Harvard Forest
Long Term Ecological Research Program

(a) 1830

(b) 1999

forest
data not available

Abstracts from the 14th Annual
Harvard Forest Ecology Symposium
12 February 2003
Forest cover in Massachusetts, 1830 and 1999. Since 1830 was near the peak of agricultural land clearance in Massachusetts, this map serves as a reasonable estimate of the maximum extent and pattern of forest clearance (see Hall et al., this volume).
Harvard Forest
Long Term Ecological Research Program

(a) 1830

(b) 1999

Abstracts from the 14th Annual
Harvard Forest Ecology Symposium
12 February 2003
# LONG TERM ECOLOGICAL RESEARCH AT HARVARD FOREST

12 February 2003

Audrey Barker Plotkin, Julie S. Pallant and Dottie Recos-Smith, Editors

## Harvard Forest Long Term Ecological Research Program

<table>
<thead>
<tr>
<th>Topic</th>
<th>Pages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Background, Rationale and Design</td>
<td>1</td>
</tr>
<tr>
<td>Forest Dynamics in Central New England</td>
<td>2</td>
</tr>
<tr>
<td>Ecological Questions Concerning New England Forests</td>
<td>5</td>
</tr>
<tr>
<td>Design and Structure of the Harvard Forest LTER Program</td>
<td>5</td>
</tr>
<tr>
<td>Research Approaches</td>
<td>6</td>
</tr>
<tr>
<td>Spatial Scales of Investigation</td>
<td>7</td>
</tr>
<tr>
<td>Education Integrated with Research</td>
<td>8</td>
</tr>
<tr>
<td>Summary</td>
<td>10</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>11</td>
</tr>
</tbody>
</table>

## Harvard Forest Ecology Symposium

<table>
<thead>
<tr>
<th>Topic</th>
<th>Pages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Titles of Abstracts</td>
<td>16</td>
</tr>
<tr>
<td>Contributors</td>
<td>19</td>
</tr>
<tr>
<td>Abstracts</td>
<td>22</td>
</tr>
<tr>
<td>Publications of the Harvard Forest LTER</td>
<td>67</td>
</tr>
<tr>
<td>Acknowledgement of Support</td>
<td>94</td>
</tr>
</tbody>
</table>
Background, Rationale and Design

Temperate forests are dynamic ecosystems that have been shaped through geologic and historical time by natural changes in the biotic and abiotic environment. Over millennial time scales climate variation has produced large shifts in the distribution and abundance of organisms, the intensity and return intervals of disturbance processes, and the productivity of ecosystems (Foster and Zebyrk 1993, Fuller et al. 1998). At century scales ecosystems have been impacted by broad-scale disturbance and long-term meteorological trends (Boose et al. 1994, 2001). On very short time scales interannual, seasonal, and diurnal variation has occurred in both physical forcing factors and biotic response (Wofsy et al. 1993; Goulden et al. 1996). Retrospective research and long-term studies document that temperate forests have been remarkably resilient to this wide range of natural environmental change and physical disturbance (Foster et al. 1990).

Despite this apparent resiliency, novel human-imposed disturbances and stresses have impacted temperate regions with increasing frequency over past centuries and may surpass the ability of forests to recover and to control important ecosystem processes (Aber et al. 1989, 1998). Massive land-use change has altered the extent and structure of forests as well as hydrological, meteorological and pedological processes. Changes in the global earth-atmosphere system have resulted in significant increases in the deposition of air pollution and may rapidly alter energy budgets in north temperate regions (Bazzaz 1996, Melillo et al. 1995). Introduced pathogens and exotic organisms continue to produce selective changes in the abundance of major forest species (Foster 1993, Orwig and Foster 1998, Orwig et al. 2002). An important question facing ecologists, natural resource managers, and policy makers is: are temperate forests as resilient (and/or resistant) to these novel physical, chemical and climatic stresses as they are to natural disturbance and environmental change?

In 1988 the Harvard Forest Long Term Ecological Research program was initiated to address this and related questions through an analysis and comparison of important natural disturbances, environmental change and historical and projected human impacts in terms of their effect on ecosystem structure, composition and function. Among the suite of disturbance and stress processes investigated emphasis has been placed on (1) hurricane and other wind impacts; (2) climate change; (3) changing land-use and land cover, (4) altered atmospheric chemistry and increased nitrogen deposition; and (5) projected increases in global temperature.

Our research design has involved assembling an interdisciplinary group of scientists that uses three complementary approaches to long-term study: (1) retrospective research that employs paleoecological, archaeological, dendrochronological and other historical techniques to interpret past conditions and the development of modern ecosystem structure and function; (2) ongoing measurements that assess current structure and function and allow the detection of variation and future change; and (3) experimental manipulations that enable the integrated study of ecosystem response to specific disturbances and stresses under relatively controlled conditions (Table 1). Through studies across a broad range of spatial and temporal scales we seek to understand the modern forest landscape of central New England, to develop information and approaches with broad relevance to fundamental ecological issues, and to train researchers and develop databases that have strong application to societally relevant environmental concerns (Table 2, Fig. 1).

Table 1. Design of the Harvard Forest LTER Program

Research Approaches

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.
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.
Figure 1. Spatial scales of investigation in the Harvard Forest LTER program.
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.
4. Integration through modeling, comparative studies, regular meetings, annual symposia, and synthetic publications.
5. Application to ecological theory, conservation biology, environmental policy, and forest management.

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

Disturbances, Stresses, and Environmental Processes Investigated
1. Climate change
2. Hurricane and lesser windstorms
3. Fire
4. Native and introduced pathogens
5. Land-use: aboriginal, Colonial, and current
6. Changes in atmospheric chemistry and deposition.

Education Integrated with Research
1. Summer Research Program for Undergraduates 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)

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 (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 (Fig. 2). 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 (Figs. 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
Figure 2. Long-term fluctuations in annual temperature and precipitation as recorded at Amherst College, 40 km southwest of Harvard Forest, and global annual surface temperature. The latter is depicted as the anomalies from the period 1961-1990. Modified from Bradley (1997 and unpublished) and the University of East Anglia Climate Research Unit.
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>
</tr>
</thead>
<tbody>
<tr>
<td>Area Size</td>
<td>New England</td>
<td>C Massachusetts</td>
<td>Petersham</td>
</tr>
<tr>
<td>Elevation</td>
<td>1000 km</td>
<td>100 km</td>
<td>10 km</td>
</tr>
<tr>
<td>0 - 1870 m</td>
<td>30 - 610 m</td>
<td>190 - 425 m</td>
<td>280 - 425 m</td>
</tr>
</tbody>
</table>

**RECONSTRUCTION**

- Paleocoeology
- Archaeology
- History
- Dendrochronology
- Hurricane Modeling
- Ecosystem Modeling

**MEASUREMENT**

- Vegetation Surveys
- Soil Surveys
- Fauna/Flora
- AVIRIS/LANDSAT
- Atmosphere Exchange

**EXPERIMENTAL MANIPULATION**

- Hurricane Pulldown
- Nitrogen Saturation
- Soil Warming
- Organic Matter
- Controlled Environment

**APPLICATION**

- Atmospheric Deposition
- Water Management
- Forest Management
- Land Protection
- Land Use Planning
- Education
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.
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 C followed by broad-scale abandonment of agriculture and massive natural reforestation (Figs. 5 and 6). Vast areas of New 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 (Fig. 7; Orwig and Foster 1998). 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 (Fig. 8; Aber et al. 1993, 1997). While photochemical reactions in the upper atmosphere deplete the stratospheric 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 - CO$_2$, CH$_4$, and N$_2$O may be leading to a regional annual increase of temperature of 3-4°C within the next century. Meanwhile, the increase in CO$_2$ (as well as N and O$_3$) 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
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).
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.

Ecological Questions Concerning New England Forests

This brief overview of New England history highlights many changes in the physical, biotic and human environment that have led to a range of dynamics in terrestrial and aquatic ecosystems. Although the specific details may vary, the questions that are central to understanding current conditions and processes in this landscape and the application of that information in the anticipation and management of future change are broadly relevant to all natural ecosystems.

What are the historically important environmental factors and disturbance processes that have shaped forest ecosystems and landscapes in the region? The preceding has raised many questions concerning the way in which environmental change, natural disturbance, and human activities have operated at a stand to regional scale and through time. Of specific interest are the details of the natural disturbance regimes, the intensity, frequency, impact and geographic variation in wind, pathogens and fire, and the way in which these have interacted with pre-historic and historical human activity.

What is the contrasting effect of natural, physical disturbance versus novel anthropogenic stress on forest ecosystem function? Increasingly, forest ecosystems are being subjected to chemical and climatic stresses and introductions of exotic organisms that are qualitatively novel or exceed the previous range in dose or rate of natural change.

Recognizing that forest species evolved within a context of natural disturbance, it is important to assess whether forest ecosystems retain the same degree of control over ecosystem processes (e.g., nutrient cycling, hydrology) under novel conditions as they do under historically important disturbances.

What is the magnitude of forest ecosystem response to intensive, regional land-use activity and how persistent are the physical and biological legacies of this historical disturbance? Large areas of northwestern Europe, Latin America, and eastern North America have or are undergoing a landscape transformation analogous to the forest-deforestation- reforestation history of New England. Major issues emerge at a regional to site scale concerning the process of forest recovery from such intensive disturbance, the ability of forest structure, composition and process to return to pre-disturbance conditions, and the duration of the impacts of historical land-use on community and ecosystem characteristics.

What application do answers to these questions have for ecological theory and policy-relevant issues such as understanding (a) global earth systems (e.g., CO₂ exchange, response to global change); (b) forest ecosystem response to multiple stresses and disturbances; (c) the ability of natural ecosystems to be resistant or resilient to natural versus human disturbance; and (d) the contribution of long-term and retrospective approaches of ecological research to the interpretation and management of natural ecosystems? As we develop an improved understanding of modern forest ecosystems, their history of change and the anticipated magnitude of future change we can bring this information to bear on fundamental ecological questions concerning the patterns and process 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 and Structure of the Harvard Forest LTER Program

In order to address the ecological questions raised above, the research effort at the Harvard Forest has been organized to integrate studies across disciplines, scientific approaches and a wide range of spatial scales (Foster et al. 1997). By seeking to augment the existing long-term record of ecosystem
change at the Harvard Forest we have selected historically important and currently relevant processes for extended investigation. Finally, we have expanded existing programs at the Harvard Forest in order to make public outreach and the education of a broad range of students a major product of these investigations (Table 1).

Research Approaches

We use a complementary suite of scientific approaches in order to identify important ecological processes, create a very long-term series of measurements, and assess ecosystem response and dynamics. Retrospective studies utilize a range of paleoecological, dendroecological, historical, and modeling approaches to assess environmental, human and biological dynamics over scales of decades to millennia. These studies provide key insights into ecological processes as well as assist in the establishment of baseline conditions and the selection of important phenomena for studies or experimental manipulations (Foster et al. 1992). Ecological history revealed through retrospective studies provides insights into the range of environmental conditions and natural and human disturbance processes that have been historically operative in a landscape. This information enables us to identify processes and ranges of responses that are critical to study in order to understand ecosystem structure and process. It also contributes to an understanding of the relative role of historical factors versus environmental factors in controlling modern conditions. Many critical ecological processes, such as broad-scale disturbance, succession, ecosystem development, and migration operate on decadal to millennia time-scales that are difficult or impossible to measure through conventional studies. Reconstructive techniques enable the evaluation of such processes, frequently providing multiple examples to contrast and compare and may allow these observations to be placed within the context of post-glacial and geological environmental change (Foster and Zebrnyk 1993, Foster et al. 2002).

Long-term measurements of ecosystem structure, composition, process and dynamics are a central part of HF LTER that are conducted in diverse ways. Permanent plots and repeat sampling enable us to continue long-term observations that were initiated in the early 20th C at the Harvard Forest. Remote sensing provides a means of scaling some measurements across two or more of our spatial scales of observation (e.g., plot to landscape to region) at intervals of a decade or more (Martin and Aber 1997, 2000). Control areas, coupled with experimental studies, provide baseline measurements and may be linked with flux studies of atmosphere-biosphere exchange at the environmental measurement station, which provides integrated ecosystem measurement of physical and biological processes (Aber et al. 1996, Wofsy et al. 1993, Barford et al. 2001).

In order to evaluate infrequent though historically important processes, and to anticipate ecosystem response to predicted ranges of climatic and chemical stresses, we have undertaken a series of long-term measurements on experimental field manipulations and under controlled environmental conditions in growth chambers and glasshouses (Bazzaz 1997). These studies have focussed on a subset of extremely important, though contrasting disturbances and stresses. Field manipulations (Fig. 9) have included simulation of windthrow from a major hurricane (Cooper-Ellis et al. 1999, Bowden et al. 1993a), clearcutting, enhanced deposition of N (Magill et al. 1997, 2000), soil warming as a component of climate change (Peterjohn et al. 1993, 1995, Melillo et al. 2002), and alteration of above- and below-ground inputs of organic matter to soils (Bowden et al. 1993b). In the case of historically important processes such as hurricanes and forest harvesting, results of these studies can be compared directly to long-term measurements on "natural experiments," such as the 1938 hurricane or land-use history, that have occurred through time in the Harvard Forest. Other manipulations can be compared to parallel studies in other ecosystems (e.g., N saturation at Bear Brook; soil warming at Abisko, Sweden; organic matter manipulation at the University of Wisconsin). In all cases, the integrated measurements of ecosystem structure and pattern enable comparison among these important manipulations.

Controlled environment studies have taken advantage of an unusually complete experimental facility at Harvard University in order to evaluate plant
response to particular changes in key environmental resources, including moisture, light, nutrients and CO₂ (Bernston and Bazzaz 1997a, b). The coupling of response measurements under laboratory control with those obtained from field experiments and under natural conditions makes it possible to understand the separate and interactive effects of specific resources on plant and ecosystem function (Crabtree and Bazzaz 1993a, b).

Long-term studies that include the development of suites of measurements of ecosystem pattern and process can link with and carry forward observations of current condition and results from reconstructive studies. In particular, extended ecosystem measurements provide assessments of seasonal and interannual variation, long-term trends and trajectories, and ecosystem function under varied and contrasting conditions. The baseline assessments of ecosystem pattern and process represent a framework for long-term experimental manipulations that seek to provide integrated measurement of ecosystem response to infrequent disturbances (e.g., windstorm or fire), to historically important events (e.g., gypsy moth defoliation), to anticipated stresses within the range of expected conditions (e.g., enhanced atmospheric deposition of nitrogen), or to novel stresses resulting from human activity (e.g., global change). The coupling of retrospective studies and long-term measurement of intact and experimentally manipulated ecosystems consequently enables an integrated assessment of ecosystem dynamics and function under a range of historical, modern, and simulated conditions (Foster et al. 1998).

Spatial Scales of Investigation

Research in the Harvard Forest LTER operates at four primary scales: site, landscape, sub-region and region (Fig. 1). Intensive, individual-investigator studies at the scale of individual organisms, a sample plot, and study site represent the heart of our long-term research. Most of these studies occur on the three main tracts of the Harvard Forest (approximately 1200 ha) where great diversity of vegetation, site conditions, and history, ninety years of continuous long-term studies, and ease of access to sites and laboratories provide ideal conditions for long-term measurements and experimental manipulations (Fig. 9). Infrastructure improvements such as access to below-ground electrical and communications service into the center of one tract, development of canopy access and environmental measurement towers, extensive deer exclosures, and control of vehicular access enable a wide array of experiments to be conducted under secure conditions. GIS-based data management systems enable current field sampling to be integrated with such diverse sources of information as low elevation airborne sensing, satellite imagery, radiotelemetry traces, and historical surveys and vegetation maps.

Many important processes, including natural and human disturbance and hydrology occur at a landscape scale where physiography, slope position, or vegetation pattern may determine environmental conditions (Foster and Boose 1992). In central New England, the area of an individual township (approximately 10 x 10 km) captures substantial landscape variation within the general physiographic setting of small-scale relief and gentle hill and valley topography that has a general south to north orientation. The town of Petersham, Massachusetts serves as one of our central areas for landscape studies as it includes the major tracts of the Harvard Forest and represents a typical upland rural village in New England. Given the politically independent structure of New England government, much of the geographical, social and environmental data relevant to ecological studies is collected or aggregated by public agencies at a township level making this a particularly convenient scale of study (Foster 1992). LTER studies on the Petersham landscape have the added advantage of access to a unique historical data base that has developed through 90 years of study of the town by Harvard Forest scientists.

In order to place site and landscape-level studies in a broader context and to examine variation in environmental, social and biotic processes, considerable research is conducted on the sub-region of central Massachusetts (Foster et al. 1998; Golodetz and Foster 1997) and the regional-scale of New England and adjacent New York (Ollinger et al. 1995). Selection of these study areas was based both on ecological and pragmatic motivations. The central Massachusetts region (Fig. 1) encompasses a wide
Figure 9. The northern part of Petersham, Massachusetts, showing major study sites in the Harvard Forest LTER program.
range of the physical and biological variation of inland Massachusetts as well as substantial variation in social history through aboriginal and European times (Fuller et al. 1998). The ability to place intensive studies within the context of major cultural and environmental gradients is extremely useful for interpreting results from the Harvard Forest and for understanding the broad-scale controls over major ecological processes. On the practical side, the study area comprises 50 townships in four counties, which present a major though manageable challenge for the collection and management of archaeological, historical and modern data. Data for this region are primarily of three kinds - continuous spatial coverage (e.g., elevation, cover maps), township level (e.g., population, agricultural and forestry statistics), or site-specific (e.g., sample plots, pollen sites). Recently, this approach has been extended to the entire state, to develop a comprehensive database of land-cover change in Massachusetts (Hall et al. 2002).

Considerably greater variation in environmental conditions occurs across the New England region and the dynamics and impacts of many of the important disturbance processes and modern anthropogenic stresses such as air pollution deposition can only be understood at this scale. In order to evaluate processes that are relevant at the regional scale we are conducting a select number of studies utilizing diverse historical, modern and modeling approaches. These studies yield data that may be continuous, aggregated at the county scale, or site specific. At the heart of these efforts are questions relating regionalization or extrapolation of point data to larger spatial scales and the use of models to project current results into a changing future.

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 15-20 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.

Research Group

Studies at the Forest are conducted by an interdisciplinary group of researchers from diverse institutions including the Harvard Forest (Barker-Pplotkin, Boone, Colburn, Ellison, Foster, Hadley, Motzkia, O’Keefe, Orwig, Pallant and Von Holle), Department of Earth and Planetary Science (Munger and Wofsy), Department of Organismic and Evolutionary Biology (Bazzaz), Arnold Arboretum (Del Tredici), the Ecosystems Center at Woods Hole (Meliilo, Nadelhofer and Steudler), the University of New Hampshire (Aber, Magill and Ollinger), and the University of Massachusetts (Kittredge and Mulholland). Particular strengths of the group include organismic, community and ecosystem ecology, modeling and atmospheric sciences.

Site Location and Description

The 1200-hectare Harvard Forest in north-central Massachusetts (Fig. 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).

Facilities

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, backhoe, 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 LTER Bibliography). This research background provides baseline data for the LTER project.

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, Nadelhoffter 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. (See Harvard Forest web page for data from recent projects.)

Summary

Thus, the Harvard Forest has a major commitment to long-term research on important ecological issues in the temperate forests of eastern North America and the application of these results of fundamental ecological questions and management concerns on a local to global scale. In approaching this research we take a very strong historical perspective and attempt to place site-specific studies within a broad regional context. As these studies unfold we seek to involve researchers from diverse fields and perspectives and students of all kinds in our activities.
Literature Cited


atmosphere in a temperate forest following a simulated hurricane blowdown. Biogeochemistry 21: 61-71.


New Haven, CT.
American Scientist 71: 54-57.
Harvard Forest Ecology Symposium 2003
Titles of Abstracts and Presentations (*denotes summer student)


A. Barker Plotkin, D. Orwig, J. Guzman* and D. Foster. Hemlock Forest Dynamics at Harvard Forest.


S. Barry, D. Foster and B. Hall. The Little Ice Age Signal in New England: A Survey of Pre-settlement Climate Change.

E. Boose, E. Colburn and A. Barros. Hydrological Stations.


E. A. Colburn and D. A. Orwig. Effects of Hemlock Decline on Forest Stream Communities.


P. Franks, M. Zwieniecki and N. M. Holbrook. The Regulation of Transpiration Rate in Plants.

S. D. Frey and M. Knorr. Chronic Nitrogen Enrichment Affects the Structure and Function of the Soil Microbial Community.


B. Hall, G. Motzkin, D. Foster, M. Syfert and J. Burk. 300 Years of Forest Change in Massachusetts: Forest Cover in 1830.


D. Köster, R. Pienitz, B. Wolfe, S. Barry, D. Foster and S. Dixit. Paleolimnological Assessment of Human-Induced Impacts on the Nutrient Balance of Walden Pond (Massachusetts, USA) During the Last Three Centuries Using Diatoms and Stable Isotopes.


P. J. Melcher, M. A. Zwienecki and N. M. Holbrook. Vulnerability of Xylem Vessels to Cavitation in Acer saccharum (Marsh.): Sealing from Individual Vessels to Whole Branches.


J. M Mettillo, P. A. Steudler, H. Lux, F. P. Bowles, S. Morisseau and E. Burrows. Soil Warming, the First Decade and Beyond.


G. Motzkin, D. R. Foster, B. Hall and D. MacDonald. Incorporating Regional-Historical Perspectives into Conservation of Uncommon Plant Communities: a Study of the Northeastern Coastal Region.


K. L. Musgrove* and E. A. Colburn. Using Hydroperiod and Historical Vegetation Data to Explain Patterns in the Distribution of Malacostracan Crustaceans in Massachusetts Vernal Pools.


D. Orwig and D. Foster. Landscape-Level Analyses of Hemlock Woolly Adelgid Outbreaks in Massachusetts.

S. Parnes. The Changing Spatial Distribution and Abundance of Tsuga canadensis and Pinus strobus between 1733 and the Present in Petersham, Massachusetts, USA.


T. W. Sipe. Photosynthetic Responses by Forest Herbs and Tree Seedlings to Near-ground Enriched Carbon Dioxide and Irradiance Regimes.


B. Stadler, T. Miller, D. Orwig and R. Cobb. The Impact of Hemlock Woolly Adelgid on Throughfall Chemistry and Microorganism Abundance.

