dates on which measurements were taken. Error bars represent ± 1 standard error.

Figure 4. Average above ground biomass for vertical sections of ragweed plants grown in ambient (360 µL L⁻¹) and elevated (720 µL L⁻¹) CO₂ concentrations, represented by closed and open bars, respectively. Error bars represent ± 1 standard error.

K. Stinson and F. Bazzaz
Figure 5. Relationships between maximum photosynthetic rates and total branch length (size) of ragweed plants. Larger plants have proportionally greater photosynthetic rates than smaller plants in ambient compared to elevated CO₂ treatments. Open and closed symbols represent measurements for individual plants under ambient (360 µL L⁻¹) and elevated (360 µL L⁻¹) CO₂ concentrations, respectively. (ANCOVA, p<0.01).

Figure 1. An invasive population of garlic mustard (Alliaria petiolata) in a forest site in Berkshire County, Massachusetts.

K. Stinson
Figure 2. Native understory plants species are more evenly distributed in plots with experimentally reduced garlic mustard (A. petiolata) cover. The base of each bar represents percent A. petiolata cover. Other shades show key native forest species. These data correspond with significant increases in the Shannon Diversity Index.

Figure 3. Reproductive success of plants from sunny and forest habitat a) in field populations at Harvard Forest, 2003; and b) when grown together in experimental light treatments. Fecundity is higher in open/sun sub-populations. Plants from sun (solid line) and shade (dashed line) sub-populations are equally less fecund in experimental low light treatments.

K. Stinson
Figure 4. Map of garlic mustard populations at Harvard Forest, showing relationship between presence of invasive populations and history of human disturbance (agricultural use). The mapping project will continue in 2004.

K. Stinson

landscape. These 352 plots were within natural areas, half within Cape Cod National Seashore, MA. This region experienced intensive land use during European settlement of the area, followed by large-scale reforestation in the last century and fire suppression in the last 60 years. Historic disturbances, current vegetation, edaphic properties and other environmental conditions were determined for each plot using historic and field methods. These factors were assessed for their influence on exotic species richness and cover with multiple linear regressions and canonical correspondence analyses. The most influential factors for non-indigenous plant cover and richness were current soil nutrient conditions. While land use history in Cape Cod National Seashore is a strong determinant of native community assemblages, this is not the case for non-native species in natural areas. The resistance of these natural areas may be due to the harsh conditions provided by the depauperate soils in this area. In addition to this modeling study, two observational field studies were undertaken in the summer of 2003, to investigate further the determinants of invasibility of habitats in Cape Cod National Seashore.

Differential effects of natural and anthropogenic disturbances on habitat invasibility: Habitat invasibility to plant invaders was investigated in the highly resistant Cape Cod ecosystem through a field survey of native and nonindigenous plant species cover along gradients of current natural and anthropogenic disturbances. We surveyed 100 transects, each containing 3 field plots (20 x 20m) located perpendicular to and 2, 50 and 100 meters from typical anthropogenic (roads, trails and parking lots) and natural (salt spray and wind) disturbances. Nonnative and native species richness and abundance values decreased linearly with distance from current
anthropogenic disturbances. Nonnative species richness and abundance values also decreased linearly with distance from natural disturbances, however native species richness and abundance showed a typical intermediate disturbance response, increasing curvilinearly with distance from coastal bluffs. While there was a trend towards higher nonnative species richness in the anthropogenically-disturbed plots, this was statistically nonsignificant. Native and nonnative species clearly have categorically different responses to natural disturbances and similar responses to anthropogenic disturbances, which suggests that these disturbance types mediate habitat invasibility in distinctive ways.

Facilitations between the introduced N-fixing tree, *Robinia pseudoacacia*, and nonnative plant species in upland forests: Black Locust, *Robinia pseudoacacia*, was identified as the nonindigenous species with the greatest impact on the native communities of Cape Cod National Seashore (CCNS). We initiated this project to determine the impact of Black Locust on plant species distribution and to estimate the spread of this species within the National Seashore. We censused 20 x 20m plots for species cover and environmental characteristics in the center of twenty randomly-selected *Robinia pseudoacacia* stands. Additionally, paired plots were surveyed under native overstory stands, comprised largely of Pitch Pine (*Pinus rigida*). These native stands were located 20m from the edge of the sampled Locust stand, and had similar land use histories. To determine the historical expansion of Black Locust, we digitized and georeferenced historical aerial photographs of randomly-selected stands in CCNS from 1970 to 2002. Nonnative plant species richness and abundance values were statistically significantly higher within *Robinia* stands than within the paired native stands (Fig. 1). *Robinia* stand area significantly decreased over time, however this decrease depended upon the distance of the stand from roads. *Robinia* stands closer to roads experienced the greatest declines in size, possibly owing to the vulnerability of this species to wind damage, which is greater near open areas. The introduction of a novel functional type (nitrogen-fixing tree) into this upland forested ecosystem resulted in ‘islands of invasion’ within this otherwise resistant ecosystem. However, because of the significant natural decline of this species in this ecosystem, we recommend no active management of this species at this time. We will investigate the relationship between native and nonnative species richness with stand age to understand the effect of succession on species dynamics in these stands. Additionally, we will undertake spatially-explicit analyses of similarity values of nonnative species composition within Locust stands to understand if there is inter-patch movement of nonnative plant species.