K. A. Stinson And F.A. Bazzaz. Does Selection on Ecophysiological Traits Facilitate Invasion of Alliaria petiolata?


B. Von Holle, D. Foster and G. Motzkim. Disturbance Histories as a Predictor of Habitat Invisibility in a Mosaic Landscape: Cape Cod National Seashore.
CONTRIBUTORS
(* denotes summer student)

Bayreuth Institute for Terrestrial Ecosystem Research, University of Bayreuth

B. Stadler

Brown University, Department of Ecology and Evolutionary Biology

L. Dorn

Centre for Agricultural Landscape and Land Use Research, Paulinenau

T. Müller

Dickinson College, Carlisle, PA

S. Pears*

Environmental Canada, Ontario, Canada

S. Dixit

Franklin and Marshall College, Department of Biology, Lancaster, PA 17604

T. Sipe

Harvard University, Department of Earth and Planetary Sciences, Cambridge, MA 02138

J. Wofsy
S. Wofsy

Harvard University, Harvard Forest, Petersham, MA 01366

A. Barker Plotkin
S. Barry Musielewicz
E. Boose
J. Burk
C. Burton
P. Burton
E. Colburn
R. Cobb
A. Ellison
D. Foster
J. Hadley
B. Hall
A. Ingerson
H. Jensen-Herrin
M. Kizlinski
D. MacDonald
G. Motzkin
K. Musgrove*
J. O’Keefe
D. Orwig
S. Parnes
M. Syfert
B. Von Holle

Harvard University, Department of Organismic & Evolutionary Biology, Cambridge, MA 02138

M. Albani
G. Bauer
F. Bazzaz
P. Cowan
K. Donohue
P. Franks
N. Holbrook
N. Jaikumar
S. Kaufman
K. Lewis
P. Moorcroft
C. Polisettty
L. Sack
R. Spicer
K. Stinson  
S. Takao*  
N. Wender*  
A. Wheeler  
M. Zwieniecki  

International Paper, Maine  
P. Malerba  

Ithaca College, Biology Department, Ithaca, NY 14850  
P. Melcher  

Lawrence Berkeley National Laboratory  
M. Torn  

Marine Biological Laboratories, Ecosystems Center, Woods Hole, MA 02543  
F. Bowles  
E. Burrows  
H. Lux  
J. Melillo  
P. Micks  
S. Morrisseau  
P. Steudler  

Massachusetts Audubon Society, Wachusett Meadow Wildlife Sanctuary  
J. Choiniere  
C. Dunn  

Massachusetts Department of Environmental Management, Wachusett Mountain State Reservation  
D. Williams  

National Science Foundation, Arlington, VA  
K. Nadelhoffer  

NOAA Climate Monitoring and Diagnostics Laboratory, Boulder, CO  
J. Elkins  

Oregon State University, Department of Botany and Plant Pathology, Corvallis, OR  
D. Hibbs  
K. Lajtha  

St. Edward's University, Austin, TX  
J. Guzman*  

State University of New York, Atmospheric Sciences Research Center, Albany, NY 12205  
M. Czikowsky  
D. Fitzjarrald  
Q. Min  
R. Sakai  
R. Staebler  
A. Tsuyosih  

Tree Ring Laboratory, Lamont-Doherty Earth Observatory and Columbia University, Palisades, NY  
G. Jacoby  
N. Pederson  

University of California, Berkeley  
J. Bird  
T. Dawson  
S. Mambelli  

University of California, Earth System Science Department, Irvine, CA 92717  
S. Trumbore  

University of California, Santa Cruz  
J. Gaudinski  

University of Colorado, Denver  
H. Sievering  

University of Georgia  
M. LeClerc
Université Laval, Quebec, Canada

D. Köster
R. Pienitz

University of Maine, Department of Plant, Soil and environmental Sciences, Orono, ME 04469

B. Dail
I. Fernandez
E. Gaige
S. Goltz
J. Lee
C. Rodrigues
J. Walsh

University of Massachusetts, Holdsworth Natural Resource Center, Amherst, MA 01003

D. Kittredge

University of New Hampshire, Institute for Study of Earth, Oceans and Space, Durham, NH 03824

J. Aber
G. Bernston
A. Magill
S. Ollinger

University of New Hampshire, Department of Natural Resources, Durham, NH 03824

J. Aitkenhead-Peterson
S. Frey
M. Knorr
W. McDowell

University of Utah, Salt Lake City, UH 84112

C. Lai
J. Ehleringer
A. Schauer

University of Vermont, Burlington, VT

N. Gotelli

University of Wisconsin, Madison, WI

C. Barford

USDA Forest Service, Durham, NH

D. Hollinger
S. Long
R. Minocha

Wilfrid Laurier University, Waterloo, Ontario, Canada

B. Wolfe

Woods Hole Research Center, Woods Hole, MA 01543

W. Borken
E. Davidson
H. Hughes
K. Savage
N. Scott

Yale University, School of Forestry and Environmental Studies, New Haven, CT 06511

X. Lee
C. Oishi
J. Sigler
H-J. Wu
Sources and Dynamics of Dissolved Organic Carbon and Nitrogen in a Hardwood Forest Floor

J. Atkkenhead-Peterson, W. McDowell, K. Lajtha, P. Micks and K. Nadelhoffer

The ongoing DIRT experiment (Detritus Input and Removal Treatments) at Harvard Forest enabled us to quantify the importance of several sources of soil solution dissolved organic carbon (DOC) and nitrogen (DON) in a mixed hardwood forest floor.

The goal of the DIRT project is to assess how rates and sources of plant inputs control the accumulation and dynamics of organic matter and nutrients in forest soils over decadal time scales. Long-term treatments begun in 1990 include double annual leaf litter input (DL), zero annual leaf litter input (NL), root exclusion (NR), root and leaf litter exclusion (NL), controls (C) and removal of the O and A horizons (OA-less), in replicated 3m x 3m plots. Similar experiments in Pennsylvania, Wisconsin, Oregon, and Hungarian forests provide insights into links between microbial processes, labile C and N pools, and plant inputs to forest soils.

The objective of this study was to quantify the contribution of DOC and DON from above- and below-ground litter, live roots, and organic soil to soil solution. We hypothesized that removal of organic matter sources would reduce DOC and DON fluxes, and that double leaf litter would increase DOC and DON fluxes. While our hypothesis was not fully supported by the results, we were able to apportion the sources of DOC and DON to soil solution.

Soil solution was collected from zero-tension lysimeters installed at the interface between the forest floor and mineral soil in each plot. Samples were taken within 24 hours after fifteen rainfall events from May - November 1997 (yr 7 of treatments). Volume-weighted mean DOC and DON concentrations were significantly higher in DL than in controls, and significantly less in OA-less soils. Response was mixed in the litter and/or root-excluded treatments (Table 1).

Sources of DOC and DON were quantified using mean annual fluxes calculated from volume-weighted mean concentrations and the PnET-II model (Aber et al. 1995) (Fig. 1).

Based on differences between controls and treatments, the Oea horizon contributes 40% to soil solution DOC, leaf litter contributes 44%, and root exudate and decay contributes 16%. DON source partitioning was less straightforward because roots appeared to be a sink for DON produced in the forest floor. Oea soil appears to contribute 107% and leaf litter 39% to soil solution DON.

Mean annual DOC flux was strongly related to forest floor C:N ratio ($R^2 = 0.95 \ p < 0.01$) (Fig. 2) but DON flux was not. Mean annual DOC and DON fluxes were positively related to fungal biomass ($R^2 = 0.78$ and $R^2 = 0.70$ respectively, $p < 0.05$), suggesting that fungal biomass may be responsible for a large proportion of DOC and DON production. A seasonal effect was observed where DOC:DON ratios were significantly narrower in root-intact treatments DL, NL, and C in summer compared to autumn. This decoupling of DOC and DON with manipulated organic matter inputs and season contrasts the traditional model which suggests that DOC and DON are produced in relatively fixed ratios.

DOC fluxes in year 7 show overall patterns similar to cumulative DOC and CO$_2$ release from incubated Oea soils collected in year 5. They also correspond to treatment patterns of CO$_2$ efflux measured in the field in year 8. Continuing soil solution analysis will allow us to track DOC and DON fluxes and examine their linkages to long-term organic matter dynamics in this forest soil.

Table 1. Volume-weighted mean growing season (May-November) concentrations of DOC and DON and ratios of DOC to DON in soil solution beneath the forest floor. Values are the means of replicate plots (n=6 control, n=3 for all other treatments) ± 1SD. Significant differences from the control at p < 0.05 are indicated by different letters.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DOC (mg L⁻¹)</th>
<th>DON (mg L⁻¹)</th>
<th>DOC:DON</th>
</tr>
</thead>
<tbody>
<tr>
<td>Double Litter Input (DL)</td>
<td>29.1ᵇ ± 1.5</td>
<td>0.81ᵇ ± 0.1</td>
<td>36.0ᵇ ± 2.1</td>
</tr>
<tr>
<td>Control (C)</td>
<td>22.1ᵃ ± 3.0</td>
<td>0.52ᵃ ± 0.1</td>
<td>43.2ᵃ ± 8.8</td>
</tr>
<tr>
<td>No Litter Input (NL)</td>
<td>19.9ᵃ ± 4.3</td>
<td>0.59ᵃ ± 0.1</td>
<td>33.4ᵃ ± 2.8</td>
</tr>
<tr>
<td>No Roots (NR)</td>
<td>18.5ᵃ ± 1.4</td>
<td>0.52ᵃ ± 0.2</td>
<td>36.9ᵃ ± 8.4</td>
</tr>
<tr>
<td>No Inputs (NI)</td>
<td>18.4ᵇ ± 1.8</td>
<td>0.54ᵇ ± 0.3</td>
<td>39.1ᵇ ± 3.6</td>
</tr>
<tr>
<td>OA-less (-OA)</td>
<td>13.9ᵇ ± 5.2</td>
<td>0.44ᵇ ± 0.1</td>
<td>31.4ᵇ ± 4.7</td>
</tr>
</tbody>
</table>

Figure 1. Contribution of organic soil, leaf litter and roots to annual soil solution DOC and DON flux. Numbers on bars denote % contribution to soil solution.

Figure 2. Relationship between annual DOC flux (g m⁻²) and soil C:N ratio. Soil C:N ratios are the mean values of samples taken in 1995 and 2000. ** The relationship is significant at p < 0.01.

Aitkenhead et al.
Modeling the Impact of Hemlock Loss on New England Forests with the Ecosystem Demography Model

M. Albani and P. Moorcroft

The Hemlock Woolly Adelgid (Adelges tsugae, HWA), an exotic aphid pathogen of eastern hemlock (Tsuga canadensis), is spreading unchecked across the eastern United States. As the pathogen spreads north, New England's forests are expected to experience substantial losses of hemlock both directly from the pathogen and by associated preemptive and salvage logging. Since eastern hemlock is the dominant species in several forest ecosystems, its loss and replacement by birch and other hardwoods will likely lead to a dramatic cascade of biological, biogeochemical, and physical changes.

We plan to 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 ecosystem structure and function.

Using data for other investigations at Harvard Forest, we will modify ED to incorporate the impact of HWA on the physiology and demography of hemlock. Concurrently, we will develop and calibrate a predictive, spatially-explicit model of pathogen infection that will be used to predict the spatio-temporal pattern spread of the adelgid as it advances northward.

Hemlock Forest Dynamics at Harvard Forest

A. Barker Plotkin, D. Orwig, J. Guzman* and D. Foster

Hemlock (Tsuga canadensis) forests in New England are changing rapidly with the invasion of the hemlock woolly adelgid (HWA, Adelges tsugae), an exotic insect pest that kills hemlock trees. The adelgid is just beginning to be observed at Harvard Forest, making this the right moment to begin intensive physiological, ecological and monitoring studies of our hemlock forests. We gathered detailed baseline information for several hemlock stands across Harvard Forest. We surveyed community vegetation structure and composition, and began to monitor soil nitrogen cycling. These measurements will allow us to link the long-term history of these hemlock stands to other current studies of hemlock response to adelgid infestation (Orwig 2002), and will provide the basis for intensive study of hemlock dynamics with the stands' anticipated decline.

The five sites in this study include existing plots with known land-use and paleoecological histories (Foster and Zebrayk 1993, McLachlan and Foster 2000). Currently, all sites are healthy with no observed HWA. Overstory trees and saplings were sampled in fixed-radius plots. Hemlock had importance values between 65-84% (Table 1), with white pine, black birch, red maple and red oak as common minor components. Nearly all saplings were hemlock; sapling densities ranged from 183 - 1645 stems/ha. Understory flora characteristics were sampled in 10-1m² subplots within each overstory plot. Across all sites, herb and shrub cover was very low, reflecting the dense shade and deep organic layer present in these hemlock stands (Table 1). Species richness ranged from 6 - 15 understory species found in each 20x20 or 30x30m plot. Compared to a suite of hemlock study sites established in Connecticut in 1995 (Orwig and Foster 1998), these sites have more white pine and a deeper organic layer, suggesting that vegetation dynamics following hemlock decline may differ from the Connecticut sites.

We initiated baseline measurements of N pools, net N mineralization and nitrification rates and N availability at the Hemlock Grid and Slab City sites. We will continue to monitor vegetation and nutrient dynamics in these stands as HWA becomes established at Harvard Forest. These sites represent a cross-section of the hemlock forests present at Harvard Forest (Fig. 1) and provide a basis for future intensive studies. HWA has been observed this winter at a few sites at Harvard Forest, so these stands are likely to experience hemlock decline and major changes in vegetation composition, forest structure and nutrient cycling within the next decade.
Table 1. Overstory importance values (average of relative density and relative basal area), sapling density and understory characteristics of Harvard Forest hemlock sites, showing baseline data from Summer 2002 (Hemlock Grid overstory data is from 1999). The Hemlock Grid and Slab City sites are averages of 3 20x20m plots, whereas the others are single 30x30m plots. The overstory is defined as live trees ≥8cm dbh. Saplings are ≥1.3m tall but <8cm dbh. Other species include black cherry, beech, green ash, paper birch, red spruce and yellow birch.

<table>
<thead>
<tr>
<th></th>
<th>Hemlock Grid</th>
<th>Slab City</th>
<th>PH2</th>
<th>PH7</th>
<th>SC9</th>
<th>SC10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemlock</td>
<td>71</td>
<td>76</td>
<td>84</td>
<td>81</td>
<td>65</td>
<td>65</td>
</tr>
<tr>
<td>Black birch</td>
<td>1</td>
<td>11</td>
<td>1</td>
<td>3</td>
<td>18</td>
<td>1</td>
</tr>
<tr>
<td>Red maple</td>
<td>7</td>
<td>9</td>
<td>2</td>
<td>4</td>
<td>7</td>
<td>13</td>
</tr>
<tr>
<td>Red oak</td>
<td>2</td>
<td>---</td>
<td>---</td>
<td>8</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>White pine</td>
<td>15</td>
<td>---</td>
<td>13</td>
<td>3</td>
<td>---</td>
<td>12</td>
</tr>
<tr>
<td>Other</td>
<td>4</td>
<td>3</td>
<td>---</td>
<td>1</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Total BA (m²/ha)</td>
<td>60</td>
<td>55</td>
<td>59</td>
<td>53</td>
<td>49</td>
<td>52</td>
</tr>
<tr>
<td>Total Density (stems/ha)</td>
<td>725</td>
<td>808</td>
<td>455</td>
<td>966</td>
<td>811</td>
<td>666</td>
</tr>
<tr>
<td>Sapling Density (stems/ha)</td>
<td>183</td>
<td>742</td>
<td>1645</td>
<td>833</td>
<td>344</td>
<td>455</td>
</tr>
<tr>
<td>Herb cover (% ± SE)</td>
<td>1.7 ± 0.6</td>
<td>0.1 ± 0.06</td>
<td>*</td>
<td>*</td>
<td>0.2 ± 0.1</td>
<td>8.2 ± 3.9</td>
</tr>
<tr>
<td>Shrub cover (% ± SE)</td>
<td>6.9 ± 1.6</td>
<td>0.1 ± 0.04</td>
<td>---</td>
<td>---</td>
<td>0.4 ± 0.3</td>
<td>0.4 ± 0.4</td>
</tr>
<tr>
<td>Seedling cover (% ± SE)</td>
<td>13.9 ± 3.4</td>
<td>0.5 ± 0.02</td>
<td>10.0 ± 5.9</td>
<td>0.9 ± 0.3</td>
<td>0.7 ± 0.1</td>
<td>0.6 ± 0.1</td>
</tr>
<tr>
<td>Seedling density (#/m² ± SE)</td>
<td>25 ± 4</td>
<td>4 ± 0.4</td>
<td>42 ± 14</td>
<td>4 ± 1</td>
<td>10 ± 2</td>
<td>8 ± 2</td>
</tr>
<tr>
<td>O layer depth (cm ± SE)</td>
<td>7.8 ± 0.5</td>
<td>5.0 ± 0.3</td>
<td>8.7 ± 1.1</td>
<td>8.1 ± 0.8</td>
<td>7.0 ± 1.1</td>
<td>4.5 ± 0.8</td>
</tr>
<tr>
<td>Understory Species Richness (# ± SE)</td>
<td>11 ± 2</td>
<td>6 ± 2</td>
<td>8</td>
<td>6</td>
<td>6</td>
<td>15</td>
</tr>
</tbody>
</table>

* <0.1%

Barker et al.
Figure 1. Hemlock forests at Harvard Forest. Stands mapped from aerial photographs by J. Stone.


Evaluation of Greenhouse and Ozone-Depleting Gases in Rural New England

D. Barnes, S. Wofsy, J. Elkins, M. McElroy and E. Gottlieb

This study provides an independent measure of emissions of ozone-depleting species for the first years (1996-2001) following the full implementation of the Montreal Protocol. The measurements were taken at Harvard Forest in western Massachusetts, a site that receives air from the northeastern urban/industrial corridor of the U.S. 30-40% of the time. These data exhibit well-correlated spikes in concentrations of CO, CFC-11 (CCl3F), CFC-12 (CCl2F2), and methyl chloroform (CH3CCl3). The annual and seasonal emissions of CFC-11, CFC-12, and CH3CCl3 are estimated by correlating their concentrations with that of CO, and the extensive inventory data for CO emissions in the U.S. (EPA) was used to infer sources strengths for these species. For further details on the method used, see Barnes (2000).

The emissions of CFC-11, CFC-12 and CH3CCl3 in two other regions of the U.S. were estimated by applying the same statistical methodology used for the Harvard Forest data to measurements from NOAA/CMRD instruments located in North Carolina (WITN: data for 1995-1998) and Wisconsin (WLEF: data for 1996-2000).

Summarized in Figure 1 are the annual emissions of CFC-11, CFC-12, and CH3CCl3 for these three regions of the U.S.

- Methyl chloroform emissions are continuing at rates higher than anticipated. Emissions of CH3CCl3 were expected to drop to zero in 1996 or shortly thereafter, based on the pattern of usage for CH3CCl3. Prior to the 1996 ban, the solvent was utilized within a year of purchase. The continuation of the CH3CCl3 emissions has significant implications for OH radical calculations by atmospheric modelers.

- Emissions of CFC-12 are decreasing as expected. Residual emissions of CFC-12 and CFC-11 were expected following the 1 January 1996 ban, due to leakage from long-term reservoirs of these two gases, particularly from refrigerants.

- CFC-11 emissions have remained steady or increased slightly during the six years since the ban in 1996.

- Our CFC-11 and CH3CCl3 emission results suggest that long-term reservoirs are larger than previously thought, that users stockpiled the substances in large quantities in anticipation of the ban, or that a black market has developed in violation of the ban.


The Little Ice Age Signal in New England: a Survey of Pre-settlement Climate Change

S. Barry, D. Foster and B. Hall

The “Little Ice Age”, ca. 1450 to 1850 A.D., was an apparently global climatic period characterized in the Northern Hemisphere by highly variable conditions, frequent long winters and short, cool summers. In northwestern Europe environmental signals of this period are recorded in glacial activity, coastal sediments, tree rings, and historical documents, which indicate a period of cool and variable weather including shorter growing seasons and increased storminess. More recently, glacial, tree ring, lake level, and historical data indicate coincident changes in terrestrial and aquatic ecosystems in North America.

The low-resolution and poor temporal control of most pollen and stratigraphic data has restricted reconstructions of subtle paleoclimatic changes in New England. Furthermore, the end of the “Little Ice Age” coincides with the period of European settlement and broad-scale deforestation. However, some studies suggest that significant environmental and vegetation changes occurred prior to settlement. For example, our recent studies of the southern New England landscape determined that the major changes since European settlement, including the decline in beech and hemlock and the regional homogenization of vegetation composition, were actually initiated some 300-500 years before European arrival.

In this current multi-proxy study, we combine pollen data from new sites, the Global Pollen database, and the Harvard Forest archives with detailed historical land-use and land cover maps to analyze vegetation and environmental change in Massachusetts over the past 2000 years. Massachusetts is a particularly good study region because it was colonized early, is covered by unique historical records, and embraces a wide range of vegetation, environments, and cultural conditions. We analyzed records from over 20 ponds arrayed across the state’s gradients in physiography, climate, geology and natural disturbance. Chronological control was provided through lead-210 and radiocarbon dating and sediments were sampled at high-resolution intervals. Small (<10 ha) and primarily spring-fed kettle lakes were selected to emphasize the local to sub-regional vegetation signal. Historical data include archaeological information and pre-settlement vegetation derived from witness trees records in early land surveys. Collaborators at Laval University have provided isotopic analyses and diatom surveys from several of our sites, increasing our understanding of regional changes.

Preliminary results suggest that the “Little Ice Age" effects varied geographically with the magnitude and nature of vegetation changes differing by vegetation type and ecoregion. A decrease in beech and hemlock is most evident in high-elevation sites, while low elevation sites of oak-hardwood forest composition show relatively little change. In many cases, changes in forest composition dynamics are accompanied by coincident changes in aquatic vegetation and % organic matter, presumably reflecting changes in water balance and lake levels or watershed clearing.

Hydrological Stations

E. Roose, E. Colburn and A. Barros

Permanent hydrological stations are planned for two small headwater streams in the Prospect Hill Tract. The first station (funded) will be located on the stream that drains the Black Gum Swamp and adjacent woodlands and flows near Shaler Hall on its way to Nelson Brook and the Millers River. The second station (funding pending) will be located on the stream that drains the steep valley to the west of Prospect Hill and flows through the wetland north of the EMS on its way to Bigelow Brook and the Swift River. Both streams have surface flow for an estimated 10-12 months of the year. The first watershed and all but the uppermost 5-10% of the second watershed are owned by Harvard University.

Each station will include a weir, piezometer array, sensors, and datalogger to measure and record surface discharge, water temperature, and subsurface flow. Stations will be provided with electricity and a communications link to networked computers in Shaler Hall and the EMS Shack. Heating cables and hoods will be
used to prevent ice buildup in winter. Measurements will be posted on the Harvard Forest web page in near-real time, and contributed regularly to the LTER HydroDB database. Construction is planned for spring and summer 2003. Additional funding will be sought to deploy piezometers and soil moisture sensors at upstream locations in both watersheds.

The two watersheds, though adjacent and comparable in size, differ significantly in topography, soils, hydrology, land-use history, stream biota, and forest vegetation (including abundance of hemlock). Long-term measurements from both stations (and the Fisher Met Station) should greatly improve our understanding of the relationships among climate, soils, groundwater, surface streamflow, and stream biota. The two watersheds may also provide some control for disturbances that impact one watershed more than the other, including the anticipated loss of hemlock from the hemlock woolly adelgid.

Effects of Experimental Drought on Soil Respiration and Radiocarbon Efflux from a Temperate Forest Soil

W. Borken, K. Savage, E. Davidson and S. Trumbore

Soil respiration is clearly affected by both soil temperature and water content. Relying upon natural variation of temperature and precipitation does not permit a clear distinction between them as factors controlling seasonal and interannual variation in soil respiration. To clarify the effects of summertime drought on soil respiration processes, we conducted a drought experiment at the Harvard Forest of central Massachusetts. Both control and throughfall exclusion plots experienced the same temperature, but different moisture regimes. In addition to measuring the effects of drought on respiration, we also measured radiocarbon content of soil CO₂ to determine if heterotrophic and autotrophic respiration are affected differently by drought.

Three replicate throughfall exclusion roofs (5x5m) and 3 control plots were established in a well-drained, mixed hardwood stand. The roofs were translucent corrugated plastic panels about 1 m above the ground surface. In 2001, 168 mm of throughfall were excluded over an 84 day period, and in 2002, 344 mm were excluded over 126 days. Soil respiration was measured weekly using a portable infrared gas analyzer and 4 manual chambers in each of six plots. Soil moisture and temperature probes were installed in all plots. The water content of the O-horizon was measured using DC half bridges. In the summer of 2002 we installed an automatic chamber in each of the six plots, which made hourly measurements. Radiocarbon of the soil CO₂ profiles was measured from the throughfall exclusion and control plots several times over the summer period.

Mean soil respiration was lower in the exclusion plots when the panels were in place in both years (Fig. 1a) with the cumulative difference between treatments of 100 g C m⁻² per 84 days in 2001 and 210 g C m⁻² per 126 days in 2002. Soil temperature varied little between treatment plots (Fig. 1b). Litter layer water content in the control plots responded dramatically to rainfall events (Fig. 1c, d). The high resolution sampling frequency of the automated chambers allowed us to capture the rapid response of soil respiration to precipitation events (Fig. 2a-d). Many of the highest fluxes were measured shortly after a wetting event (Fig. 3a). Fluxes can remain high up to 3 days following the precipitation event (Figs. 2a and 3a). The residuals of the temperature function were positively correlated with litter layer water content (Fig. 3b).

Higher Δ¹⁴C values were observed when CO₂ concentrations were low (Fig. 4), which occurred at low water content. In the control plots this is a response to natural late summer drought, but it is more pronounced in the throughfall exclusion plots. When the soil is moist, high rates of root respiration and decomposition of young substrates result in high soil CO₂ concentrations with low Δ¹⁴C values. Under dry conditions, root respiration produces less CO₂, while gradual decomposition of old, radiocarbon-rich substrate continues at low rates, resulting in low CO₂ concentrations with high radiocarbon content.

In summary, experimentally imposed summer drought caused a reduction of soil
Figure 1. a) Two years of soil respiration measurements using manual chambers in control and throughfall exclusion plots (n=12), b) soil temperature, c) O horizon water content, control dashed line, exclusion solid line, d) daily precipitation.

Borken et al.
Figure 2: a) Mean hourly flux from the 3 control site autochambers, b) soil temperature, c) O horizon water content, d) hourly precipitation

Borken et al.
Figure 3. a) Exponential response ($y = Ae^{BT}$) of soil respiration to temperature; and (B) correlation of litter layer water content with residuals from the temperature curve.
Figure 4. Radiocarbon content of CO$_2$ collected at 3 depths during the summer of 2001 in control and throughfall exclusion plots as a function of soil CO$_2$ concentration.

**Control**

- 8 cm
- 15 cm
- 53 cm

**Dry down**

- 7 cm
- 11 cm
- 53 cm

Borken et al.
respiration by 1 - 2 Mg C ha⁻¹, which is 10 - 30% of the annual rates (7-8 Mg C m⁻² ha⁻¹). Rainfall caused rapid increases in soil respiration, which lasted several days. A significant fraction of the variation in soil respiration not explained by soil temperature was correlated with water content of the litter layer. Radiocarbon data demonstrated that respiration of recently fixed C substrates was more strongly affected by drought than decomposition of older substrates. This experiment clearly shows that soil water content, and particularly the water content of the litter layer, is an important factor controlling daily, seasonal, and interannual variation in soil respiration of this temperate forest.

Tree Regeneration and Understory Vegetation in an Eastern Hardwood Forest 20 Years After Creation of Small Forest Openings

P. J. Burton, C. M. Burton, T. W. Sipe and D. E. Hibbs

Some suggest that forest harvesting methods mimicking the scale of natural gap dynamics can both regenerate desired tree species and maintain the conservation value of mature forests. In central New England, the process of hardwood regeneration in small openings has not been explored as thoroughly as in other regions. Fifteen roughly circular forest openings were created at Harvard Forest in the winter of 1983 to address the differential effects of opening size, and location within openings, on the establishment, survival and growth of local tree species. The experiment was established in a mixed hardwood and conifer forest dominated by red oak (Quercus rubra), red maple (Acer rubrum) and white oak (Q. alba), with lesser amounts of white ash (Fraxinus americana), black oak (Q. velutina), white pine (Pinus strobus) and several other incidental tree species. Timber harvesting created a series of canopy gaps ranging in size from 30 m² to 700 m² (6 to 30 m average diameter). Mean canopy height of residual trees soon after logging was 15.5 m. The study site is located in Compartment 9 (west of Route 32) of the Prospect Hill Tract, on gently rolling bouldery terrain formerly cleared for agriculture.

In the mid-summer of 1984, the second growing season after logging, forest regeneration was sampled in intersecting transects of contiguous 2 m x 2 m quadrats running north-south and east-west across each gap and into the adjacent uncut forest. A total of 384 quadrats were used to map and count tree seedlings and sprouts, and to estimate the cover of dominant understory species. Height and basal diameter were measured for the tallest regenerating stems of each tree species. In the late summer and early fall of 2002, 20 growing seasons after gap creation and 18 years after the previous monitoring, all quadrats were relocated and resampled. Data recording for this most recent round of sampling was done on copies of the 1984 data sheets, which facilitated the relocation of mapped tree seedlings and sprouts. Stems of all tree species were measured for basal diameter and height, and the percent cover of all vascular plant species was estimated.

Forest regeneration both 2 and 20 years after logging was dominated by sprouts of red oak and red maple and by seedlings of black birch (Betula lenta), which collectively formed a closed canopy in most gaps when surveyed in 2002. Many of the stems mapped in 1984 survived to 2002, but clumps of sprouts from the same stump had thinned out considerably. Some black birch and yellow birch (B. alleghaniensis) trees had attained heights of more than 13 m after 20 years of growth, and trees of many species were found to be more than 10 m tall. Approximately as many trees had established after the 1984 survey as before it. But most late-establishing regeneration was of small stature, suppressed by the earlier cohort. Preliminary data analysis suggests that length of the north-south gap axis is a stronger determinant of regeneration dynamics than simple gap area. It appears that a north-south gap diameter of 21 m (135% of canopy height) may constitute a threshold for the processes governing successful tree establishment and growth (Fig. 1).

Ground-level vegetation in 1984 was very dense, especially in the larger gaps, and was dominated by hay-scented fern (Dennstaedtia punctilobula). By 2002, where regenerating trees formed a closed canopy, this vegetation had receded considerably, but not quite to the cover levels found in the uncut forest nearby. The 2002
Figure 1. Maximum height of regenerating trees within 3.2 m of the center of experimental gaps created in 1983, as measured in 2002. Tree growth has been a linear function of gap size, but only for gaps with a north-south axis measuring less than 21 m. In larger gaps, the stocking and growth of regeneration has been much more irregular, often constrained by a dense cover of herbs and shrubs that prevailed soon after logging.
vascular plant community in the experimental gaps was dominated by flowering-ferns (*Osmunda* spp.), wild sarsaparilla (*Aralia nudicaulis*), and wild blueberries (*Vaccinium* spp.) as well as hay-scented fern. We are currently analyzing how the abundance of individual species and the composition of the plant community are related to gap size and gap position.

**The Effects of Hemlock Woolly Adelgid Infestation on Decomposition in Eastern Hemlock Forests**

*R. Cobb and D. Orwig*

For the last four years we have been working to quantify decomposition changes that occur as eastern hemlock (*Tsuga canadensis*) ecosystems decline. Our study has focused on three key drivers of decomposition: (i) changes in foliar quality due to HWA herbivory, (ii) changes in forest floor microclimate that occur as the canopy thins, and (iii) the effect of species composition change. All three have had an impact on decomposition. Furthermore, our data suggest that these changes are coupled with N-cycling dynamics and may helped to elucidate the mechanisms driving increased N availability in these forests.

We sampled hemlock foliar N, C, and lignin along an extensive gradient of hemlock forests. These stands range from uninfested to forests with complete hemlock mortality and currently dominated by black birch (*Betula lenta*) (see Orwig and Foster 1998). Foliar % C and lignin were not affected by HWA infestation; however, foliar N was higher in infested stands (S. Meyer unpublished data; see Cobb et al. this volume). Higher initial foliar N was found to increase the rate of N immobilization in decomposing foliage. Additionally, our data suggest that in many forests infested foliage may switch from a net sink to a net source of N more rapidly compared to uninfested foliage. This may be an important contribution to increased N availability in infested forests (Jenkins *et al.* 1999)

Altered microclimate has had an important effect on foliar decomposition. Surface litter decomposition was slowed in many infested forests due to poor conditions for microbial establishment on litter. However, our work suggests this effect may be limited only to litter at the forest floor surface. Cellulose paper buried at the forest floor mineral soil interface had significantly greater mass loss in infested stands. We also observed that as surface litter became buried, its rate of mass loss increased in infested stands.

In 2001 we began a comparative study of hemlock, black birch, and mixed litter decomposition. During 2002 we collected litter bags after six and twelve months of decomposition. Results after six months show that black birch litter decomposed more rapidly than hemlock and mixed litter (Fig. 1). The higher rates of litter decomposition that occur after the switch from hemlock to black birch litter-fall are likely a major mechanism of forest floor mass loss after hemlock mortality and logging (Kizinski *et al.* 2002).

Taken as a whole, our study illustrates the dynamic effects of hemlock woolly adelgid infestation on decomposition in eastern hemlock forests. All stages of infestation studied had significant effects on decomposition by altering the chemical changes in litter, altering litter inputs (hemlock to black birch), and soil microclimate conditions.


Figure 1. Percent mass remaining from three litter types distributed after six months of decomposition at 8 hemlock sites in Connecticut and at Harvard Forest's Prospect Hill (ph). BB is black birch (*Betula lenta*), HEM is eastern hemlock (*Tsuga canadensis*), and MIX are bags with an equal mix of the two species. Data are medians within quartile plots. The ph, sr, and cr sites have very low levels of HWA infestation.

Cobb and Orwig
Seasonal Dynamics of Hemlock Woolly Adelgid and Eastern Hemlock Foliage Chemistry

R. Cobb, B. Stadler and D. Orwig

We documented the seasonal dynamics of hemlock woolly adelgid (Adelges tsugae – HWA) densities and eastern hemlock (Tsuga canadensis) foliar chemistry (% C and N) over the 2002 growing season. We sampled 12 trees at three dates, May 31st, July 1st, and September 1st. Three branches from each tree were selected at random, cut and returned to the laboratory. We determined HWA density, length, and number of needles for each age class of hemlock foliage. HWA were recorded as egg-sack forming (individuals that matured over the 2001 winter) or non-egg sack forming (current generation). Considerable overlap of HWA generations occurred during our sampling, especially on July 1st when as many as 15 life cycle stages may be present on a single tree (McClure et al. 2001). Egg sacks were removed, foliage was dried at 45°C for 48h, ground to pass 800 um screen, and analyzed with a Fison CHN dry-combustion autoanalyzer. We found HWA densities and population distribution to be highly seasonally dependent. Our initial sampling occurred before current year foliage was elongated and no HWA were found on this age class at the beginning of the field season (Fig. 1). However, current year foliage is the preferred substrate, infestation increased to 100% by July and this age class supported the greatest number of individuals. In May and July, egg-laying sistens (individuals that survived over winter) dominated the HWA population on 1-year-old foliage. The relatively high percentage of HWA on the 2-year-old age class in May suggests that the crawling progredien-sexuparae (present in early May) may be forced to establish on the low quality substrate where survivorship is probably poor. The 2-year-old age class supported the least number of individuals but was the only age class with egg sacks at the end of the growing season. This suggests that HWA grows and differentiates more slowly on this substrate and may produce a small population of mobile HWA late in the growing season.

Foliar chemistry tended to be highest during the early portion of the growing season but did not vary significantly. Percent foliar N was greatest in HWA infested trees (Table 1). HWA density and foliar % N were positively correlated (Fig. 2) suggesting that chemical induction occurs in hemlock after infestation by this insect. This conclusion is supported by the increase in volatile organic compounds emissions documented from infested trees (Broekling and Salom 2003). However, we cannot determine if increased N is a function of improved HWA performance on higher quality foliage or an effect of HWA herbivory. A simple study of pre and post infestation foliar N levels would be useful for resolving this question.


Vernal Pools in the New England Landscape

E. A. Colburn

Relationships between short- and long-term changes in physical factors, biotic interactions, and species’ distributions remain a key focus of ecological investigation. Vernal pools are small, shallow, seasonally flooded, fishless forest ponds that provide breeding habitat for forest amphibians and support diverse invertebrate fauna. They are tightly coupled to surrounding uplands through transport of materials and movement of animals. Short- and long-term variations in water levels and flooding duration are dramatic and may be cyclic. We hypothesize that species’ distributions in pools reflect integrated responses to hydrology and other pool-specific physical factors, current watershed conditions, and historic influences. Our long-term studies of vernal pools provide an opportunity to examine the influence of climate, hydrology, and landscape-scale factors on the distributions and abundances of aquatic organisms.
Figure 1. Distribution and abundance of HWA during the 2002 field season. Panel A shows the amount of HWA hatched in 2002 as a percent of the total and their distribution across three hemlock foliar age classes. Panel B shows the absolute amount of HWA. Data are means from twelve trees. Notice that for current year foliage no infestation had occurred before the May sampling.
Table 1. Foliar %N concentration from eastern hemlock trees across a range of HWA infestation levels. Data are means from three seasonal collections with one standard error. Lowercase letters indicate statistical significance at $P=0.10$.

<table>
<thead>
<tr>
<th>Needle age</th>
<th>Current year</th>
<th>1 year</th>
<th>2 years</th>
</tr>
</thead>
<tbody>
<tr>
<td>HWA Uninfested</td>
<td>1.68 (0.12)a</td>
<td>1.21 (0.08)a</td>
<td>1.14 (0.10)</td>
</tr>
<tr>
<td>Moderate infestation</td>
<td>2.28 (0.21)b</td>
<td>1.50 (0.11)b</td>
<td>1.06 (0.07)</td>
</tr>
<tr>
<td>Severe infestation</td>
<td>2.28 (0.25)b</td>
<td>1.76 (0.09)c</td>
<td>1.23 (0.09)</td>
</tr>
</tbody>
</table>

Figure 2. Association between HWA density and eastern hemlock foliar N content. Needle percentages $>100\%$ indicate more than one adelgid per needle.

Cobb et al.
Macroinvertebrate and vertebrate species' distributions and reproductive success in vernal pools are correlated with hydroperiod, geography, vegetation, and water quality. Hydrologic differences are associated with high within-year faunal heterogeneity between pools. Between years, vegetation and fauna change with variations in hydroperiod, and effects may carry over to the next year. Relationships among long-term hydrologic patterns, land use and plant cover in the watershed, pool vegetation, and pool fauna are unclear. Existing data suggest that periodic hydrologic cycles may extend over decades for some pools. Three unanswered questions are: (1) For a given pool, is there a predictable long-term pattern of hydrologic variation? (2) Among pools, are there parallel patterns in plant and animal distributions and abundances? (3) How do short- and long-term patterns in hydrology interact with other physical and biological variables to shape species' distributions and abundances?

We are analyzing a long-term database of aquatic invertebrates and habitat conditions from a cluster of 14 pools in the Cape Cod National Seashore (CACO), 3 additional Cape pools, a cluster of 7 pools in central Massachusetts, and a subset of 18 pools elsewhere in the state. Single-date samples taken from an additional 50 pools complement the long-term data set. Processing of samples and identification of organisms is ongoing for some sites. This long-term study (6-12 years of data per site over 19 years) of macrofaunal community dynamics in southern New England vernal pools investigates within-pool biological responses to year-to-year variations in climate and pool hydroperiods, between-pool differences in habitat and aquatic community composition, and the influence of landscape-scale variables within the broader context of long-term climatic variation and watershed changes.

Patterns appearing in our preliminary analysis include chemistry, vegetation, and historic land use. A pH gradient occurs across the central Massachusetts pool cluster, and it fluctuates between years in relation to changes in maximum water depths. Distributions of molluscs and fairy shrimp within the pool cluster suggest a threshold pH tolerance for these taxa. In the CACO pools, a gradient of pH associated with the relative abundance of Sphagnum sp. is evident.

The distributions of a number of invertebrates, including a northern caddisfly, Phanocelia canadensis, are correlated with pH and Sphagnum in these pools (Colburn and Garretson 2003, submitted). In individual pools across the state, the distributions of some species of aquatic insects and amphibians closely track patterns in hydroperiod from one year to the next. Between pools, differences in vegetation and canopy closure, as well as average hydroperiod, explain some of the variation in species' distributions, as does past history of forest clearing for agriculture (see abstract by Musgrove and Colburn, this volume).


Establishing a Long-term Monitoring Protocol for Freshwater Macroinvertebrates at the Cape Cod National Seashore

E. A. Colburn and H. Jensen-Herrin

Freshwater lakes, ponds, and wetlands, and the plants and animals that they support, are among the most important natural resources of the Cape Cod National Seashore. The development of an inventory of the biological resources of the Seashore's fresh waters, and the establishment of a program for long-term biological monitoring to detect changes in water quality and other parameters in Seashore waters, are high priorities for the National Park Service (Godfrey et al. 1999). We are beginning a process of research designed to categorize freshwater bodies in the Cape Cod National Seashore; to carry out an inventory of a selected subset of those water bodies in order to identify indicator species, assemblages, or metrics useful for monitoring changes over time; to develop a protocol for use by Seashore staff for long-term monitoring of the ecological state of the water bodies over time; to present the National Park Service with a report detailing the results of the initial classification of
water bodies, inventory, and method development; and to provide the Seashore with a step-by-step protocol for implementation of the monitoring program.

Development of a protocol for monitoring the Seashore’s fresh waters will involve several steps. Preliminary work requires preparation of a list of water bodies, classification of these waters into categories, selection of freshwater bodies of interest within each category, assessment of likely threats to each water body and of potential impacts of those threats, and identification of major habitat types within each chosen water body. Once study sites have been chosen and target habitats identified, we will sample for macroinvertebrates using several different techniques at different times of year. Identification of collected animals, and analysis of the results of the sampling in relation to the water body classes and a variety of physical, chemical, and habitat data will allow us to determine sampling methods and target taxa or associations that promise to provide the best resolution for monitoring long-term environmental changes of interest.

Effects of Hemlock Decline on Forest Stream Communities

E. A. Colburn and D. A. Orwig

The invasion of an Asian insect, the hemlock woolly adelgid (Adelges tsugae), is focusing attention on hemlock and its ecological role in northeastern forests. The adelgid attacks both mature trees and seedlings. Infested trees die within a few years and are usually replaced by hardwoods (Orwig and Foster 1998). Preliminary research in the Delaware Water Gap (DWG) suggests significant differences in water quality and biota of streams draining hemlock- and hardwood-dominated stands (Snyder et al. 2002). Hemlock is an important component of New England’s forests, including many nature reserves and water-supply watersheds, and the effects of adelgid-induced hemlock mortality on stream water quality and biodiversity are of concern.

Soils under conifers tend to be acidic, high in organic carbon, and low in nitrogen and phosphorus (Howard and Howard 1993, Lapin 1994). Streams in hemlock-dominated watersheds tend to have higher dissolved organic carbon (DOC) and lower dissolved nutrients than streams in hardwood catchments (Snyder et al. 2002). Adelgid-induced hemlock decline may increase decomposition and nitrogen cycling in the forest soil (Yorks et al. 1999), potentially contributing to increased nutrient export in groundwater and streams. In the DWG, hemlock-dominated streams are more thermally stable, remain cooler in summer and warmer in winter, and appear to be less susceptible to seasonal drying than hardwood-dominated streams (Snyder et al. 2002). Hemlock streams also support a richer aquatic macroinvertebrate fauna and a higher proportion of predatory fish species, and they appear more likely to sustain populations of native brook trout than hardwood streams. We predict that adelgid-induced hemlock decline in New England will alter habitat, increase algal primary production, change aquatic community composition, and affect the relative abundance of different functional feeding groups of invertebrates and vertebrates in streams draining catchments currently dominated by hemlock.

In late summer, 2002, we began collecting baseline data on habitat structure, water flow, temperature, stream salamanders, and aquatic macroinvertebrates in 17 headwater streams dominated by hemlock or hardwood in central Massachusetts. In summer, 2003, we plan to expand our surveys to a number of streams located along a space-for-time transect of hemlock decline from southern Connecticut to northern Massachusetts (Orwig and Foster 2002). We will also intensify sampling in headwater streams in hemlock and hardwood watersheds at Harvard Forest. Our stream data will be tied to analysis of vegetation composition and structure, soil decomposition, and nutrient cycling in the adjacent forest.


Physical and Biological Characteristics of Headwater Habitat Streams in Central Massachusetts: A Preliminary Assessment

E. A. Colburn, J. Choiniere, H. Jensen-Herrin, D. Williams and C. Dunn

Intermittent headwater streams are poorly understood and receive limited regulatory protection in Massachusetts. This research is evaluating the role of headwater streams as habitat for salamanders and aquatic invertebrates, with a long-term goal of contributing to volunteer monitoring of these systems. Starting in late summer, 2002, we mapped and sampled 17 intermittent headwaters tributary to 6 perennial streams in Westminster, Princeton, and Petersham, northern Worcester County, Massachusetts. We flagged each stream at 20-m intervals, recording GPS coordinates and describing channel characteristics, substrate, gradient, flow, riparian vegetation, and land use between flags. Based on the mapping results, we subdivided each stream into 50-m study reaches for biological sampling. In late fall we began intensive visual surveys and net sampling for stream salamanders (Gyrinophilus p. porphyriticus, Desmognathus f. fuscus, and Eurycea bislineata) and terrestrial salamanders (Plethodon cinereus, Notophthalmus viridescens) in randomly selected, area-constrained transects 1 m wide by 4 x mean channel width in each reach. Salamander sampling is complemented by dip-netting for aquatic macroinvertebrates in square-meter quadrats upstream of each salamander transect. Sampling is ongoing and will continue until after the streams have dried in summer, 2003.

Some of the study areas were cleared historically for agriculture but have regrown to forest over the past century; some were not farmed but have been harvested for forest products; others have been continuously forested. All of the streams are small, one half to one kilometer long and one-to-three meters wide, and most of them flow into impoundments created by farmers in past centuries, or by beavers in recent decades. The history of intensive land use in central Massachusetts is reflected in the presence of unpaved roads at varying distances upgradient of all of the headwater channels, and some streams receive high loads of eroded sand from these roadways.

Our preliminary analysis shows that these streams do not follow the expected longitudinal pattern of ephemeral channels leading to interrupted, then interstitial sections before reaching perennial flow. Wooded wetlands with no surface flow or evident channels are interspersed along the length of several of the headwater streams. Perennially flowing sections occur upstream of wetlands and seasonally dry channel reaches. In most of these headwater streams, reaches of high gradient with boulders are interspersed among gravel stretches and meandering reaches with seasonally deep pools. Fountain mosses (Fontinalis sp.) are common on cobbles and occur in seasonally dry stream reaches. Preliminary data on benthic invertebrates
from the streams suggest strong similarities in species composition both along the length of the headwaters and between streams.

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


Roughly 90% of nitrogen oxides (NOx) in the atmosphere are emitted as a result of human activities. The Midwestern and northeastern United States, and parts of Canada, are recipients of much of this nitrogen (N), deposited as both wet and dry deposition. Northern forests are thought to be limited in growth by the availability of N. Increased N inputs have coincided with increased carbon (C) contents reported in northern forest inventories. The fate of anthropogenic N, its residence time, and the potential N-fertilization effect on forest growth remains unknown. We report throughfall findings from an ecosystem-level N addition made as wet precipitation to the canopy of a spruce-hemlock forest in central Maine. Beginning in the growing season of 2001, ammonium nitrate was sprayed on 21 hectares of forest canopy by helicopter in six applications from May through September. The addition rate was 18 kg N ha\(^{-1}\) yr\(^{-1}\); approximately 3X wet-estimated dry ambient atmospheric deposition for this site. Additional fertilizer N at a 1% \(^{15}\)N enrichment was aerially applied to 30x100 m (0.3 ha) plots during each fertilization. These smaller plots received N as either \(^{15}\)NH\(_4\) or \(^{15}\)NO\(_3\). We measured “throughfall” N reaching the forest floor the day of the fertilizations, and also in throughfall on an event basis after all precipitation events prior to winter.