**Hurricane Damage Exerts Long-Term Effects on Forest Development**

*K. Wilson*, *A. Barker Plotkin and D. R. Foster*

Central to the Harvard Forest LTER is examination of natural disturbance and anthropogenic stress. Hurricane blowdown is a major natural disturbance process in New England, and has been studied at Harvard Forest through large-scale manipulation, historical reconstruction and modeling. Permanent plot data allow us to expand our understanding of long-term hurricane effects on forest dynamics; here, we use permanent plot data to illustrate the persistent effects of hurricane damage 30-60 years after the great hurricane of 1938. A 2.9 hectare hardwood forest plot was established in 1969 at Harvard Forest. All living and dead trees were censused in 1969, 1975, 1987-92 and 2001. Based on distribution of windthrown stems and damage boundaries delineated immediately after the 1938 hurricane, the site was divided into severe (91-100% damage, 0.3 ha), moderate (51-75% damage, 0.9 ha) and low (11-25% damage, 1.7 ha) damage areas.

Intensity of hurricane damage continues to shape forest development, 30-60 years after the initial disturbance event. Stand development in the severely damaged area lagged about 30 years behind the low and moderately damaged areas (Fig. 1). There were also marked differences in species compositon
Satellite-Based Modeling of Gross Primary Production in a Deciduous Broadleaf Forest

X. Xiao, Q. Zhang, B. Braswell, S. Urbanski, S. Boles, S. Wofsy, B. Moore III and D. Ojima

Net ecosystem exchange (NEE) of CO₂ between the atmosphere and forest ecosystems is determined by gross primary production (GPP) of vegetation and ecosystem respiration. Continuous CO₂ flux measurements at individual CO₂ eddy flux sites provide valuable information on the seasonal dynamics of GPP. Satellite images also provide systematic observations of leaf and canopy processes. The linkage between flux tower sites and satellite remote sensing offers an opportunity to help interpret flux data and scale-up site-specific flux data for the regional analysis. In this presentation, we report the results from analyses of a temperate deciduous broadleaf forest at Harvard Forest, Massachusetts, using satellite images and site-specific CO₂ flux and climate data (1998-2001). First, we conducted analyses of improved vegetation indices in relation to the seasonal dynamics of GPP. The 10-day composites from the VEGETATION (VGT) sensor onboard the SPOT-4 satellite (4/1998 – 12/2001) and the 8-day composites from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor onboard the Terra satellite (1/2001 – 12/2002) were used, respectively. Three vegetation indices, Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI) and Land Surface Water Index (LSWI), were evaluated. Multi-year (1998-2001) data analyses have shown that EVI had a stronger linear relationship with GPP than did NDVI. A combination of LSWI and EVI describes well the seasonal dynamics of leaf phenology (green-up (leaf flush, full leaf expansion), senescence and leaf-off). Secondly, we ran the satellite-based Vegetation Photosynthesis Model (VPM) to estimate GPP of forest at the flux tower site in Harvard Forest. The VPM model is built upon the conceptual partitioning of photosynthetically active vegetation and non-photosynthetic vegetation within the leaf and canopy. The input data of the VPM model are satellite-derived vegetation indices (EVI, LSWI), air temperature and photosynthetically active radiation. Seasonal dynamics of predicted GPP values from the VPM model, when using vegetation indices from the 10-day VGT composites over 1998-2001, agreed reasonably well with observed GPP of the deciduous broadleaf forest at Harvard Forest, in terms of phase and magnitude (Fig. 1). Predicted GPP from the 8-day MODIS composites in 2001 also had a good agreement with observed GPP from the flux tower site (Fig. 2). In comparison, predicted GPP from the standard MODIS GPP/NPP product provided by the MODIS Land Science Team do not agree well with observed GPP of forest at Harvard Forest in 2001. This study has highlighted the biophysical performance of improved vegetation indices in relation to GPP and demonstrated the potential of the VPM model for scaling-up of GPP of deciduous broadleaf forests.
Figure 1. Plot richness of native and nonnative species in *Robinia pseudoacacia* and paired native stands.

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Figure 1. Basal area and stem density trends in the different damage areas over time. Stand development in the severely damaged area appears to lag behind the other areas.

Figure 2. Species composition changes from 1969 – 2001 in the low, moderately and severely damaged areas. Red oak dominated basal area in the low and moderately damaged areas, whereas red maple, birch species and white pine were collectively more important in the severely damaged area.

K. Wilson* et al.
Figure 1. The seasonal dynamics of predicted gross primary production (GPP) from the VPM model and observed GPP of forest at the flux tower site in Harvard Forest during 4/1998 – 12/2001. Vegetation indices (EVI, LSWI) derived from the 10-day VGT composite images (VGT-S10), site-specific air temperature and PAR data were used in simulation of the VPM model.

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Figure 2. A comparison between the predicted and observed gross primary production (GPP) of forest in 2001 at the flux tower site in Harvard Forest, Massachusetts. Vegetation indices derived from the 8-day MODIS Surface Reflectance Product (MOD09A1), and site-specific air temperature and PAR data were used in simulation of the VPM model.

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