Filter paper randomly placed on the forest floor the day of three fertilizations was retrieved ~2 hours post-fertilization and leached with a 2M KCl solution to remove mineral N. Approximately 9% (range: 4 to 20%) of the N applied was reaching the forest floor immediately after the foliar application. An additional 30% of the total N added to the canopy was recovered in throughfall over the course of the growing season. Finally, 5-10% of the experimentally added 18 kg N ha\(^{-1}\) yr\(^{-1}\) was returned to the atmosphere by gaseous release of, mainly, NH\(_3\). Thus, about 50-60% of the experimentally added N was retained within the canopy, lost by way of stemflow, gaseous losses from the canopy, or translocated within the trees. We are using recovery of \(^{15}\)N in foliage samples taken at the end of the growing season to assess total N uptake by the canopy. The N uptake fraction = (foliage\(^{15}\)N \\ - background\(^{15}\)N) * (canopy N mass + applied N)/(applied \(^{15}\)N applied N mass). Using this latter approach, we estimate a very different value for canopy N retention. The \(^{15}\)N technique suggests uptake may be as low as ~10%. The \(^{15}\)N approach is likely to underestimate canopy uptake because it assumes no isotopic exchange or redistribution within the canopy. The mass balance approach may be an overestimate since gaseous N losses from the canopy might account for greater losses of the applied N. Both methods suggest that some of the applied N is being retained by the canopy, and further sampling of woody tissue should demonstrate whether significant translocation is occurring. The effects of N uptake by the canopy on C exchange and ecosystem C storage has not yet been detected after two years of eddy covariance and biometric measurements, and long-term monitoring of these processes is continuing.

QTL Analysis of Parental Effects on Seasonal Dormancy in Arabidopsis thaliana

K. Donohue, S. Takao*, A. Wheeler and L. Dorn

Seed dormancy is an important life history character that can strongly influence fitness. Appropriate germination responses to environmental cues may contribute to persistence in a variable environment or expansion into novel environments. This research investigates the genetic basis and adaptive significance of germination responses to seasonal cues in Arabidopsis thaliana. Using a combination of quantitative trait loci (QTL) mapping and manipulative selection studies in the field, we will determine which QTL contribute significantly to variation in seasonal dormancy and how variation in seasonal germination timing influences fitness.
This research program focuses on germination responses to two seasonal cues: the photoperiod under which maternal parents mature seeds, and the temperature experienced by seeds after dispersal. Plants can mature seeds in the late spring under long photoperiods or in late autumn under short photoperiods. Seeds dispersed in spring experience hot temperatures immediately after dispersal, while seeds dispersed in autumn experience cold temperatures. We therefore manipulated the photoperiod experienced by maternal plants and the temperature experienced by seeds in order to determine their effects on germination.

In one summer project, we used seeds collected from replicates of recombinant inbred lines that had been grown in either a long day or short day photoperiod under controlled conditions. After the seeds afterripened for six months, we exposed them to different incubation temperatures in the dark before putting them in the light at temperatures that promote germination (23°C). Incubation temperatures included two weeks at 31°C, two weeks at 23°C, and two weeks at 31°C followed by five days at 4°C.

The incubation temperature significantly influenced the percentage of seeds that germinated. Warm incubation caused less germination, while cold broke the dormancy induced by warm incubation. Seeds incubated at 23°C displayed no dormancy. Maternal photoperiod did not influence percentages of germination in these fully afterripened seeds. Significant genetic variation was detected for the percentage of seeds that germinated in both treatments that included a warm incubation period. Genetic correlations between germination in the different incubation treatments were strong, but significant genotype-environment interactions were also detected. Therefore, different genotypes responded differently to the different incubation treatments. A very preliminary analysis identified one chromosomal region associated with variation in germination in both the warm incubation and warm/cold incubation treatments. Evidence for effects of a different chromosomal region was found for germination in only the warm incubation treatment. Therefore, one gene appears to be associated with variation in germination regardless of incubation treatment, whereas another gene may determine germination only under certain conditions.

Quantitative Genetic Architecture and Plasticity of Seed Dispersal in *Arabidopsis thaliana*

*K. Donohue, N. Wender* and *C. R. Polisetty*

This project addressed the genetic basis of seed dispersal and its plasticity in *Arabidopsis thaliana*, a model organism for molecular genetic studies. Our goal was to determine whether dispersal ability has a genetic basis so that we can predict whether dispersal can evolve in response to natural selection. We also characterized plasticity in dispersal in response to density and seasonal conditions. By determining whether genetic variances and covariances change with density, we will be able to predict how the evolutionary potential of dispersal changes as dispersal itself evolves.

The most significant finding from this project to date is evidence for a novel genetic constraint on the evolution of dispersal that is mediated by phenotypic plasticity. First, we identified maternal plant traits that significantly influenced dispersal. Branching angle, branch number, silique length, percent fruit dehiscence, and the percentage of fruits on the primary stem all influenced seed dispersion patterns. Second, we found significant genetic variation for these maternal traits. The genetic variation for maternal traits that influence seed dispersion patterns, moreover, did not differ with density. However, these plant traits determined dispersal much more strongly when plants were grown at high density than when they were grown at low density. Therefore, genetic variation for dispersal itself would be greater at high density than at low density. As increased dispersal ability evolves and plants experience lower densities as a result, the expression of genetic variation for dispersal is expected to decline. Thus, a limit to the evolution of dispersal may result. Genetic constraint can thereby be mediated by the evolution of the trait itself.

We found substantial plasticity in dispersal in response to density. Plants that grew in high density dispersed their seeds shorter
distances, and their seeds experienced less sibling competition although non-sibling density was very high. Thus plants that were themselves efficiently dispersed and consequently grew in low density also dispersed their own seeds efficiently. This dynamic can create a positive environmentally-induced correlation between generations for seed dispersal that may accelerate responses to selection on dispersal.

Effects of Nutrient Stress on a Co-evolved Food Web

A. M. Ellison, and N. J. Gotelli

Ecological communities are made up of interacting species that have evolved in response to particular types, frequencies, and intensities of stress and disturbance. Environmental cycles with lengthy return times, natural and anthropogenically-induced climate change, and unintentional or deliberate alterations of the environment may modify the types, frequencies, or intensities of stressors. The consequences of such stressors for species interactions and community structure are unknown, and may be especially severe for communities of strongly co-evolved species. In the summer of 2003, we will begin a three-year research project to determine how a novel stressor – atmospheric deposition of nutrients – is changing the dynamics of the detritus-based food web that has co-evolved with its host, the northern pitcher-plant Sarracenia purpurea. The focus of this research is on a detritus-based food web, because 70-90% of all primary productivity enters food webs as detritus. However, the development of model systems for understanding the structure and dynamics of detritus-based food webs has not paralleled similar developments in studies of grazing food webs, in which the basal trophic level is composed of phytoplankton, algae, or vascular plants. Specifically, in the course of this research, we will test three null hypotheses using a combination of greenhouse and field experiments:

1) Nitrogen derived from atmospheric sources and nitrogen from captured prey are used equivalently by the Sarracenia food web and the plant itself;
2) The trajectory of assembly of the Sarracenia food web is independent of initial starting composition, habitat type, and the type of, and rate at which, nutrients are supplied;
3) Host plant growth morphology is independent of food web structure and nutrient supply.

The results will be used to develop Markov models of community assembly and coupled differential equation models of food web dynamics. These models will be used to predict the responses of integrated communities to environmental stress. This research project will reveal the importance of anthropogenic stressors on co-evolved systems, and contribute to a deeper understanding of the assembly of food webs by contrasting effects of top-down and bottom-up forces on the dynamics of non-equilibrial assemblages. It also will lead to an appropriate model system for the experimental study of detritus-based food webs.

Biology of Loss and Replacement of Core Species Caused by an Invasive Insect

A. M. Ellison, D. R. Foster, D. Orwig and the FIBR collective

We describe a new five-year project aimed at elucidating and modeling how a single core species – Eastern Hemlock – determines the biological, biogeochemical, physical, and ecological processes of the ecosystem it creates. We propose to document and predict how the elimination of that core species, its replacement, and subsequent community re-assembly change these fundamental biological and ecological processes. This research program uses as a model system the current elimination of eastern hemlock by an invasive, exotic insect, the hemlock woolly adelgid.

The four objectives of this project are to:
1. Develop a comprehensive understanding of the way that a single core species can create and maintain an environment that supports a wide variety of other organisms.

2. Predict how a biological community is reorganized and reassembled following the loss of that core species and assess the implications of this loss at local, landscape, and regional scales.

3. Elaborate a mechanistic understanding of the biological, biogeochemical, and physical processes associated with this reorganization and reassembly.

4. Produce a predictive, general model of how coupled biological-physical systems will respond to loss and replacement of core species.


D. R. Fitzjarred, R. M. Staebler, M. Czikowsky, R. K. Sakai and A. Tsosyref

1. Forest phenology and streamflow. We hypothesize that the greatly enhanced growing season evapotranspiration (ET) by 'robbing' streams of runoff provide a phenological indicator. In last year’s abstract, we identified three independent runoff characteristics that accompany spring onset and leaf emergence. These are the return of the P-R curve to pre-snowmelt pulse values, the streamflow recession time constant for return to base flow after a rain event, and the amplitude of the diurnal streamflow signal. At some level, replacement of pasture with forest should alter the long-term hydrological balance in an analogous manner, but these observed effects of reforestation on watershed runoff are often subtle. However, we detected long-term changes in the streamflow recession time constant that may be attributed to successional forest growth (Czikowsky 2003).

Two competing factors are at work that could change the length of streamflow recessions due to successional forest growth. The more apparent factor is that growing-season streamflow recessions should be shortened due to increased ET. The less apparent factor comes from application of the variable source concept of hydrology (Dunne 1978). Successional forest growth not only results in increased forest cover, but in an increasingly well-developed rooting system. Greater soil infiltration at depth should occur from a better-developed rooting system. With greater soil infiltration, a larger proportion of precipitation will seep deeper into the soil column and result in delayed baseflow runoff rather than the more quickly contributing overland flow. Consequently, streamflow recessions should be lengthened. In the Wappinger Creek, NY watershed, there has been about a 40 percent increase in forest cover since streamflow records became available in 1928. Note that recession lengths here (Fig. 1) increased in the long-term during the late spring period, owing to higher soil infiltration and a greater delayed runoff contribution which lengthened recession times. During the growing season, the effect of increased ET demand by the successional forest cover dominates as recession lengths are shortened in the long-term. By contrast, we observed an increase in the recession lengths in the middle of the growing season during the 1970-2000 period for a central Massachusetts watershed of similar size but with a different land-use history, the East Branch of the Swift River (Fig. 2). Forest cover fractions on this watershed have changed less than 10 percent over the period of record. The longer recession times may indicate that the aging forest of this region is transpiring less than it was earlier in the 20th century.

After identifying the three methods that we used to infer spring onset, we examined which watershed characteristics are related to these indicators. The diurnal streamflow signal appears in the smallest watersheds (< 200 km²) more frequently (Fig. 3) and with greater amplitude (Czikowsky 2003). The fraction of time the diurnal streamflow signal appears as well as its amplitude \( \frac{s'}{s} \) scale to watershed area \( A_w \) through the power-law \( \left( \frac{s'}{s} \right) \sim A_w^{0.34} \). Mainstream length (Eagleson, 1970) and total stream length (Rosso and Bacchi 1991; Crave and Davy 1997) have also been found to scale to watershed area (\( \beta \approx 0.5 \)). If we hypothesize that the riparian area has approximately constant width, \( A_r \) is proportional to total stream length \( (L) \), increased riparian area fraction in small watersheds
contributes to the greater likelihood of the diurnal streamflow signal being observed there.

Until the late 1990's, only daily-averaged streamflow data were available for nearly all of the USGS streamflow observing sites. Reasons for not archiving high-frequency data included limited storage capacity and that daily data was believed to be sufficient for most hydrological studies. The recent practice of archiving 15-minute streamflow data at the USGS gauging sites is clearly of great utility and should be continued.

2. Canopy-atmosphere exchange processes. We continue our efforts to understand the physics of subcanopy flows and their connection to potential CO2 flux deficits. Fluxnet carbon budgets now rely on an empirical rule of thumb to account for respiration on calm nights. To understand flows on calm nights, we developed a microkinematic approach, the DRAINo experiments performed from 1999-2002.

Canopy structure. In 2002, subcanopy measurements of the wind and CO2 fields in a 120x120m grid around the EMS tower were conducted from mid-April to early December, covering the whole growing season. In addition, in collaboration with G. Parker of SERC, detailed canopy structure measurements were made using the methods of Parker et al. [2002], walking horizontal transects through the forest with an upward-looking laser range finder. Laser return readings were taken at 170Hz and binned in horizontal 2m sections along the path walked, equivalent to about 680 data points. Corrections were performed to correct for the bias to closer targets by assuming that leaves are Poisson randomly distributed [MacArthur and Horn, 1969]. An absolute canopy area density (CAD) is then derived using an empirical relationship between leaf area indices measured by leaf litter collection and laser return signals [Parker and Lefsky, 2003].

Six 80m transects covering the “DRAINo grid” were made, with the EMS tower roughly in the middle. The northeast transects were distinctly bottom-heavy, primarily because of the dense, low hemlock found along this transect. Transects oriented towards the southwest indicated more evenly distributed canopy elements. Here the forest is dominated by maples and oaks. The average of all CAD profiles reflects these two types of canopy encountered near the EMS tower, and displays a bimodal distribution (Fig. 4). 90% of all canopy area is found below 20m, although some canopy elements are found as high as 25m.

Direct observation of understory winds. Understory flows in complex terrain are affected by four physical forces, as shown in the momentum equation, here simplified to two dimensions:

$$\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} + v \frac{\partial v}{\partial y} = -\frac{\partial p}{\partial x} - \nu \frac{\partial^2 u}{\partial x^2} - \nu \frac{\partial^2 u}{\partial y^2}$$

where $h$ represents the topography, $\tau$ is the stress tensor, $\theta_V$ is the virtual potential air temperature and $\theta_L$ the local departure from it. $FD$ represents the sum of all drag forces. The Boussinesq approximation has been applied, and the rotation of the Earth and molecular dissipation neglected.

The first force is coupling with the flows aloft, which can take the simple form of momentum transfer into the canopy through the stress, term [4] in Eq. (1). The second force [5] is gravitational, when radiative cooling near the ground creates negative buoyancy, which will cause the colder air to flow downhill. Term [6] (pressure perturbation) is also potentially important, especially in the lee and wake of hills. Upon generation, these understory flows are then modified by the immediate local topography and by obstacle effects (e.g. the vegetation). At any given place and time, different combinations of these forces and complications can be expected.

Drainage flows. Depending on which force dominates, the subcanopy flow should have different distinguishing characteristics. In Fig. 5, the effect of the buoyancy term [5] is made clear. As the fraction of this force in the sum of all forces increases, the north and northwest wind directions starts to dominate. This direction agrees with the longest continuous slopes at Harvard Forest.

Consequences of understory flows on the carbon budget. We describe the CO2 budget in a conceptual box of height $h=29m$ and horizontal size of the Draino grid in terms of the equation of conservation of $c$: 

37
<table>
<thead>
<tr>
<th>Study period</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of nights with all data</td>
<td>70</td>
<td>66</td>
<td>46</td>
<td>128</td>
<td>310</td>
</tr>
<tr>
<td>Number with CO$_2$ flux deficit (N)</td>
<td>40 (57%)</td>
<td>38 (57%)</td>
<td>24 (52%)</td>
<td>79 (62%)</td>
<td>181 (58%)</td>
</tr>
<tr>
<td>Number of these N with $u_* &lt; 0.2$ m/s</td>
<td>15 (38%)</td>
<td>15 (39%)</td>
<td>9 (38%)</td>
<td>36 (46%)</td>
<td>75 (41%)</td>
</tr>
<tr>
<td>Number of these N with drainage flow</td>
<td>27 (68%)</td>
<td>27 (71%)</td>
<td>20 (83%)</td>
<td>51 (65%)</td>
<td>125 (69%)</td>
</tr>
<tr>
<td>Number of these N with stress flow</td>
<td>1 (3%)</td>
<td>2 (5%)</td>
<td>0 (0%)</td>
<td>7 (9%)</td>
<td>10 (6%)</td>
</tr>
<tr>
<td>Number of these N with pressure flow</td>
<td>10 (25%)</td>
<td>6 (16%)</td>
<td>4 (17%)</td>
<td>17 (22%)</td>
<td>37 (20%)</td>
</tr>
</tbody>
</table>

Table 1: Summary of nightly conditions. The last four rows refer to the subset of nights with CO$_2$ flux deficits. Drainage, stress and pressure flows refer to nights when the corresponding terms in Eq. (1) ([15], [4] and [6]) were dominant. Note that the last three rows may not always sum to 100% because on some nights no one of the forcing terms clearly dominated.

<table>
<thead>
<tr>
<th>Deficit Nights</th>
<th>Eddy Flux</th>
<th>Storage</th>
<th>Vertical Advection</th>
<th>Horizontal Advection</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1.4 ± 0.1</td>
<td>0.49 ± 0.02</td>
<td>-0.01 ± 0.27</td>
<td>0.67 ± 0.08</td>
<td>2.6 ± 0.3</td>
</tr>
<tr>
<td>Non-deficit Nights</td>
<td>2.6 ± 0.4</td>
<td>0.40 ± 0.03</td>
<td>0.10 ± 0.36</td>
<td>0.34 ± 0.11</td>
<td>3.4 ± 0.6</td>
</tr>
</tbody>
</table>

Table 2: Summary of the 2002 (DOY 117-330) results. All values are in $\mu$moles/m$^2$/s.

Fitzjarrald et al.
Figure 1. Mean streamflow recession time constant, Wappinger Creek, NY. The solid line refers to the 1928-1958 period, the dashed line the 1970-2000 period. The standard error bars are shown. The rows at the bottom of the figure labeled E and L are the number of observations in the early and late period respectively. The points on the graph represent the midpoint day of the period during the recession times were taken.

Figure 2. Same as figure 1, but for the East Branch of the Swift River, Hardwick, MA. The solid line refers to the 1937-1958 period.

Fitzjarrald et al.
Figure 3. Watershed area ($A_w$) vs. diurnal signal time fraction (solid line). The diurnal signal time fraction is defined as the fraction of time the diurnal streamflow amplitude ($S'/S$) exceeds 2% of the total streamflow. The error bars indicate the upper and lower 95% confidence intervals for the median. The values listed above the x-axis indicate the number of station-years included for each watershed size range. The dashed curves represent the power-law relationship between watershed area and streamflow amplitude, 
\[
\frac{S'}{S_c} \sim A_w^{-\beta}
\]
Labels above the curves denote $\beta$ values from 0.5 to 0.8.

Fig. 4. The average CAD distribution near the EMS tower at Harvard Forest. Dotted lines delimit the standard error. Dashed line represents the winter (leafless) profile of a similar mixed deciduous stand about 1 km southwest of the EMS tower.

Fitzjarrald et al.
Fig. 5: Wind roses as a function of the relative importance of the buoyant (drainage forcing) term in the sum of the forces. The $bfrac$ percentages represent the fraction of the buoyant forcing term in the sum of all forces. The last panel represents a "slope rose", showing the total elevation drop in each direction to the next significant topographic inflection point. Negative slopes are indicated by dashed, positive by dotted lines. The arrow heads point downslope. Note that the sum of upwind and downwind slope appears to dictate the preferred drainage direction.

Fig. 6. Mean diurnal cycles of the eddy flux, storage term, vertical and horizontal advection terms for the growing season 2002. The horizontal $x$ and $y$ coordinates are oriented west-east and south-north. The bottom right corner shows mean ± standard error. Diurnal means for each component for the growing season are given at lower right.
\[ \int_0^h \frac{\partial}{\partial t} dt + \int_0^h \frac{\partial}{\partial z} \left( \frac{\partial}{\partial t} \right) dt + \int_0^h \frac{\partial}{\partial y} \left( \frac{\partial}{\partial t} \right) dt + \frac{\partial}{\partial x} \left( \frac{\partial}{\partial t} \right)_h = \int_0^h \frac{\partial}{\partial t} dt \]

Term 1 is the storage term, 2\([2]+3\) the horizontal advection, 4\([4]\) the vertical advection term advocated by Lee \([1998]\), 5\([5]\) the eddy covariance flux at \(z=h\), and 6\([6]\) the sum of all sinks and sources between \(z=0\) and \(z=h\), including everything crossing the lower boundary at \(z=0\).

Table 1 summarizes the statistics of the relationship between nights when the eddy covariance fails to properly measure the respiration flux of CO2 ("deficit nights") with subcanopy flow conditions for all four years of "Draino" observations. Nights with drainage flows do indeed correlate well with nights with missing eddy fluxes. In fact, high buoyant fractions describe these nights significantly better than the commonly used \(u^*\) criterion.

Fig. 6 summarizes the mean diurnal variation of all measured components of the CO2 budget. Both the measured eddy covariance (EC) and the \(u^*\)-corrected signals are shown. The advective terms are significant at night and disappear during the day. The sum of EC, storage and advective terms agree within limits of error. Table 2 separates nights with clear deficits from those with apparently correct EC fluxes. Horizontal advective terms increase during deficit nights. However, adding the advection term does bring deficit and non-deficit nights into closer agreement, within the resulting error limits.


The Regulation of Transpiration Rate in Plants

P. Franks, M. Zwieniecki and N. M. Holbrook

The survival of all land plants depends primarily on their ability to maintain hydration while performing photosynthesis. Central to this task is the regulatory role of stomata. Increasingly dry air is a threat because the hydraulic gradients required to sustain higher transpiration rates, particularly in trees, may constitute an intolerable state of cellular desiccation or induce air embolisms in xylem. To protect against this, stomata appear to have evolved functionally to down-regulate transpirational water loss as air becomes drier. The intensity of this regulation is known to vary considerably between species (Fig 1), but little is known about both the mechanism of this regulatory process, or the basis of its variation across species.

Recent data on the hydromechanical properties of stomatal guard cells and hydraulic conductivities of leaf fine veins suggests that control of transpiration rate must depend heavily on the nature of the hydraulic resistances of the non-vascular tissue between leaf xylem elements.
**Figure 1.** Illustration of the range of stomatal control of transpiration rate under increasing transpiration demand. All terrestrial vascular plants studied so far exhibit some control, but there is a broad range of responses between weak and strong control.

![Graph showing transpiration rate and demand with control levels](image)

**Figure 2:** Leaf cross section diagrams showing two possible variations in leaf hydraulic properties that may influence the mode of stomatal transpiration control: (a) No change in hydraulic resistance between vein and guard cells/sub-stomatal-chamber; (b) Higher hydraulic resistance (round symbol) between subsidiary cell and adjacent guard cell.

![Diagram of leaf cross sections](image)

Franks et al.
and sites of evaporation on the guard cell walls and/or sub-stomatal chamber walls. Our hypothesis is that variations in leaf tissue hydraulic resistances (Fig. 2) influence the mode of stomatal control of transpiration rate. It is possible that these differences in hydraulic properties are determined by different leaf anatomical characteristics. Our objective in this study is to use micro-probe techniques to manipulate and measure the degree of hydraulic coupling between leaf veins and different points along the hydraulic flow path between veins and evaporative sites near stomata, and to use this quantitative information to develop a mechanistic model of transpiration control.

This study will yield insights into the role played by leaf hydraulic resistances in stomatal control of transpirational water loss. Information gained from this will greatly improve our understanding of the linkages between leaf anatomy, leaf hydraulic properties and regulation of transpiration rate in plants. Application of this information to both living and fossilized leaf material will aid our interpretation of plant evolution and provide an improved mechanistic basis for understanding forest responses to changing climates.

Chronic Nitrogen Enrichment Affects the Structure and Function of the Soil Microbial Community

S. D. Frey and M. Knorr

Inputs to the terrestrial N cycle have doubled in the past century due to anthropogenic activities, particularly fertilizer use and fossil fuel combustion. The biota in many terrestrial ecosystems evolved under low N conditions and thus, one anticipated consequence of elevated N inputs is the change in species composition and/or diversity. There are still major uncertainties in our understanding of how N enrichment will impact the soil community and ultimately ecosystem function. We have begun a study to examine the effects of N enrichment on the relative abundance, diversity, and activity of bacteria and fungi in forest soils exposed to chronic N additions. During fall 2002 we collected and analyzed soil samples from the Chronic Nitrogen Addition Plots at Harvard Forest. One soil core (5.6 cm diam; O horizon plus 10 cm of mineral soil) was collected from four of the 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. The samples were analyzed for active bacterial and fungal biomass, microbial functional diversity, and the activities of cellulolytic and ligninolytic enzymes. To date, we have found that long-term N additions have decreased total microbial biomass, relative fungal biomass, functional diversity, and lignin-degrading activity (Fig. 1). Total microbial biomass was 35 and 38% lower in the high N compared to control plots in the hardwood and pine stands, respectively. The proportion of the microbial community comprised of fungal biomass declined from 70-94% in the control plots to 45-53% in the high N treatments. Catabolic evenness, assessed by measuring the respiratory response of the microbial community to the addition of 25 different C sources, indicates that the functional or metabolic diversity of the microbial community is reduced under long-term N additions. Finally, the activity of phenol oxidase, a lignin-degrading enzyme, was significantly reduced by N enrichment, with a particularly strong effect observed in both the low and high N plots in the hardwood stand. We expect that these changes in the microbial community will be reflected in the quantity and quality of the active soil organic matter pool. During the coming year we will be measuring the concentrations of the amino sugars muramic acid and glucosamine in order to quantify the relative contributions of bacteria and fungi, respectively, to the production of microbial-derived organic matter. We will also conduct an experiment to examine the relative contributions of mycorrhizal and saprotrophic fungi to N immobilization in these soils.
Fig. 1. Total microbial biomass, relative fungal biomass, functional diversity, and phenol oxidase activity in soil samples collected from the hardwood and pine stands at the Chronic Nitrogen Addition Plots. Error bars represent one standard error.

Frey and Knorr
Quantifying the Importance of Belowground Plant Allocation for Sequestration of Carbon In Soils

J. Gaudinski, M. S. Torn, T. Dawson, J. Bird and S. Mambelli

How much carbon is pumped belowground by root growth in temperate forests? How long do roots live and how does the fate of this belowground productivity compare to the microbial and humic transformations of leaf and needle productivity? These are pressing questions for global change and carbon sequestration research, as well as for ecological theory about plant allocation strategies and their nutrient feedbacks.

Our work aims to better characterize dynamics of carbon cycling belowground for roots versus aboveground plant allocation. We are (1) Quantifying the stocks and lifetime of live fine and coarse roots; (2) Determining the lower bound of NPP "pumped" into soil carbon through these roots; (3) Comparing leaf and root decomposition including rates, microbial communities and humification products; (4) Characterizing the turnover times of soil organic matter pools, and (5) Tracking the partitioning of recent plant photosynthetic to rapidly lost root respiration and exudate mineralization, and more slowly lost root tissues and soil organic matter (SOM). Our approach will take advantage of several new methods (radiocarbon analysis of roots and SOM, $^{13}$C tracking of decomposition products, and isotope-label PLFA analysis). The radiocarbon method in particular allows direct determinations of root age, a measure not currently possible with any other technique. At four northern latitude forest research stations, including Harvard Forest, MA, we will make comparisons of belowground allocation sequestration potential based on species and forest type, including deciduous vs. conifer and re-growing vs. mature managed forests. At Harvard Forest we are focusing on items 1-3 discussed above, namely fine root dynamics and the decomposition dynamics of roots vs. leaves.

Estimates of high belowground net primary productivity (50% or more) in forest ecosystems are often based on assumptions that all fine roots (< 2 mm in diameter) live and die within one year. Recent radiocarbon ($^{14}$C) measurements of fine root cellulose in three eastern temperate forests of the United States show that at least a portion of fine roots are living for more than 8 years (Gaudinski et al. 2001) and that fine root lifespans likely vary as a function of both diameter and position on the root branch system. New data from Harvard Forest, MA, further support the idea of large variations in fine root lifespans. We have sampled soil cores in the O, A and B horizons and sorted all roots (removing fern roots) into five size classes (< 0.3, 0.3-<0.5, 0.5-<0.8, 0.8-<1.1 and 1.1 - 2 mm in diameter) and live versus dead root categories. Samples have also been analyzed for age as a function of position on the root branching system for red maple. Additionally, we have compared $^{14}$C-derived- and mini-rhizotron-derived lifespans for sugar maple from Michigan (in collaboration with Kurt Pregitzer). Our preliminary results are (1) position on the root branching system shows a correlation with age, with ages up to 7 years for 4th order roots of red maple (Fig. 1). (2) The method by which roots are sampled also affects the ($^{14}$C)-estimated age, with roots sampled via soil cores showing longer lifespans and less variation in lifespan relative to roots sampled by position on the root branch system (when similar diameter classes are compared). (3) Mini-rhizotron and radiocarbon lifespan estimates agree well when a correction is made to account for the age of carbon making up new root tissues (~ 1 year). This age correction is right within the resolution range of our bomb-$^{14}$C technique and thus this value comes from parallel work being done at Oak Ridge National Research Park (where there is an enriched $^{14}$C signature ecosystem wide). In the near future we hope to compare our $^{14}$C-derived data with mini-rhizotron data from Tom Gower's research group working in the same area at Harvard Forest.

To predict the sequestration potential of plant C inputs, it is essential to better understand the biological and chemical regulation of the conversion to stable soil organic matter (SOM). Much of the recent research in forest ecosystems has focused on the initial decomposition of aboveground litter. We are examining both aboveground (needles and leaves) and below-ground inputs (fine roots), and determining
Figure 1. Radiocarbon ($^{14}$C) derived root ages for live roots sampled as a function of position on the root branch system at Harvard Forest, MA and the Michigan Peninsula. The ages have been corrected to account for a storage time in the plant of 1.5 years prior to new root growth. Also shown is the independently derived minirhizotron (MR) estimate of average age of first and second order roots combined for sugar maple (Kurt Pregitzer, personal communication). First order roots are the smallest most distal roots. Error bars are range when $n = 2$, otherwise $n = 1$. However each run for $^{14}$C represents composites of three samples. We thank Kurt Pregitzer for providing us sugar maple root splits from the Michigan Peninsula and fostering comparison of our $^{14}$C data with his mini-rhizotron data.

Gaudinski et al.
decomposition rate as well as the conversion of C inputs into stable SOM fractions. Our objectives are to assess the effects of soil depth (O vs. A horizon) and litter type (roots vs. needles or leaves) on C and N stabilization rates and humification pathways in temperate forest soils. As part of this goal, we are conducting a litter bag study at Harvard Forest, MA (deciduous forest) and Blodgett Forest, CA (conifer forest). In fall 2001, litter bags were placed in the organic and mineral (O and A) horizons at Blodgett Forest and Harvard Forest. The litter types are: three sizes of classes of roots, needles (Blodgett); leaves (Harvard Forest), and a common wood substrate placed at all sites. By placing each kind of litter at both soil depths and having a substrate common to the forests, the results will enable us to evaluate the influence of soil environment, litter type, and litter chemistry on litter decomposition rates.


Carbon Exchange Measured in a 55-Year-Old Oak-Maple Forest on a Dry Upland Site in 2002

J. Hadley

Carbon exchange was measured using the eddy covariance technique on an upland site near the center of a forest fire that destroyed about 20 ha of forest in 1957. The forest within 200 m to the SW and NW of the carbon exchange site is dominated by red oak and red maple, which established after the fire, along with smaller numbers of black oak, white birch, black birch, eastern hemlock and white pine. Beyond 200 m to the SW is a 70-year-old red pine plantation and older forest outside the burn, while to the NW are older oaks, maples, black birch and some white pine.

Eddy covariance measurements were begun in May 2002, along with measurements of soil respiration using chambers and a portable gas analyzer. Daily net carbon storage by the forest was first observed on May 21, but cold and cloudy weather prevented consistent daily net carbon storage until after May 29. The forest stored 1.1 to 1.4 Mg/ha of carbon per month in June, July and August, and slightly less than 1 Mg/ha in September. Data from the dormant period beginning in October are being evaluated.

One of the challenges for estimating carbon exchange of the relatively young forest in the area burned in 1957 is the relatively small size of the burned area. A mathematical model to estimate the source area for measured carbon fluxes (footprint model) based on the work of Schmid (1994) was created using a detailed wind profile above the canopy. The model shows that nighttime footprints are much larger than the 1957 burn, but in daytime the footprint is sometimes primarily in this area. A detailed analysis of measured carbon exchange rates as a function of footprint area is currently underway.

Soil respiration was measured at 30 locations to the SW and NW of the tower where eddy covariance measurements of carbon exchange were conducted. Soil respiration was primarily affected by temperature, which explained over 90% of the variation in the average rate of the 30 sites. However, during July and August low soil moisture also limited soil respiration, as indicated by a large increase in respiration rate soon after a precipitation event. The highest average soil respiration rate for all 30 sites was about 5 μmol m⁻² s⁻¹ (215 mg m⁻² s⁻¹), similar to that measured at other sites at Harvard Forest, except during very wet years (Savage and Davidson 2001). There was no clear difference in soil respiration between the forest established after the 1957 fire and older forest outside the burn, but total basal area of trees within 6 m of a particular site was positively correlated with the soil respiration rate, as was the basal area of oak trees in particular.


300 Years of Forest Change in Massachusetts: Forest Cover in 1830

B. Hall, G. Motzkin, D. Foster, M. Syfert and J. Burk

In 1830 the Commonwealth of Massachusetts mandated that all towns make maps at a scale of 100 rods to an inch (19,800:1). All towns depicted cultural features such as roads and important industrial, educational and governmental buildings; most maps also show environmental features such as woodland cover, meadows, and water bodies. Since 1830 was near the period of maximum agricultural land clearance in Massachusetts, the maps serve as a reasonable estimate of the maximum extent of forest clearance. This map series has proven to be an invaluable source for historical woodland cover data. While other sources, such as tax evaluations, censuses, and State Foresters’ Reports list only total area of forest, the town maps are spatially explicit and allow spatial analysis and description of forest cover and subsequent change at the local level.

The Harvard Forest has recently finished digitizing the town maps for the whole state into a Geographic Information System (GIS) to facilitate future analysis. Such analysis will be valuable in archeological, historical, and natural resource assessment, planning, and management. Recent and current studies have used the woodland data to identify potential primary forest sites and areas of historic agriculture, to describe long-term trends in forest cover, and to compare with other sources of long-term data.

Ecosystem-Atmosphere CO₂ Exchange in a Maine Spruce-Hemlock Forest: Updated Results


Measurements of carbon dioxide exchange between a spruce-hemlock forest and the atmosphere have been carried out since 1996. The complete flux data set was recently re-evaluated with corrections applied for low frequency flux losses. CO₂ fluxes were examined as a function of the friction velocity, u*, and a minimum threshold of 0.25 (rather than 0.20 as used previously) used for accepting nocturnal flux values. These and other minor changes result in the following integrated NEE values for the Howland Forest for 1996-2001: 158, 153, 133, 178, 271, and 175 g C m⁻² y⁻¹. On average, the revised values are about 5% lower than previous estimates. Interannual variability of NEE is due about equally to variation in respiration and GPP. A variety of factors including total incident quantum flux, temperature, and precipitation affect either or both GPP (photosynthesis) and respiration. The 1996-2002 period of flux measurements at Howland (especially since 1998) represents a time of unusually warm summer temperatures, based on a 50-year climate record from the Millinocket National Weather Service Station.

Carbon Cycling at the Harvard Forest, a Bottom-up Approach


Agricultural land use and active management have changed the vegetation dynamics of the New England landscape. Temperate deciduous forests have been identified as a potentially significant carbon sink (Curtis et al. 2002). Our study uses a bottom-up approach to quantify carbon pools and fluxes thereby allowing us to independently test the findings of the EMS tower (see Urbanski et al. abstract) and understand the linkage between the forest and the atmosphere. We are specifically looking at variables driving the seasonal and annual dynamics of carbon within Harvard Forest. A second experiment was initiated in 2001 to directly measure the long and short-term changes in the carbon cycle resulting from active management.

Forest carbon cycling is not singularly driven by accrual in live wood, but encompasses a multitude of other variables. The forest’s mortality and recruitment demographics
characterize the future composition of the live biomass and create the material for decomposition (See Liu et al. abstract). Litter fall and chemistry provide a metric for assessing inter-annual variation in photosynthetic capacity and nutrient cycling.

In 1993, forty vegetation plots with a radius of 10-m, were established within the fetch of the EMS tower. In 1998, the vegetative plots were resurveyed and a suite of high frequency biometric measurements was added to the study. All trees greater than 10-cm in diameter were outfitted with spring mounted stainless steel dendrometers. Using fine resolution dendrometry measurements we could examine variations in tree growth and responses to long and short-term climatic forcing. In 1999, an active forest management study was created by combining three of the original study plots with six additional plots to monitor ecosystem responses to a typical New England harvest. From February through November 2001, the harvest site was selectively logged. Litter inputs have been monitored at both of these sites since the commencement of the biometric measurements.

Total carbon uptake by live trees showed significant inter-annual variation (Table 1). Late season growth appears to differentiate the total strength of the carbon sink (Fig. 1a). Severe summer drought followed by late season rain in 1999 likely dampened the total rate of carbon uptake. A sunny and warm 2002 growing season may have helped propel the growth rate into the fall. Prior to logging, the harvest site contained approximately 81-MgC ha\(^{-1}\), 42.8-m\(^3\) ha\(^{-1}\) of wood was removed leaving 56.1-MgC ha\(^{-1}\) in post-logging live biomass. The total stock of coarse woody debris more than doubled following harvest (Table 2). The harvest site showed a dramatic increase in carbon uptake in 2002, rebounding to near pre-harvest levels in one-year (Fig. 1b). Continued monitoring of these two sites will provide valuable insight towards understanding the effects of natural variations and anthropogenic activities on the carbon cycle.


Using History for Land Management in New England

A. E. Ingerson

I am investigating whether, how, and why landowners and managers in New England are (or are not) using long-term or historical methods and data to make and evaluate practical decisions, through qualitative interviews with the staffs of nonprofit organizations and public agencies, as well as some private landowners and consultants.

Much science policy focuses on improving access to research, by broadening distribution or simplifying the language used to report results. However, my interviews to date have not identified accessibility as a critical issue. Instead, they have drawn attention to issues of institutional design and practice, for both management and research:

1. **Turnover** State and federal resource management agencies are now shifting from a generation of employees trained to value institutional memory and long-term record keeping to a generation trained to respond to changing public values and implement "state of the art" research and policies. In the private sector, data and plans developed for short-term transactions (timber, land, or easement sales and donations) are seldom archived for future use.

2. **Continuity** Some data collection has been motivated by the threat of potential litigation, or by a need for economic valuation. Paradoxically, data may neither be collected nor archived for land in uncontested, stable ownerships that are not expected to produce periodic income.

3. **History as a static "past"** History is often used to identify "reference" states to which ecosystems should be returned, or in which they should be maintained. Although many managers are skeptical of strict preservation as an approach to both ecological systems and human institutions, there is a dearth of practical examples using historical methods and analyses to understand, manage, or promote rather than prevent ecological and institutional change.
Table 1 – Above Ground Woody Increment (MgC ha\(^{-1}\) year\(^{-1}\))

<table>
<thead>
<tr>
<th>Year</th>
<th>EMS Plots (Total)</th>
<th>EMS Plots (n = 34)</th>
<th>Harvest Plots (n = 9)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>0.94 (n = 40)</td>
<td>1.03</td>
<td>NA</td>
</tr>
<tr>
<td>1999</td>
<td>1.24 (n = 40)</td>
<td>1.37</td>
<td>0.94</td>
</tr>
<tr>
<td>2000</td>
<td>1.48 (n = 40)</td>
<td>1.61</td>
<td>1.30</td>
</tr>
<tr>
<td>2001</td>
<td>1.51 (n = 34)</td>
<td>1.51</td>
<td>0.69</td>
</tr>
<tr>
<td>2002</td>
<td>1.62 (n=34)</td>
<td>1.62</td>
<td>1.02</td>
</tr>
</tbody>
</table>

Table 2 – Changes in Coarse Woody Debris Biomass (MgC ha\(^{-1}\))

<table>
<thead>
<tr>
<th>Classification</th>
<th>Pre-harvest</th>
<th>Post-harvest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stumps</td>
<td>0.16</td>
<td>1.17</td>
</tr>
<tr>
<td>Logs</td>
<td>3.65</td>
<td>10.95</td>
</tr>
<tr>
<td>Snags</td>
<td>6.04</td>
<td>3.73</td>
</tr>
<tr>
<td>Fine Debris</td>
<td>0.76</td>
<td>6.86</td>
</tr>
<tr>
<td>Total</td>
<td>10.62</td>
<td>22.71</td>
</tr>
</tbody>
</table>

Figure 1a – EMS Plots Total AGWI

Figure 1b – Harvest Site AGWI
4. History as retrospective explanation. By explaining the past too thoroughly, history can make past actions appear “overdetermined” or inevitable, and thus irrelevant to current decisions—which usually seem anything but inevitable. Historical ecology may compound this problem by documenting mostly the actual consequences of human actions, while managers face mostly choices between competing routes to the same intended consequences, or between competing intentions.

These tentative findings suggest several new or nonstandard approaches to promoting the practical application of historical ecology:

- **Support place-based partnerships between management and research**, to encourage the integration of long-term knowledge from different specialties (including history and ecology, or the social and natural sciences), to help research and management “co-evolve” over time, and to provide visible intermediate benefits from long-term research and data archiving.

- **Promote a stronger flow of ideas about change management between the managers of cultural and natural resources** (for example, between practitioners of ecologically “adaptive management” and practitioners of “adaptive reuse” in historic preservation).

- **Create new models of historical research and teaching**, centered on critical empathy, which could be used to help policymakers and the public understand the intentions of past and present managers, while still judging management choices by their long-term ecological consequences; such models would make historical methods and data more directly useful for adaptive management.

**Landscapes Dominated by Non-Industrial Private Forest (NIPF) Ownership:**

**Sustainability at Woodlot and Regional Scales**

*J. Burd and J. Burk*

These NIPF lands comprise the dominant forest ownership in many parts of the United States, and represent an important part of the greater forest landscape matrix even in parts of the region where industrial and/or public lands dominate. In northeastern states, NIPF lands can represent 75% or more of total forest area. While forest landowner attitudinal survey work in the past several decades has explored reasons for ownership, motivations, and perspectives on traditional management (e.g., do you intend to harvest in the next 10 years?), little if any study has focused on attitudes and, importantly, documented behaviors related to sustainability on their lands. Some forest owner attitudes pertaining to the notion of sustainability can be inferred from earlier work (e.g., documented interest in wildlife habitat and nature, aesthetics, and privacy), but these do not directly link to sustainability or timber productivity on their own lands.

As the urban-rural interface expands from metropolitan centers, though this wooded landscape may appear to be forested from the air, it no longer sustains a number of benefits upon which society has grown to depend. In particular, timber harvesting declines as a viable and sustainable land use activity. We will use the assembled Massachusetts timber harvest spatial database to: 1. Study the decision-making process, priorities, and behaviors of different types of NIPF owners, in terms of sustainable harvesting, and sale/development; and 2. Use landscape-scale spatial data and associated community-level demographic data to assess the extent to which such landscapes can remain sustainable producers of wood products in the face of expanding urban/suburban influence. In so doing, we will identify characteristics of a NIPF landscape in which harvesting or the production of timber is no longer sustainable.

**Logging as Disturbance in Massachusetts**

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

In a pilot study in the 19-town North Quabbin region, we captured the spatial location and associated information describing all
commercial timber harvesting from 1984 to 2001 (Kittredge et al. in press). Analysis indicates that harvest occurs randomly within this heavily forested region. There is no pattern of spatial occurrence with respect to terrain, forest cover type, soils or other natural features. There is likewise no pattern of occurrence with respect to roads. The only pattern that emerges is with respect to ownership. Some state agencies actively harvest, and others are more passive and their level of harvest is not proportional to the amount of the landscape they control. Interestingly, non-industrial private landowners collectively own roughly 60% of the forest, and were responsible for 64% of the harvested area, suggesting a relative interest in harvest that is not matched by attitudinal surveys which portray owners as disinterested in this form of disturbance on their land.

Based on the results of our pilot study, we are expanding data collection to cover the entire state of Massachusetts. The process is ongoing, and to date we have captured commercial harvest information for approximately 300 of the state’s 350 communities dating back to 1984. Data has been gathered for 4 of the 5 DEM regional districts, covering all of eastern MA, central MA west to the Connecticut River Valley, and Berkshire County. This represents 9,212 harvest operations over this period, and a total of over 141,400 hectares. The average harvest operation is 15 hectares. More than 3/4ths of the harvest occurrences are on non-industrial private land, mirroring the forest ownership pattern in the state. 4.4 percent of the harvests have occurred on DEM state lands, and 8.8 percent have been conducted by the MDC. Detailed species data has been recorded for each harvest, and added to all files in the pilot study. With the exception of portions of Middlesex and Essex Counties, harvest records are available across the state for the 18-year period.

Data collection for the remaining western MA towns and verification of all spatial information should be completed by Summer 2003. We will use this information to study the influence of widespread harvesting disturbance on successional trajectories and future forest composition. Vegetation sampling in harvested versus unharvested areas will also enable us to evaluate the impact of harvesting on native and invasive species distribution and abundance. Together with spatial data on harvesting patterns, our results will provide information that is critical for guiding conservation planning across the region.


Paleolimnological Assessment of Human-Induced Impacts on the Nutrient Balance of Walden Pond (Massachusetts, USA) During the Last Three Centuries Using Diatoms and Stable Isotopes

D. Köster, R. Pienitz, B. Wolfe, S. Barry, D. Foster and S. Dixit

The evaluation of human disturbance on ecosystems and the development of effective and appropriate restoration and conservation management strategies require knowledge of natural pre-disturbance ecosystem structure. The catchment and lake of Walden Pond, Massachusetts, have experienced multiple historical anthropogenic impacts, a site which has attracted much attention since the publication of the American classic “Walden” by the natural philosopher Henry David Thoreau. Despite the public interest in the protection of the lake as a natural and historical monument, no comprehensive study of the pre- and post-disturbance limnology of Walden Pond has been conducted.

As part of a multi-proxy analysis of a sediment core spanning 1600 years from Walden Pond, fossil diatoms reveal substantial changes in the nutrient status over the past 250 years, resulting from anthropogenic impacts on the lake and watershed. Following a period of environmental stability from about 430 AD to 1750 AD, the abundance of the diatom Cyclotella stelligera increased (Fig. 1), organic content declined, and bulk organic $^{13}$C decreased and bulk organic $^{15}$N increased. These changes coincided with logging in the watershed, and are mainly
Fig. 1. Diatom stratigraphy of Walden Pond with major zonation, diatom valves-to-chrysophyte scales ratio, diatom-inferred pH (DI-pH, using WA$_{im}$) and TP (DI-TP, using WA-PLS) and analysis of dissimilarity using the program ANALOG. The sample-specific error for DI-pH and DI-TP (for TP back-transformed to μg·L$^{-1}$) is indicated by horizontal bars. Dashed vertical lines in the ANALOG graph indicate the 75% and 95% confidence limits. Values lower than the 75% limit indicate good analogs, values between the 75% and the 95% limit indicate poor analogs. Levels with poor fit to pH and TP are labelled with asterisks. (from: Köster et al. submitted).
attributed to an increase in detrital input of inorganic sediment from the watershed. With the beginning of intensive recreational development of Walden Pond in the mid-20th century, oligotrophic diatom species were largely replaced by diatom indicators and the diatom-inferred lake pH increased by 0.5 units, while the bulk organic carbon and nitrogen stable isotope composition markedly shifted to lower and higher values, respectively. These changes reflect higher nutrient availability and primary production due to inorganic inputs from erosion related to trails, beaches, and construction as well as increased nutrient inputs by waste water seepage into groundwater and massive swimmer use. During the last 25 years, diatom assemblages stabilized, suggesting that initial management measures have been effective in reducing the rate of eutrophication.

From about 600 AD to the period of European Settlement, a gradual increase in the abundance of *Tabellaria flocculosa*, which has been recently observed during spring overturn and late summer in Walden Pond, might indicate longer full circulation periods due to lower summer temperatures or earlier ice-breakup than before 600 AD.

Notably, the human-induced changes observed over the past 250 years are well beyond the range of natural variability of the past 1600 years, yet the pre-disturbance record provides a useful target for developing additional restoration and conservation measures to ensure future environmental protection of this historical site.


Variation in Ecosystem Respired CO₂ in a Deciduous Forest Is Related to Climatic Drivers

C. Lai, A. Schauer and J. Ehleringer

The carbon isotope ratios of carbon dioxide fluxes from terrestrial ecosystems are key measurements needed to constrain interpretations of sinks in carbon cycle analyses. The current research began in January 2001 and is a multi-faceted effort addressing photosynthetic and respiratory isotope exchanges across the biosphere-atmosphere boundary at four AmeriFlux sites (Harvard Forest, Howland Forest, Konza Prairie, and Wind River). We have developed, tested, and established automated CO₂ sampling devices at these sites, capable of continuously sampling CO₂ concentration and filling air flasks for subsequent isotope ratio analyses. We focus on understanding the magnitude of changes in the carbon isotope ratio of ecosystem respiration (δ¹³Cᵣ) through the growing season and a mechanistic basis for observed isotope changes. Observations at the Harvard Forest in 2001 indicate that δ¹³Cᵣ varied ~ 2.4 per mil during the growing season and were significantly correlated with the changes in environmental variables. These observations appear to relate directly to water stress and stomatal closure dynamics within this temperate deciduous ecosystem. After leaf fall, δ¹³Cᵣ varied by nearly 10 %, from −26.4 to −35.9 %, far exceeding the natural range of this ecosystem. It is suggested that fossil fuel combustion might have contributed significantly during winter.

Focusing at AmeriFlux sites provides a direct link to NEE measurements. Over the next 2 years, we will continue to measure seasonal observations of the isotope ratio of CO₂ fluxes. In addition, we will be combining eddy covariance and isotope observations to partition NEE into assimilation and respiratory components. This will provide an independent estimate of flux components over a growing season in response to seasonal stresses.

Both short-term and long-term monitoring of the seasonal and interannual variations in ecosystem ¹³C values feed directly into regional and global CO₂ inversion models as a constraint
on land-ocean partitioning. Our data sets complement long-term observations of tropospheric CO₂, which are the best available long-term data sets constraining interannual estimates of global productivity. Our data sets are being linked with global CO₂ inversion modeling efforts (e.g., TRANSCOM) to better understand the seasonal dynamics of tropospheric CO₂, particularly with respect to how much land/ocean partitioning varies on an interannual basis.

Rapid and Transient Response of Soil Respiration to Rain

X. Lee, H. Wu, J. Sigler and C. Oishi

The need for a precise understanding of the terrestrial carbon sink and climate feedback has motivated extensive studies on environmental influences on soil respiration. However, current knowledge of soil respiration is based in large part on field research in fair weather conditions, and the process during rainstorms and its role in the ecosystem carbon balance are not well understood. Here we combine the data from eddy covariance (EC), rain simulation and incubation experiments to show that, for a mixed temperate forest at Great Mountain, Connecticut, soil respiration increases rapidly and instantaneously in response to the onset of rain and returns to the pre-rain rate shortly after the rain stops. The pulse-like flux, most likely caused by the release of active carbon compounds from the litter layer, amounts to an annual loss on the order of 0.2 t C ha⁻¹ yr⁻¹ to the atmosphere, or as much as 20% of the net ecosystem production (NEP) of mid-latitude forests. If precipitation becomes more variable in a future warmer world, the rain-induced flux should play an important part in the transient response of the ecosystem carbon balance to climate, particularly for ecosystems on ridge-tops with rapid water drainage.

Evolution of Defense Chemistry in Alliaria petiolata Since Introduction into North America

K. C. Lewis and F. A. Bazzaz

Invasive species threaten the integrity and function of ecosystems across the globe. However, prediction of and prevention of invasion have thus far proved elusive because of the dearth of commonalities among invasive species that might predict invasiveness. One of the characteristics common among invasive plant species is escape from herbivory in their new range. It has been predicted that plants released from herbivory will adjust their resource allocation to reduce investment in defense, particularly when defenses are costly. This could result in increased availability of resources for other activities such as growth and reproduction. In invasive plant species, this may contribute to strong competitive ability and rapid spread. Alternatively, release from specialists and continued selection pressure from generalists in the new range could increase investment in defense if these are mainly effective against generalists. By using a cruciferous invasive species, Alliaria petiolata, which has costly defenses, I am investigating whether and how this species might shift resource allocation between chemical defenses and other fitness-related traits. If this is an important contributing factor to invasiveness, then potential for release from herbivory and response flexibility in resource allocation could be important screening tools to predict which species may become invasive when introduced outside their home range.

Using field populations of these plants in New England (including Harvard Forest) and in Hungary, I have been measuring growth, herbivory, defense chemistry, and reproductive capacity to determine whether invasive US populations differ significantly from native-range European populations. Using herbivore exclusions, I will also be able to distinguish between constitutive (inflexible) defense expression and defenses induced by herbivore damage. These data will provide insight into the changes that have occurred since introduction in these plants and the role of defense chemistry in competitive ability and invasiveness.
Respiration of Coarse Woody Debris in Adjacent Shelterwood-Cut and Mature Central Hardwood Stands

W. Liu, D. M. Bryant, L. Hutyra and S. C. Wofsy

Carbon cycle investigations have recently noted the potential importance of dead woody biomass as a storage pool of organic C (Barford et al. 2002). In addition, dead wood provides food and shelter for multiple trophic levels from microbes to macrovertebrates. The decay of CWD transfers nutrients from to the forest floor thus influencing forest productivity (Harmon et al. 1986).

Coarse woody debris (CWD) is generally defined as the deadwood portion of litter fall measuring > 10cm diameter and includes snags (dead trees), logs and stumps. CWD stocks, mass loss rates and density changes are well characterized for forests of the Pacific Northwest Region but data for the Northern Hardwood forests remains sparse.

Logs of the dominant hardwood genera (Betula, Acer, Quercus) and conifers within the footprint of the EMS tower and the adjacent cut site (south of Pierce Farm Rd) were tagged and numbered, measured for diameter at the midpoint. The current state of decay of each log was categorized to five decay classes. Locations were logged with a handheld GPS unit.

Cross-section disks were removed from the midpoint of logs that were randomly chosen from this tagged population. Respiration of decay organisms within the wood is trapped in the pore spaces resulting in accumulation of CO₂ that often reaches 10%. Consistent with Chambers et al. (2002) we exposed CWD samples to ambient air, under shade, for 3 hours prior to measurement. Three replicates of each factorial class (genus X decay class X diameter class) were measured in each of the two stands.

Flux of CO₂ from cross-sections was measured in the headspace of one of 2 static chambers depending on the size of the sample. Concentration of CO₂ in the sample stream was measured at 5 sec intervals with an Infra-red Gas Analyzer (IRGA). The rate of concentration change was determined by the slope of the time vs. concentration regression.

Disks were weighed prior to flux measurement. Samples were measured for volume by water displacement and dried in a 105° oven to constant mass. Moisture content of the disks was calculated as a function of oven-dry vs. fresh cut mass. Density is the oven-dry mass per unit volume.

Individual regressions of temperature, moisture and sample density against flux rate (flux = µg CO₂, g sample⁻¹, sec⁻¹). Correlations were weak for all variables in the following order: density (r² = 0.31, p < 0.01), > moisture (r² = 0.23, p < 0.01) > Temperature (r² = 0.029, p < 0.02). Combining temperature and moisture as independent variables vs. flux in a multiple regression improved the fit slightly (r² = 0.26, p < 0.01). Including density in the model further improved the multiple r² but only slightly above the fit of density alone (r² = 0.36, p < 0.01).

A three-factor nested model ANCOVA was performed with genera, decay class and diameter as categorical factors; temperature and moisture were included as continuous variables. Flux among genera was found to be significant, but only Betula and Quercus varied significantly in pair-wise comparisons (p = 0.0247, see Table 1). No significant pattern was found for flux among decay class. A single factor ANOVA of fluxes across genus and decay class showed a significant difference of flux rates between the cut site and the adjacent undisturbed stand (p = 0.027). Including moisture and temperature in the ANCOVA model of stand flux showed no significant effect of stand. Therefore, the microclimate difference between these stands appears responsible for the variation in flux rate. The effect is particularly apparent when scaling fluxes to inventoried CWD in both stands. The total estimated growing season flux rate (genus mean x biomass x 6 mos) of the cut stand was 784 kg/ha/yr almost 294 % greater than the adjacent mature forest (268 kg/ha/yr). The greater volume of CWD in the cut stand (see Hutyra et al., this vol. Table 1) produced a much greater areal flux rate. However, turnover rate of the total stand biomass was higher in the mature stand than the cut site (5.5 % yr⁻¹ vs 4.1 % yr⁻¹ respectively). These differences will likely diminish as the canopy closes and residual stocks of CWD decline during regrowth of the cut site.


Table 1. Mean (s.d.) Flux rates of CWD in adjacent shelterwood cut and mature stand. Units are nanogram CO\(_2\), gm CWD\(^{-1}\), sec\(^{-1}\). (nanogram = \(\mu g \times 10^{3}\))

<table>
<thead>
<tr>
<th>Genus</th>
<th>Decay Class:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Shelterwood cut</td>
<td></td>
</tr>
<tr>
<td><strong>Acer</strong></td>
<td>1.1 (0.6)</td>
</tr>
<tr>
<td><strong>Betula</strong></td>
<td>2.3 (1.5)</td>
</tr>
<tr>
<td><strong>Quercus</strong></td>
<td>1.9 (0.9)</td>
</tr>
<tr>
<td><strong>Conifer</strong></td>
<td>1.2 (0.6)</td>
</tr>
<tr>
<td>Mature Stand</td>
<td></td>
</tr>
<tr>
<td><strong>Acer</strong></td>
<td>3.2 (2.9)</td>
</tr>
<tr>
<td><strong>Betula</strong></td>
<td>3.2 (4.4)</td>
</tr>
<tr>
<td><strong>Quercus</strong></td>
<td>3.5 (2.6)</td>
</tr>
<tr>
<td><strong>Conifer</strong></td>
<td>2.5 (2.1)</td>
</tr>
</tbody>
</table>

Vulnerability of Xylem Vessels to Cavitation in *Acer saccharum* (Marsh.): Scaling from Individual Vessels to Whole Branches

*P. J. Melcher, M. A. Zwieniecki and N. M. Holbrook*

The relation between xylem vessel age and vulnerability to cavitation of *Acer saccharum* Marsh. was quantified by measuring the pressure required to force air across bordered pit membranes separating individual xylem vessels. We found that the bordered pit membranes of vessels located in current year xylem could withstand greater applied gas pressures (3.8 MPa) compared to bordered pit membranes in vessels located in older annular rings (2.0 MPa). A longitudinal transect along six-year-old branches indicated that the pressure required to push gas across bordered pit membranes of current year xylem did not vary with distance from the growing tip. To understand the contribution of age-related changes in vulnerability to the overall resistance to cavitation, we combined data on the pressure thresholds of individual xylem vessels with measurements of the relative flow rate through each annual ring. The current year's annual ring contributed only 16 % of the total flow measured on 10-cm-long segments cut from six-year-old branches, but more than 70 % of the total flow when measured through six-year-old branches to the point of leaf attachment. The vulnerability curve calculated using relative flow rates measured on branch segments were similar to vulnerability curves measured on six-year-old branches (P\(_{50}\) = 1.6 to 2.4 MPa), whereas the vulnerability curve calculated using relative flow rates measured on six-year-old branches were similar to ones measured on the current year's extension growth (P\(_{50}\) = 3.8 MPa). These data suggest that, in A saccharum, the current year's xylem can withstand larger xylem tensions than older wood and dominates water delivery to leaves.

The Barre Woods Megaplot Soil Warming Experiment

*J. M Melillo, P. A. Steudler, H. Lux, F. P. Bowles, S. Morriseau and E. Burrows*

Two of the major results of our original soil warming study were that: (1) warming stimulated the decay of a labile soil carbon pool; and (2) it also increased the availability of inorganic nitrogen to plants. Because of the small size of the original warming plots an important question we have not been able to answer conclusively is:

- Has the increase in available nitrogen led to an increase in carbon storage in the vegetation?
Figure 1. Total standing biomass (kg ha$^{-1}$) in the control and to be heated plots. Biomass for each tree was estimated using allometric equations (M.T. Ter-Mikaelian, 1997).

Figure 2. Under-story biomass (kg ha$^{-1}$) in the control and to be heated plots. Biomass was estimated using allometric equations for woody ($R^2 = 0.96$) and herbaceous ($R^2 = 0.97$) plants. Equations were obtained using a regression of stem number times mean height against above-ground biomass for clipped plots outside the study area. Control and heated plots were not significantly different. Error bars represent the standard error of the mean ($n = 10$, 1 meter squared sub-plots) for each treatment.

Figure 3. C:N ratios of maple and oak foliage in the control and to be heated plots. Oak and maple trees represent the two dominant tree species occurring in the plots. Error bars represent the standard error of the mean ($n = 5$ maple trees and 9 oak trees) for each treatment.

Figure 4. Seasonal trend in soil CO$_2$ efflux for the control and to be heated plots (November 2001 – November 2002). Error bars represent the standard error of the mean ($n = 9$ sub-plots) for each treatment. Paired $t$-test results show that there is no significant difference between the control and to be heated plots.

Melillo et al.
And if yes, how much?

In a systems context an additional question is:

What is the balance between the carbon lost from the soil and the carbon stored in the vegetation in response to soil warming?

We are now addressing these important questions with a new warming experiment in the Barre Woods area of the Harvard Forest. The Barre Woods site was chosen because of its similarities to the Prospect Hill site - stand age, tree species composition, and soil type. There is no evidence of a plow horizon at the Barre Woods site, though surrounding stone walls indicate past use as pastureland. Historical records indicate the site was destroyed during the 1938 hurricane and then regrew naturally.

During the summer and fall of 2001 we buried 3.4 miles of heating cable in a 30 x 30m plot. Cables were buried at a 10cm depth, spaced 20cm apart. A second 30 x 30m area was delineated 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.

In April 2002, we began a one-year period of baseline measurements before turning on the heat in the new megaplot. These measurements included nitrogen mineralization, trace gas fluxes (CO₂, CH₄, N₂O), tree growth (dendrometer bands), and under story species survey, canopy foliage analysis (C:N, NIR), and lysimetry. Thermistors were installed in both plots to begin tracking soil temperatures. The baseline measurements have confirmed that there are no significant differences between the two plots for key ecosystem processes prior to the initiation of the warming manipulation (Figs. 1-4).

We will turn on the power in April 2003 to begin the "manipulation phase" of this study. From this study, we expect to determine whether or not warming results in the movement of nitrogen from the soil to the trees and to learn how this movement affects the net carbon balance of the ecosystem.

Soil Warming, the First Decade and Beyond


In the first decade of the soil warming experiment in the Prospect Hill site at the Harvard Forest, we have documented changes in soil carbon and nitrogen cycling and here we consider some of the consequences of these changes for the climate system. For the first time we have shown that while soil warming accelerates soil organic matter decay and CO₂ fluxes to the atmosphere, this response is small and short-lived for a mid-latitude forest because of the limited size of the labile soil carbon pool (Fig. 1a, b). We have also shown that warming increases the availability of mineral nitrogen to plants (Fig. 2a, b). 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.

By the twelfth year of the soil warming study, the effect of warming on soil nitrogen availability has declined dramatically. The once large increase in available nitrogen created in response to warming has almost disappeared by year twelve (Fig. 3a, b). We do not know where the "excess" available nitrogen has gone. We speculate that over time most has become tied up in nitrogen pools with long storage times such as refractory soil organic matter and the woody tissue of the trees.

A Regional Climatology of Cloud and Aerosol for Forest-Atmosphere Exchange

Q. Min

Carbon uptake by forest is enhanced on partly cloudy days due to the enhancement of diffuse component scattered by cloud droplets (Min 2002, and references herein). Furthermore, ecosystems affect both cloud formation through the process of evapotranspiration, and cloud properties, by influencing aerosol and water vapor concentrations. These studies point to the needs for regional climatological measurements of clouds and aerosol, and for establishing the link between the microphysics of cloud and aerosol,
Figure 1a. A decade of soil respiration by treatment and year for the disturbance-control and heated plots at the soil warming experiment for the field measurement period of April through November (1991-2000). Soil respiration is measured using syringes to draw a time-series of gas samples from closed-top chambers (static chamber technique). Samples are analyzed in the lab using an infrared gas analyzer, and rates are calculated from changes in concentration observed over time. Error bars represent the standard error of the mean (n = 6 plots) for each treatment. Modified from Melillo et al. 2002.

Figure 1b. A decade of net N mineralization rates for the organic horizon plus the top 10 cm of mineral soil for the disturbance-control and heated plots in the soil warming experiment (1991-2000). Soil cores were incubated in situ and extracted in the lab using 2N KCl (buried bag technique). Error bars represent the standard error of the mean (n = 6 plots) for each treatment. *Rates for 1999 and 2000 were modeled using temperature and moisture data. Modified from Melillo et al. 2002.

Figure 2a. Percent increase in the amount of carbon released from the heated plots relative to the disturbance control plots. The data are presented as 3-year running means for the period from 1991 through 2000. Modified from Melillo et al. 2002.

Figure 2b. Percent increase in net nitrogen mineralization rates of the heated plots relative to the disturbance control plots. The data are presented as 3-year running means for the period from 1991 through 2000. Modified from Melillo et al. 2002.

Figure 3a. Twelve years of soil respiration by treatment and year at the soil warming experiment for the field measurement period of April through November (1991 – 2002). Error bars represent the standard error of the mean (n = 6 plots) for each treatment. Modified from Melillo et al. 2002.

Figure 3b. Twelve years of net N mineralization of the organic horizon plus the top 10 cm of mineral soil at the disturbance-control and heated plots at the soil warming experiment (1991–2002). Error bars represent the standard error of the mean (n = 6 plots) for each treatment. *Rates for 1999 and 2000 were modeled using temperature and moisture data. **2002 shows a partial year, Jan-Nov. Modified from Melillo et al. 2002.
through the PAR irradiance, for CO₂, water vapor and sensible heat exchange.

To investigate climatology of cloud for forest-atmospheric exchange, we developed a fast retrieval algorithm to derive cloud optical depth from broadband global shortwave measurements that have been taken for past ten years at the Harvard Forest site. First we compared cloud optical depths derived from this retrieval algorithm against well-validated results at the ARM SGP site where various passive and active instruments for detecting clouds are operated (Min et al., 2003). As shown in Figure 1, this simple retrieval with assumption of standard mid-latitude summer atmospheric profiles agrees within 10% of accurate narrowband retrieval. Various sensitivity studies indicate that the overall uncertainty of this simple retrieval is about 15%.

We applied this retrieval to the hourly averaged shortwave measurements at Harvard Forest from 1997 to 2000. For four years, data sets are more continuous and have better quality. Figure 2 shows the histogram of cloud optical depth over Harvard Forest. The averaged optical depths of all clouds are thicker in 1998 and 2000 than those in 1997 and 1999. The mean optical depths of thin clouds are relatively constant (about 2) for these years. Occurrences of clouds (cloud counts vs. total measurement counts) are 0.722, 0.729, 0.678, and 0.761 for 1997, 1998, 1999, and 2000, respectively. Occurrences of thin clouds (optical depth less than 5) are 0.311, 0.295, 0.317, and 0.318, which show less annual variability than that of thick clouds.

We further examine seasonal variations of clouds, shown in the Figure 3. The monthly occurrence of thin clouds shows a distinct peak in July, which is consistent with ASOS observations (Freedman, 2000). On the other hand, occurrence of thick clouds appears to have no seasonal trends, but closely links to the precipitation as we expected. The occurrence of thin clouds starts to increase as the leaves emerge, indicated by shortwave albedo as well as PAR albedo. As shown in the Figure 3, the growing season maximum of thin cloud occurrence is strongly correlated with the water vapor flux measured at the EMS tower. With the commencement of transpiration, the additional moisture is bumped into the boundary layer, resulting lower lifting condensation level and formation of boundary layer clouds. With reduction of water vapor flux in the late growing season, the occurrence of thin clouds is also reduced. Those statistics indicate that most of the thin clouds (except for high altitude cirrus clouds) are formed as a result of forest-atmospheric exchange. The thick clouds, on the other hand, are due to the large-scale circulations. However, this is a preliminary study with a limited dataset. It points to a possible direction to monitor the cloud optical properties, the exchanges of moisture, gas and energy between forest and atmosphere by using the broadband shortwave measurements.


Impact of Canopy Nitrogen Deposition on Foliar Physiology: Initial Results from a Manipulative Experiment at the Howland AmeriFlux Site

R. Minocha, D. Hollinger, S. Long, B. Dail and J. Aber

Atmospheric nitrogen (N) deposition has been identified as the probable cause of both forest decline and enhanced productivity in temperate forests. Whether N deposition has positive or negative effects on an ecosystem depends on the N status of the system and the rate and duration of N deposition. Long-term elevated N deposition typically increases the concentration of total foliar N, with or without similar changes in the base elements such as Ca, Mg and K. This increase in leaf N content also leads to significant shifts in the internal partitioning of N within the leaf. For example, in conifers N deposition significantly increases leaf N present in the form of free amino acids such as arginine.
Figure 1. Comparison of cloud optical depth inferred from broadband shortwave measurements (BSRN) and from narrowband spectral radiometer (MFRSR) at the ARM SGP site, on March 3, 2000.

Figure 3. Monthly statistics of cloud occurrences, Shortwave and PAR albedoes, water vapor fluxes, and precipitations over Harvard Forest from 1997 to 2000.

Min
Data from our laboratory show a strong correlation between soil nutrient deficiencies (e.g., Ca) and/or excess nitrogen and increased foliar free putrescine (an organic polyamine) levels, indicating that foliar putrescine can potentially be used as a marker of general stress in visually healthy trees (Minocha et al., 1997, 2000). Putrescine has also been implicated as a marker of stress remediation in sugar maple stands in PA (Wargo et al., 2002). Polyamine catabolism is not simply a degradative process but is also an important link between N and C metabolism in plants as shown in Figure 1. Preliminary data from our laboratory show also that the free amino acids (FAA), especially arginine increase many fold in response to high nitrogen input. Arginine could thus be used as a specific marker of excess nitrogen inputs in otherwise nitrogen limited forest soils. Other significant effects of acidic deposition and/or high N deposition on the stand physiology include changes in organic acid metabolism, membrane properties, chlorophyll and protein content, all currently under investigation in our lab. The physiological evaluation of otherwise visually healthy stands is essential in developing risk assessment and stress remediation strategies for forest trees prior to the onset of obvious decline.

The objective of this study is to determine the usefulness of polyamines, particularly putrescine, and amino acids such as arginine, as foliar indicators for early detection of changes in physiology in visually asymptomatic trees due to a relatively low level of nitrogen application to canopy (18 kg N ha\(^{-1}\) y\(^{-1}\) (NO\(_3\):NH\(_4\) 1:1)) at Howland Experimental Forest starting in summer of 2001. Another objective is to compare these changes in the Howland site stand physiology to those currently being measured at the Harvard Forest LTER Site where a similar experiment, underway since 1989, is adding much higher levels of nitrogen to the forest floor (Magill et al., 1997). In this latter study, most added N enters the soil and is rapidly immobilized, however physiological changes in foliar chemistry have been observed after 6 years of chronic N addition (Minocha et al., 2000). For the Howland site, we hypothesize that the smaller, foliar N addition will not exceed the capacity for N uptake by vegetation and this may lead to greater C sequestration and is unlikely to stress the foliage (e.g., there will be no change in the levels of physiological stress indicators at least for these initial years of N application). The goal is to be able to get a better grasp on the N deposition levels that elicit a stress response in a forest where NPP is assumed to be limited by N availability.

Foliation samples were collected by shotgun sampling in May, 2001 (before the inception of N fertilization), and again in July 2001 (first season N additions), July 2002 (time course study for transient changes in foliar physiology due to N application), August 2002 (annual sample collection for the 2\(^{nd}\) year of fertilization). The first-two-year data from all collections at Howland suggested no significant changes in the foliar physiology and organic nitrogen metabolism due to N application to canopy. The cellular levels of free polyamines, free amino acids, soluble proteins, chlorophyll content, and exchangeable inorganic ions did not not differ significantly between treatments. The levels of only one amino acid, glutamine, that is precursor not only for polyamines and most amino acids but also feeds into other metabolic pathways did increase transiently during the 4-25 h period that was tested immediately after one of the N applications in mid July, 2002. These initial results are reassuring in that the foliar application does not appear to stress these trees and that the primary focus of the study, whether increased N will enhance NPP, may not be compromised by foliar physiological stress.


Figure 1. Polyamine and their link between nitrogen and carbon metabolism in plants.
Nitrogen Availability and Net Primary Production in Temperate Forests: the Role of Leaf Physiology, Foliage Turnover and Canopy Structure


Atmospheric nitrogen (N) deposition has been identified as the probable cause of both forest decline and enhanced productivity in temperate forests. Whether N deposition has positive or negative effects on an ecosystem depends on the N status of the system and the rate and duration of N deposition. Most added N enters the soil and is rapidly immobilized. If the remaining available N does not exceed the capacity for N uptake by vegetation, net primary productivity (NPP) and C sequestration may be enhanced. If N deposition rates remain high, the excess nitrogen may lead to N saturation and reduced growth through major changes in carbon and nitrogen metabolism including the sequestration of nitrogen compounds in leaves and lower photosynthetic rates. It is important to understand how chronic additions of N to forested ecosystems may change their structure and function.

Temperate forests are predicted to play a key role as important sinks for atmospheric carbon dioxide. This sink could be enhanced by atmospheric nitrogen deposition. However, the predicted response may vary for deciduous and coniferous trees due to differences in photosynthetic nitrogen use efficiency. Experimental evidence suggests that the impact of N deposition on temperate forest productivity may not be as great as originally assumed. This is in part due to the limited information on processes, which take place in the canopy. We investigated how changes in N deposition rate effects the partitioning of organic N into different physiological pools, and how this in turn will affect photosynthetic capacity and foliage productivity. Our study is based at the Harvard Forest LTER site, where a 12-year long study of the addition of N on both coniferous and deciduous forests is underway. The measurements within a Pinus resinosa stand demonstrate that foliar N content has significantly increased in this species, and that this increase is accompanied by a de-coupling of the photosynthesis-N relationship. Conifers of the high N treatment do not use the surplus of N to synthesize more Rubisco, which would allow them to have a higher photosynthetic capacity. Instead this N is being accumulated as putrescine (a common polyamine and also a stress indicator) and its precursor amino acid, arginine (Fig. 1). The level of soluble proteins is also significantly higher in high N treated foliage. Needle retention time changed significantly in response to N addition. A strong decline in foliar and wood NPP has also been observed at this site. These results indicate that the increase in leaf N is not accompanied by a greater capacity for carbon assimilation in the high N treatment. These results suggest that long-term input of high dosages of mineral N into this pine stand have not been conducive for a higher net carbon sequestration.

Vegetation and Disturbance History of Ridgetop Pitch Pine and Red Pine Communities in Southern New England

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.

Our initial studies focused on the dwarf pitch pine community on the summit of Mt. Everett in the Town of Mt. Washington, Massachusetts. Dwarf pitch pines are rare across the northeastern U.S., typically occurring only on sites with extremely high fire frequencies and where pitch pines have a high frequency of cone serotiny. In contrast, we found little evidence of recent fire and no cone serotiny on the summit of Mt. Everett, suggesting that the dwarf growth form developed in response to extremely harsh edaphic and climatic conditions. During this past
Figure 1. Effects of chronic nitrogen addition on: (A) foliar free putrescine and exchangeable Ca in the organic horizon of soil; (B) relationship between foliar free polyamines and nitrogen; (C) foliar free amino acids in a pine stand at Harvard Forest. Foliar data are mean ± SE (n=60 for polyamines; n=14 for nitrogen) and soil data are mean ± SE (n=18). The data for amino acids is from canopy access towers and are mean of 2-3 samples accessible from towers.

Minocha et al.
year, we extended this study to two nearby summits in the Taconic Mountains, where preliminary data suggest that stands are uneven-aged and have also not experienced frequent fires. A fire in summer 2002 occurred east of Mt. Everett, smoldering for ~7 weeks and largely consuming the organic matter in many areas; this area will be visited again in summer 2003 to evaluate sprout and seedling dynamics after the fire.

We also visited several ridgetop sites supporting native red pine during 2002. Massachusetts is near the southern limit of red pine distribution, with fewer than a dozen sites in the state currently known that are thought to support native red pine, primarily in rocky areas in the western part of the state. Charcoal or scarring was evident in each of the red pine sites visited thus far, suggesting that fire has influenced the dynamics of these sites. Several sites have abundant red pine mortality and limited regeneration, suggesting that the long-term persistence of red pine on these sites may be threatened.

Future work will focus on comparing disturbance histories and stand dynamics among sites across the southern New England to determine whether stands with similar composition and age structure may develop on sites characterized by substantially differing histories of disturbance.

Incorporating Regional-Historical Perspectives into Conservation of Uncommon Plant Communities: a Study of the Northeastern Coastal Region

G. Motzk, D. R. Foster, B. Hall and D. MacDonald

Although the importance of determining the history of uncommon communities is increasingly recognized as critical for conservation efforts, most studies have been restricted to investigations of individual sites, with little attempt to place local results within a regional context. Such a context is necessary to determine the degree to which local dynamics are characteristic of the community type targeted for protection and to determine geographic and temporal variation in disturbance regimes, species distributions, and ecosystem processes. We are investigating the history and development of upland plant communities in the northeastern Coastal Region, an area that supports numerous uncommon species and assemblages and is highly threatened by development. Land-use and natural disturbance history vary considerably across the region; Nantucket and Block Island were almost completely cleared for agriculture in the 17th - early 20th C., whereas extensive areas on Long Island, Cape Cod, and Martha's Vineyard were never cleared for agriculture. Modern community patterns strongly reflect this history of land-use; several characteristic or rare lepidopteran species are largely restricted to sites that were never in agriculture, whereas numerous rare plant species are most frequent on sites that were disturbed intensively for historical agriculture or other uses. Land-use history is also a primary determinant of distribution patterns of common species. In the upcoming year, analysis of sediment cores from ponds on Long Island, New York will enable us to evaluate the long-term vegetation and fire history of one of the most extensive pine barrens systems in the northeastern US, including extensive areas that were never cleared for historical agriculture.

Air Quality Observations at the Harvard Forest Environmental Measurement Site: Analysis of Pollution Events in the Summer of 2002

J. W. Munger, J. Budney and S. C. Wofsy

We have made nearly continuous measurements of major air pollutants, including nitrogen oxides, ozone, and carbon monoxide at the Harvard Forest Environmental Measurement Site since 1990. A particular emphasis of these measurements has been to quantify the inputs of nitrogen and ozone to the forest canopy, and to better understand the influence of forests on regional air quality. Additionally, these data provide a long-term examination of air quality patterns in rural New England and allow us to determine the frequency and characteristics of extreme air pollution events. Air quality during the summer of 2002 illustrates key features of pollution episodes in this region.
During the first week of July, much of New England was heavily impacted by smoke from forest fires in Quebec as illustrated by satellite imagery (Fig. 1). During this event CO concentrations rose to nearly 1000 ppb at the peak on July 7 compared to background levels near 150 ppb. Total nitrogen oxides (NOx) only increased from 1500 to 3000 ppt. Ozone was not enhanced in the smoke plume (Fig. 2). In contrast, two days later on July 9 ozone concentrations reached 100 ppb along with 6000 ppt NOx and 500 ppb CO. Wind direction during this episode were southwesterly, the direction of transport from major east-coast urban corridor. A major pollution episode was observed during the week starting August 10, 2002 (Fig. 3). Ozone concentrations exceeded 100 ppb on 5 consecutive days. These concentrations are well above the thresholds for injury to sensitive plant species. Daytime concentrations of NOx increased to 6000 ppt and nighttime values increased to 18,000 ppt. The rise in pollutant concentrations commenced as winds shifted from north to southwest. Maximum daily temperatures increased steadily over the course of the event. The pattern of increasing pollutant concentrations and temperatures is typical of regional stagnation events in which urban emissions are trapped near the ground and react with abundant sunshine to generate high ozone levels.

Comparison of NOx and CO highlights important features of atmospheric chemistry in rural New England. Occasionally Harvard Forest receives relatively fresh pollutants as indicated by NOx:CO ratios comparable to what is observed adjacent to a major urban highway (Fig. 4). More typically NOx concentrations are depleted relative to CO indicating that a significant fraction of the nitrogen oxides have been converted to nitric acid and removed by wet and dry deposition. Observations during the Quebec smoke plume exhibit an especially low NOx:CO ratio. Because the smoke plume did not have enhanced O3, it is likely that these fires had relatively low NOx emissions to begin with. Observations over the last decade indicate that acute air pollution events are episodic. The frequency, duration, and magnitude of pollutant events is controlled by synoptic weather patterns that vary from year to year. Typical concentrations outside the episodes are generally below thresholds for acute injury of sensitive plants. The strong role of weather variability in controlling air pollutant levels complicates the identification of long-term trends.

Using Hydroperiod and Historical Vegetation Data to Explain Patterns in the Distribution of Malacostracan Crustaceans in Massachusetts Vernal Pools

K. L. Musgrove* and E. A. Colburn

The seasonally flooded forest ponds commonly known as vernal pools span a broad range of hydroperiod, from two-to-three months to several years. The distributions of many organisms in vernal pools are tied closely to pool hydroperiod, with life history and predator-prey interactions determining where some species occur (Wiggins et al. 1980, Schneider and Frost 1996, Schneider 1999). Branchiopod crustacean species such as fairy shrimp and clam shrimp (Eubranchipus spp., Lymnaea brachyurus) have life cycles adapted to the desiccation provided by the regular drying of short-hydroperiod pools, are intolerant of predation by fishes and many large invertebrates, and are generally considered to be vernal pool “indicator species.” Malacostracan crustaceans, including amphipods (Crangonyx sp.) and isopods (Caecidotea sp.), have historically been presumed to be restricted to permanent waters due to a lack of appropriate aestivation or other drought-resistant life history strategies. Batzer and Sion (1999) reported on the presence of malacostracans in annually drying vernal pools in New York state and suggested an association with past land use, specifically continuous forestation. For this study, we examined the relationship between malacostracan distributions in vernal pools, hydroperiod, and past land use. We analyzed previously collected data sets (1990-1999) from 36 pools throughout Massachusetts to determine the hydroperiod of pools with and without consistently sampled malacostracans. The distribution of malacostracans was random in relation to hydroperiod. We then mapped the pools using GIS and a historical vegetation data layer to determine whether or not they were forested at the statewide peak of deforestation, in 1830. In short-hydroperiod pools, the relationship
Figure 1 MODIS image during the Quebec forest fire event. Clouds appear as white, smoke is a light grey that shows as a streak emanating from the cloud mass east of James Bay and tracking south across Vermont and Massachusetts and out over the Atlantic Ocean.

Munger et al.
Figure 2 Time series of NO$_x$, CO, and O$_3$ for two pollution episodes in July at Harvard Forest. Lower panel shows surface wind directions measured at the HF EMS tower site.

Figure 3 Time series of CO (upper panel), NO$_x$ (middle panel), and O$_3$ (bottom panel) during a 10 day period in August 2002. The righthand side presents the time series of wind direction, Temperature, and relative humidity.

Munger et al.
Figure 4  Comparison of NO$_x$ and CO concentrations. The grey line indicates the NO$_x$:CO ratio that is observed for fresh exhaust emissions. Observations during a high ozone episode are far removed from this emission line, showing evidence of extensive NO$_x$ deposition. The observations during the July smoke event exhibit very low NO$_x$:CO ratios, suggesting that this fire emitted relatively little NO$_x$. The absence of any excess O$_3$ in the smoke plume is consistent with the low NO$_x$ concentration.

Munger et al.
between malacostracan presence and the absence of historical forest clearing was strong ($x^2$ value = 9.333, 1 degree of freedom, $p$ value < .005). Our results suggest that historic land use may help explain the distribution of some species in short-hydroperiod vernal pools.


Woody Species Phenology, Prospect Hill Tract, Harvard Forest - 2002

J. O'Keefe

2002 was the thirteenth year in our ongoing investigation of the timing of woody vegetation development during the growing season, however this year the scope of the study was changed somewhat. 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 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 again 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 2001-2002 was much warmer than normal with below normal precipitation. May and June brought the first below average temperatures in nine months accompanied by near normal precipitation. The remainder of the summer was warm and quite dry. Unseasonable warmth continued through mid-October, but precipitation increased in September. The first frost at Harvard Forest didn't occur until October 14th, eighteen days later than the mean first frost date since 1990, and seven days later than 1999, the next latest year within this period.

For most species initial bud break in 2002 was slightly early (Table 1/Fig. 1). Red oak was very early. Leaf development then progressed rather steadily with 75% leaf development occurring neither early nor late. Fall coloration and leaf fall in 2002 were the latest yet observed, with color peaking about October 18th, ten days later than the prior ten-year mean and three days later than the prior latest year (1999). Similarly, 50% leaf fall for the four species in Figure 1 occurred on October 25th, also ten days later than the prior ten-year mean and five days later than the prior latest year (1999). This extreme lateness expands the variability observed in leaf senescence significantly, so that it more closely resembles the variability observed in leaf emergence over the course of this study, and calls into question our previous assumption of considerably less variability in the timing of fall events. These
<table>
<thead>
<tr>
<th>Year</th>
<th>Quercus rubra (n=4)</th>
<th>Acer rubrum (n=5)</th>
<th>Betula alleghaniensis (n=3)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>IBB</td>
<td>75%</td>
<td>IBB</td>
</tr>
<tr>
<td>1990</td>
<td>127 (5/7)</td>
<td>166 (6/15)</td>
<td>121 (5/1)</td>
</tr>
<tr>
<td>1993</td>
<td>122 (5/2)</td>
<td>153 (6/2)</td>
<td>118 (4/28)</td>
</tr>
<tr>
<td>1994</td>
<td>129 (5/9)</td>
<td>154 (6/3)</td>
<td>124 (5/4)</td>
</tr>
<tr>
<td>1997</td>
<td>136 (5/16)</td>
<td>158 (6/7)</td>
<td>133 (5/13)</td>
</tr>
<tr>
<td>1998</td>
<td>123 (5/3)</td>
<td>142 (5/22)</td>
<td>120 (4/30)</td>
</tr>
<tr>
<td>1999</td>
<td>126 (5/6)</td>
<td>148 (5/28)</td>
<td>126 (5/6)</td>
</tr>
<tr>
<td>2001</td>
<td>122 (5/2)</td>
<td>149 (5/29)</td>
<td>123 (5/3)</td>
</tr>
<tr>
<td>2002</td>
<td>118 (4/28)</td>
<td>156 (6/5)</td>
<td>125 (5/5)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Quercus alba (n=3)</th>
<th>Hamamelis virginiana (n=3)</th>
<th>Acer pensylvanicum (n=4)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>IBB</td>
<td>75%</td>
<td>IBB</td>
</tr>
<tr>
<td>1993</td>
<td>124 (5/4)</td>
<td>150 (5/30)</td>
<td>121 (5/11)</td>
</tr>
<tr>
<td>1996</td>
<td>139 (5/18)</td>
<td>159 (6/7)</td>
<td>123 (5/2)</td>
</tr>
<tr>
<td>1997</td>
<td>146 (5/26)</td>
<td>164 (6/13)</td>
<td>130 (5/10)</td>
</tr>
<tr>
<td>1999</td>
<td>132 (5/12)</td>
<td>155 (6/3)</td>
<td>122 (5/2)</td>
</tr>
<tr>
<td>2000</td>
<td>132 (5/11)</td>
<td>162 (6/10)</td>
<td>126 (5/5)</td>
</tr>
<tr>
<td>2001</td>
<td>124 (5/4)</td>
<td>162 (6/11)</td>
<td>122 (5/2)</td>
</tr>
<tr>
<td>2002</td>
<td>132 (5/12)</td>
<td>(158 (6/7)</td>
<td>109 (4/19)</td>
</tr>
</tbody>
</table>

O'Keefe
FIGURE 1

O’Keefe
observations again point out the need for long-term data sets and emphasize the importance of temperature in regulating these events.

Resolving the Effects of Multiple Environmental Changes on Forest Carbon Exchange Through Time-Series Application of a Forest Ecosystem Model

S. V. Ollinger and J. D. Aber

Understanding the effects of multiple environmental change agents on forest carbon balances is important for a number of reasons. First, from a scientific perspective, identifying underlying processes behind current terrestrial carbon balances is important because different mechanisms have very different implications for future CO₂ exchange. For example, the effects of forest recovery from past land use are likely to be a more transient phenomenon than the effects of atmospheric changes that are expected to persist into the future (elevated CO₂ or climate change). Second, from a management perspective, identifying the role of individual driving variables is a crucial component of developing effective strategies for responding to human-induced environmental change.

In theory, long-term measurements from CO₂ flux towers should reveal the influence of factors such as climate variation, land use alteration, nitrogen deposition and ozone pollution, but in practice, the complexity of interactions among them makes identifying individual responses a very challenging task. The aim of this project is to improve our understanding of mechanisms affecting forest carbon balances by using an ecosystem simulation model to examine long-term, multiple factor interactions at two CO₂ flux measurement sites: Harvard Forest, Massachusetts and Howland Forest, Maine. The model used in this study (PnET-CN) has been explicitly developed to include the effects of climate, CO₂, ozone, N deposition and land use history on important physiological and biogeochemical processes.

At Harvard Forest, preliminary analyses have been conducted using long-term land use history records, climate reconstructions and estimates of historical changes in atmospheric pollutant deposition. From these simulations, we have put forth a set of hypotheses regarding the relative strength of atmospheric factors and historical disturbance (Fig. 1). By extending these predictions to other sites across the northeastern US region, we have also hypothesized that the fertilization effects of N deposition may be largely offset by simultaneous reductions in photosynthesis caused by ozone. Including climate variability in these analyses adds additional layers of complexity due to feedbacks and lag effects between temperature, drought stress, photosynthesis and N turnover in soils.

The next phase of this work involves exploring the extent to which detailed application of this model can elucidate mechanisms affecting CO₂ exchange over shorter time intervals, perhaps including new processes that have not been previously simulated (e.g. soil frost). The model's accuracy will be determined by the degree to which it recreates measured time series net flux data. A series of single- and multi-factor model experiments will then be used to extract the individual and combined effects of all environmental drivers included.

Landscape-Level Analyses of Hemlock Woolly Adelgid Outbreaks in Massachusetts

D. Orwig and D. Foster

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 are in the process of mapping 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 obtained information on forest structure and composition, crown vigor, site
Figure 1. Transient effects of various land use and atmospheric chemistry scenarios on net carbon exchange (NCE, g m\(^{-2}\) yr\(^{-1}\)) at Harvard Forest, predicted by a modified version of the PnET-CN ecosystem model. The baseline scenario included no disturbance of any kind. The land use scenario includes physical disturbances only, the CO\(_2\) + O\(_3\) + N scenario includes atmospheric effects only and the combined scenario (upper line) includes all factors together. Simulations were run from 1700 to 2000, but predictions are only shown for the period from 1880 onward for clarity. Scenarios that include land use effects begin this period with positive rates of carbon uptake following agricultural abandonment in 1850.
Figure 1. Spatial pattern of hemlock distribution in the 7500 km² CT-MA study area, derived from aerial photographs. Hemlock represents over 16,000 ha in Connecticut and over 86,000 ha in the Massachusetts study region.

Orwig and Foster
characteristics, potential replacement species, presence of HWA, and the extent and spatial patterns of canopy damage in 30 stands. Overstory *T. canadensis* importance ranged from 24 – 92% and total stand densities varied from 225 - 2025 stems ha⁻¹. Many stands were found on northern and western aspects on slopes of 20 - 30%. 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.

Adelgid was reported in 43% of the forests sampled and preliminary observations suggest that HWA densities were higher at lower elevations and, like our Connecticut results, were lower with increasing latitude. In addition, HWA was found in close proximity (a few km) to VT, suggesting it is continuing to migrate and may already be in southern portions of VT and NH. We observed low hemlock mortality levels in these stands, consistent with its more recent infestation of northern MA. We will continue to sample stands over the next few years throughout this region to examine the relationship between site and stand characteristics and intensity of infestation and extent of mortality that occurs.

Ecosystem Analyses of Hemlock Woolly Adelgid Outbreaks in Southern New England

*D. Orwig, R. Cobb, M. Kizinski and D. 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 southern New England. Healthy hemlock forests typically have slow decomposition and N cycling rates due to their low foliar N content and cool microclimate. However, thinning canopies associated with HWA infestations are starting to reverse this trend, due to dramatic increases in light levels and soil temperature. Within 8 study sites varying in HWA infestation level, we continue to investigate the magnitude and duration of N dynamics associated with HWA infestations by measuring nitrogen (N) mineralization rates using close-topped soil cores during the last five years. In addition, ion-exchange resin bags are used to estimate the spatial availability of N within sites and the extent to which NO₃ is being lost. Measurements of gravimetric moisture content and soil temperature were used with hemispherical photographs to assess microenvironmental changes. During the first five years of this study, thinning canopies from heavy HWA damage resulted in increased light, soil temperature, and mineral soil moisture, and decreased forest floor moisture content (Fig. 1). Heavily infested sites continue to have larger extractable NH₄ and NO₃ - N pools, and significantly higher net nitrification rates than healthy hemlock forests. In addition, resin bags captured more ammonium and nitrate in infested versus uninfested 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. We will continue to sample these stands 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.

The Changing Spatial Distribution and Abundance of *Tsuga canadensis* and *Pinus strobus* between 1733 and the Present in Petersham, Massachusetts, USA

*S. Parnes*

Studies conducted at the Harvard Forest and elsewhere demonstrate that historic land use influences the modern distribution of species at the stand and regional scales. These studies focus on the dynamics of all plant species that inhabit a particular area, but also demonstrate that species react individualistically to both natural and anthropogenic disturbances. Surprisingly though, no attempt has been made to follow individual species with contrasting disturbance responses through spatial and temporal planes in order to determine the extent to which their individualistic responses to disturbance have influenced the role these species play in the modern landscape. In the absence of such studies, there is also a lack of
Figure 1. Organic and mineral soil moisture content over time in infested and uninfested hemlock stands in central Connecticut.

Orwig et al.
a comprehensive understanding of the continuous effects of disturbance on species distribution.

In order to further advance the understanding of disturbance on species distribution we began a novel approach that follows the spatial dynamics of two tree species (Pinus strobus and Tsuga canadensis) with unique life histories over the last 300 years in the town of Petersham, MA. Pinus strobus and Tsuga canadensis are the dominant conifer species in Petersham and much of the Northeastern U.S. Although both are long lived, T. canadensis has a higher shade tolerance, slower growth rate, and less fire tolerance than P. strobus. The goal of this study is twofold: first, to describe how the abundance and distribution of the two species has changed from pre-settlement (1733) to present day; second, to understand the driving forces behind these changes in terms of environmental interactions and natural and anthropogenic disturbances.

Sources for data include previous palynological studies, witness tree data, an 1830 map showing remaining woodlots, 1920 and 1937 vegetation maps from a white pine blister rust control study, 1971 and 1999 aerial images classified according to land-use taken from MassGIS, a survey of P. strobus and T. canadensis conducted by the Harvard Forest in 1994, logging operations since 1984 taken from cutting plans filed with the Massachusetts Department of Environmental Management, soil and elevation maps, and various historical writings and tax records. Changes in the abundance and spatial distribution of T. canadensis, P. strobus, and land-use determined by the comparison of these data sets will be interpreted through a framework of historic and modern disturbances. These disturbances include the initial clearance of land by settlers, coppice cutting of remaining woodlots, harvesting of T. canadensis for tanbark, re-growth of forests after farm abandonment in the late 19th century, selective harvesting of second growth P. strobus, fires, the demise of Castanea dentata after 1914, and the hurricane of 1938.

While the data has not yet been analyzed, it is expected that the story of temporal change in the spatial, distribution and abundance of P. strobus and T. canadensis in the town of Petersham will highlight the dynamic nature of the historic landscape and the lingering importance of historic land-use in modern species distribution. Initial glances at the vegetation maps indicate a dramatic increase in overstory T. canadensis between 1920 and 1994 (Fig. 1), which may be a result of decreased fire and clear-cutting in the area and the gradual spread of T. canadensis from primary woodlots.

An Experimental Study of the Relation between Eddy-Flux Carbon Uptake Measurements and Tree-Ring Estimates of Growth

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

Atmospheric measurements and modeling efforts have indicated that North American forests may play a significant role in the global missing carbon sink. Ecosystem carbon exchange research at the Harvard Forest (HF) has shown consistent annual carbon sequestration. Sixty percent of this sequestration can be accounted for by tree growth, driven primarily by red oak succession and land-use history. An eastern US forest inventory data study predicted that carbon sequestration would level off in the next few decades since results indicated that land-use history, that influences ecosystem carbon accumulation, will lead to less carbon sequestration with time. However, two recent studies suggest that older forests may continue to act as carbon sinks where respiration and assimilation rates do not reach equilibrium over long successional periods. The main goal of this year’s research is to place the growth of the HF tower plot red oak population (TP) in a long-term, regional context. Growth in the TP was first compared to the Lyford Plot (LP) in the HF. The HF populations were then compared to populations from NY, northern NJ and MA growing in forests with a range of site qualities and various disturbance/land-use histories. These comparisons will allow the following questions to be answered: Is the TP’s red oak growth history representative of the HF? How does HF red oak growth trends compare to other northeast US sites?

Seventy red oaks were randomly selected and cored in the HF; 35 in the eddy-flux tower
Figure 1. Area in the town of Petersham, MA with *Tsuga canadensis* in the canopy from vegetation surveys in 1920, 1937, and 1994.

S. Parnes
footprint (TP) and 35 outside the footprint (LP). Three cores/tree were collected. Sites outside the HF were sampled using standard dendrochronological methods; at least 20 trees/site and two cores/tree. Site information can be found in Table 1.

Basal area increment curves (BAI) can be used as proxies of biomass increment. HF BAI curves had similar growth variations, although the TP trees grew slightly faster than LP (Fig. 1). Both growth curves show a general leveling of biomass increment from 1950-2001. Annual carbon increment of the 20 largest TP trees could account for more than 80% of the randomly selected 35 tree carbon increment. LP’s largest 20 trees gave similar results. This suggests that a smaller sampling size might be adequate to study long-term growth trends.

In the comparison of HF to external sites, oak trees in Mohawk Trail State Forest (MTSF) in western Massachusetts, the only population sampled less than 130 years old, had higher average radial increment than the HF red oak (Fig. 2). Interestingly, unlike the HF populations, the MTSF population showed a sharp increase in growth from 1992 to the present despite no field evidence of recent canopy disturbance in MTSF. Figure 3 shows the BAI curves of all populations. Only the HF and Prospect Mountain, NY populations show a flat or declining BAI during the latter half of the 20th century. Several factors could play a role or interact with each other to cause differences in growth trends including: disturbance history, stand density, abiotic site characteristics or population climatic sensitivity. However, it is not apparent from these data that stand age limits long-term growth trends.

Future work for this research entails sampling several red oak populations, determining the climatic sensitivity for each population and quantifying the relation between eddy-flux carbon uptake measurements and tree-ring estimates of biomass at Harvard Forest.

Incorporating Vegetation Dynamics into a Hydrological Model. Part I: Photosynthesis and Dark Respiration

J. G. Quijano and A. P. Barros

Vegetation can amplify and/or modulate the effects of climate change through atmosphere-vegetation interactions. An essential step to a quantitative understanding of such interactions is the proper integration of the hydrological cycle and photosynthesis and how this relates to other processes such as respiration and leaf - flower phenology. The goal of our research is to overcome limitations observed by hydrological models and by terrestrial biogeochemistry models in simulating atmosphere-vegetation interactions. Herein, we present the integration of a physically based land-surface hydrological model (Deacon and Barros, 2002), a biochemical model for leaf photosynthesis (Farquhar et al., 1980 and Friend, 1995), and a substrate-structure separation model for respiration (Thorinley and Cannell, 2000). Some changes have been introduced to the original formulations in order to improve the physical representation of the processes. First, the original approach used by Friend (1995) for transpiration and stomatal resistance was replaced by the existing formulation in the land-surface hydrological model. Second, to simulate a realistic diurnal cycle of photosynthesis, the temporal variation of Rubisco in leaves, which results from variations in the potential electron transport rate per unit of chlorophyll, was incorporated as per Evans (1996). Third, the approach of Thorinley and Cannell (2000) was used for total and growth respiration, but Ryan’s approach (1991) for residual/maintenance respiration was retained as used by Friend (1995). In the current study, only leaf respiration was taken into account because it is relevant for leaf elongation, and thus LAI (leaf area index), which modulates atmosphere-vegetation interactions.

The specific goals of the work reported in this paper are: 1) to assess the ability of this new-coupled model to replicate previous work, and 2) to produce realistic behavior over long periods of time. For this purpose a one-year long simulation was conducted to evaluate daily, monthly and annual cycles in Cabauw, The Netherlands, a characteristic site of mid-latitude climates.
<table>
<thead>
<tr>
<th>Site</th>
<th>Basal Area [m²/ha]</th>
<th>Sampling Density</th>
<th>Age Structure [years]</th>
<th>General Land-Use History</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goose Egg State Forest, NY</td>
<td>26.4 [27.6]²</td>
<td>21 [36]</td>
<td>163, 204, 187.5</td>
<td>Primarily old-growth; a small section of second growth; potentially burned in late-1800s for blueberry production</td>
</tr>
<tr>
<td>Harvard Forest</td>
<td>35.8 [-]</td>
<td>35 [105]</td>
<td>57, 107, 72</td>
<td>Agricultural abandonment in late 1880s?; limited logging in early 1900s?</td>
</tr>
<tr>
<td>Tower Plot</td>
<td>35.3 [-]</td>
<td>35 [105]</td>
<td>74, 102, 99</td>
<td>Agricultural abandonment in late 1880s?; limited logging in early 1900s?</td>
</tr>
<tr>
<td>Harvard Forest Lyford Plot</td>
<td></td>
<td></td>
<td></td>
<td>AGricultural abandonment in 1870s?; canopy disturbance in 1890s, 1930s;</td>
</tr>
<tr>
<td>Mohawk Trail State Forest, MA</td>
<td>39.8 [41.2]²</td>
<td>21 [42]</td>
<td>84, 130, 103</td>
<td>Canopy disturbance in 1820s, 1890s; pasture in 1820s?; hotel and cable car line built in late-1800s; fire in 1910s?</td>
</tr>
<tr>
<td>Prospect Mountain, ADK, NY</td>
<td>34.0 [35.4]²</td>
<td>23 [33]</td>
<td>95, 188, 150</td>
<td>Sugar bush and/or park in 1800s; American chestnut salvaging or logging event in 1920s</td>
</tr>
<tr>
<td>Singer Farm, NY</td>
<td>30.8 [33.8]²</td>
<td>8 [17]</td>
<td>944, 203, 127</td>
<td>A mix of old- and second-growth forest; 2nd-growth section had a canopy disturbance in 1860s</td>
</tr>
<tr>
<td>Uttertown, NJ</td>
<td>37.5 [45]²</td>
<td>20 [41]</td>
<td>112, 218, 144.5</td>
<td>Old-growth; perhaps some limited firewood cutting or grazing in 1870s; nothing too significant otherwise</td>
</tr>
<tr>
<td>Wachusett Mountain, MA</td>
<td>35.0 [-]</td>
<td>39 [40]</td>
<td>100, 325, 210</td>
<td></td>
</tr>
</tbody>
</table>

Figure 1 – Average basal area increment curves for the eddy-flux Tower Plot (solid line) and Lyford Plot (dashed line) red oak populations at the Harvard Forest.
Figure 2 - Average annual radial increment growth curves for Mohawk State Forest (solid line), HF Tower Plot (solid line with open circles) and HF Lyford Plot (solid line with open squares). The thick curvilinear lines represent decadal scale growth trends. Arrows point to gypsy moth defoliation events in 1945 and 1981.
Figure 3 – Average basal area increment curves for red oak sites from western NY to eastern MA (see Table 1 for details). The HF (TP = thick line with dotted circles; LP = thick line with open diamonds) and Mohawk Trail State Forest (thick, dashed line) curves are emphasized to compare populations of roughly the same stand age.
Forcing data was available with a resolution of half an hour, for a one-year period (i.e. 1987). Results shown here demonstrate that the coupled model is able to reproduce previous work for similar conditions, and that the daily, monthly and annual cycles of photosynthesis are well simulated and exhibit adequate sensitivity to hydrological stress (Fig. 1 - 4). The model in its current form is capable of reproducing the dynamics of dry matter production and carbon assimilation, as well as the temporal evolution of the growing season. Ongoing work is on developing the leaf phenology and crown structure parameterizations that will help in modeling energy, water and carbon exchange between the atmosphere and vegetation in a fully predictive fashion.

The 'Hydrology' of Leaves: Coordination of Structure and Function in Temperate Woody Species

L. Sack, P. D. Cowan, N. Jaikumar and N. M. Holbrook

The hydraulic conductance of the leaf lamina (K_{lamina}) substantially constrains whole-plant water transport, but little is known of its association with leaf structure and function. We measured K_{lamina} for sun and shade leaves of six woody temperate species, and tested for correlation with irradiance, and with 22 other leaf traits. K_{lamina} varied from 7.40 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPA}^{-1} \text{ for Acer saccharum} shade leaves to 2.89 \times 10^{-4} \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPA}^{-1} \text{ for Vitis labrusca} sun leaves; tree sun leaves had 15 - 67% higher K_{lamina} than shade leaves. K_{lamina} was coordinated with traits associated with high water flux, including leaf irradiance, petiole hydraulic conductance, guard cell length, and stomatal pore area per lamina area. K_{lamina} was also coordinated with lamina thickness, water storage capacitance, 1/mesophyll water transfer resistance, and, in 5/6 species, with lamina perimeter/area. However, K_{lamina} was independent of inter-related leaf traits including lamina mass per area, density, modulus of elasticity, osmotic potential, and cuticular conductance. K_{lamina} is thus coordinated with a complex of structural and functional traits relevant to liquid-phase water flux and maximum rates of gas exchange. These water flux traits are independent of other traits relating to drought tolerance and to aspects of carbon economy.

Forest Management Effects on Carbon Sequestration at Howland Forest, Maine, USA


Mid-latitude ecosystems appear to be an important carbon sink, and at several sites forests appear to contribute significantly to this sink. Forest management regimes are likely to influence the strength and longevity of that sink. In Maine, forest management regimes have changed primarily to shelterwood harvesting regimes, where a portion of the basal area is removed at different times throughout the rotation. Using a combination of eddy covariance and ground-based measurements, we are examining the net carbon consequences of this shelterwood management regime at Howland Forest in Maine, owned and managed by International Paper.

Between 1996-2000, an undisturbed old-growth stand at Howland Forest has been accumulating on average 1.6±0.2 Mg C ha\(^{-1}\) y\(^{-1}\). This old-growth stand serves as a control stand for a commercially-harvested stand located about one mile away. In the harvested area, pre-harvest live biomass was about 77 Mg C ha\(^{-1}\) and dominated by hemlock and less red spruce (Fig. 1). In our control stand, live biomass was about 110 Mg C ha\(^{-1}\), with co-dominant red spruce and hemlock. Based on measurements of truck weights and log density, harvest resulted in a removal of about 18 Mg C ha\(^{-1}\), with hemlock comprising about 25% of biomass removed (Fig. 2). For comparison, plot remeasurements combined with species-specific allometric equations suggested removals of 15 (SD=11) Mg C ha\(^{-1}\) at harvest. Slash inputs to the forest floor (branches and foliage) estimated using allometric equations were about 5 Mg C ha\(^{-1}\), increasing the size of the down-dead wood pool by about 30% (Fig. 1). Post-harvest belowground residue inputs (including stumps) were about 5 Mg C ha\(^{-1}\). These residue inputs appear to have stimulated night-time respiration rates above those observed pre-harvest, approaching those observed in the control stand with higher live biomass. In
Figure 1. Annual evolution of photosynthesis activity with highest values during the months of June till September. The growing season goes from the beginning of April till the end of October.

![Annual evolution of the dry matter production](image)

Figure 2. Monthly average values of dry matter production. Note high values during July and the effect of the intra-annual variability of daylight hours.

![Monthly average of dry matter production](image)

Quijano and Barros
Figure 3a. Diurnal cycle for soil, root and leaf water potentials for a week in July. In the simulation, water potential effectively control photosynthesis especially at midday (Fig.2). A critical value for water potential of $-1650$ J/kg was used (Friend, 1995).

Figure 3b. Effect of leaf water potential (from Fig. 3a) over dry matter production.
Figure 4. Diurnal evolution of the respiration as a fraction of the dry matter production.

Respiration fractions as a function of the dry matter production

\[ \text{Fraction} \]

12th Aug 13th Aug 14th Aug

Time

Growth respiration – Maintenance respiration – Total respiration

Quijano and Barros
Figure 1. Pre-harvest carbon pools in the harvested stand. Total includes both standing dead and live above- and belowground biomass.

Figure 2. Proportion of biomass removed at harvest as percent of total (based on truck information).

Scott et al.
2002, between Julian Day 192-270, net ecosystem exchange (NEE) in the harvested stand was about 50% of that in the control stand due both to decreased C uptake and a (not as large) decrease in night-time respiration.

Whether this management regime increases carbon sequestration rates will depend in part on the fate of wood products. During the harvest, logging contractors working with International Paper provided us with information on the fate of the wood and likely products to be produced for each truckload of wood leaving the forest. Most hardwood species (19% of wood removed) were either converted to chips or used for pulp for special types of paper – some species (birch) were used to produce more refined wood products. Hemlock (25% of wood removed) was used primarily for pulpwood to produce coated paper for books and catalogs. Smaller logs of (mostly) spruce were either converted to pulp, or used for studs and planks. Larger samples of spruce (21% of wood removed) were used for sawlogs – bark was converted to mulch. Aspen (10% of wood removed) was used to produce a waferboard-type product. Future work will quantify the expected lifespan of these products and their contribution to the overall (long-term) carbon balance of the forest.

The dynamics of carbon release to and uptake from the atmosphere depends on the fate of the wood products, post-harvest forest growth rates, and detritus decay. We are estimating each of these independently while, in addition, using eddy covariance measurements to provide integrated whole-ecosystem carbon fluxes. These results will be used in simple models to predict the long-term carbon consequences of this shelterwood management regime.

**Carbon Sequestration at the Howland Forest in Maine: Where Does the Carbon Go?**

*N. Scott, D. Hollinger, E. Davidson, J. Gaudinski, S. Trumbore, S. Goltz, H. Hughes, J. Lee, C. Rodrigues and J. Walsh*

Eddy covariance towers provide information on net carbon (C) exchange between terrestrial ecosystems and the atmosphere, but they provide little information on the location of C sources and sinks within an ecosystem. At Howland Forest (an old-growth mixed spruce/hemlock/red maple forest) in Howland, Maine, eddy covariance results from 1996-2000 suggest that, on average, the forest is accumulating about 1.6 Mg C ha⁻¹ y⁻¹. Live biomass at Howland Forest is about 110 Mg C ha⁻¹, and soils (to 1 m depth) contain about the same amount of C as live vegetation (Fig. 1). Down-dead wood (DDW) and standing-dead wood are relatively small C pools (Fig. 1), but changes in these pools could contribute significantly to net C storage. In order to understand how sustainable this C sink might be, it is important to know where C is being stored, as the residence time of C in the different pools varies greatly.

We investigated changes in whole-ecosystem C pools to determine where C is being sequestered. Measurements on permanent sample plots in 1989, 1998, and 2002 provided estimates of changes in C storage in live vegetation and standing-dead wood. Changes in DDW were based on measurements of pool size (point-relascope method), input rates and output (respiration) rates. Respiration was estimated by placing pieces of DDW in a sealed chamber and measuring CO₂ production with a portable IRGA system. We estimated inputs to the DDW pool based on the permanent plot measurements in 1989 and again in 2002. Soil C accumulation/loss was examined using radiocarbon information to constrain soil C turnover rates in a soil C model.

From 1989 to 1998, C storage in live trees increased by about 1.7 (0.2) Mg C ha⁻¹ y⁻¹; about 23% of this C is stored in roots. Between 1998-2002, however, C storage in live vegetation increased by only 1.1 (0.4) Mg C ha⁻¹ y⁻¹. Based on these same measurements, mortality was about 0.9 (1.0) Mg C ha⁻¹ y⁻¹. Down-dead wood contains about 4.1 Mg C ha⁻¹, and respiration rates of DDW correlated positively with temperature (Fig. 2); this relationship was used to estimate annual CO₂ production from DDW of 0.1 Mg C ha⁻¹ y⁻¹. Inputs to the DDW pool are about 0.3 Mg C ha⁻¹ y⁻¹, suggesting that DDW is accumulating a small amount of C over the last decade. Standing-dead wood contains about 10 Mg C ha⁻¹, but its contribution to whole-ecosystem C storage is poorly understood. Soil C could be contributing to whole-ecosystem C storage, with accumulation.
Figure 1. Carbon pools at Howland Forest around the tower site. Soil C based on Fernandez et al. 1992. Total includes both standing dead and live above- and belowground biomass.

\[
\text{Ln respiration} = 0.103 \text{Temp} - 6.808; \quad R^2 = 0.30
\]

Figure 2. Relationship between temperature and respiration rates from down-dead wood.

Scott et al.
Howland
C Inventory (gC m²)

Low Density               High Density

0   2000   4000          0   2000   4000

Decadal cycling SOM
Δ¹⁴C > 100+‰

Centennial cycling SOM
Δ¹⁴C = 0-100‰

Millennial cycling SOM
Δ¹⁴C = < 100‰

---

Figure 3. Vertical distribution of soil C stocks fractionated into low- and high-density material. Most C accumulation occurs in the low-density soil C fraction located near the surface (forest floor and mineral soil) – this material cycles on decadal time scales.

Scott et al.
rates ranging from 0-0.4 Mg C ha\(^{-1}\)y\(^{-1}\) in moderately well drained soils and from 0-0.2 Mg C ha\(^{-1}\)y\(^{-1}\) in poorly drained soils; the area weighted (based on area of different soil type) upper-limit estimate is 0.3 Mg C ha\(^{-1}\)y\(^{-1}\). Most soil C accumulation occurs near the surface (Fig. 3). Our results suggest that most of the net ecosystem carbon storage goes into live vegetation; C storage in dead wood and soil contributes at most 30% of net ecosystem C storage. Given the uncertainties, our biometric estimates of net ecosystem C storage roughly balance NEE estimates over longer time scales.

Emission and Long-Range Transport of Mercury from a Canadian Boreal Forest Fire

J. Sigler, X. Lee, W. Munger and S. Wofsy

Field observations made at Harvard Forest [Petersham, Ma., U.S.A. (42°54'N, 72°18'W)] during early July 2002 show clear evidence of long-range transport of mercury (Hg) in a smoke plume from a series of boreal forest fires in northern Quebec. From these measurements, large increases in Hg and CO were shown to be highly correlated during the plume event. Long-range transport from fires may therefore have a significant impact on short-term ambient Hg concentrations in the United States. The Hg:CO emissions ratio determined from the data (8.61×10\(^{-8}\) mol/mol) was combined with previously published information on CO emissions to determine an area-based Hg emissions rate for boreal forest fires (2.8 g Hg ha\(^{-1}\)\(^{-1}\)), annual Hg emissions from Canadian forest fires (6.4 tons), annual global Hg emissions from boreal forest fires (8-62 tons) and annual global Hg emissions from biomass burning (246-431 tons). Hg:CO emissions ratios are likely dependent on biome/species, and therefore result in different estimates when used to determine global Hg emission from biomass burning. Annual Hg emission from fires in the boreal zone is likely equal to, if not greater than, the annual sink from wet deposition, and amount to ~60% of annual Canadian anthropogenic emissions. The highly sporadic temporal and spatial dynamics of boreal forest fires suggest that a single large fire could emit enough Hg to nearly equal the total annual anthropogenic emission in Canada.

Photosynthetic Responses by Forest Herbs and Tree Seedlings to Near-Ground Enriched Carbon Dioxide and Irradiance Regimes

T. W. Sipe

The goals of this three-year project (2003-06) are: (1) to measure naturally-occurring nearground enriched CO\(_2\) (NEC) profiles and irradiance regimes, with a particular focus on sunflecks, (2) to model diurnal leaf-level carbon gain by six herbaceous and woody species across a wide range of NEC/irradiance combinations, and thereby (3) to determine the potential for NEC/irradiance interactions to elicit differences in survival, growth, and distributions of species within and across forest stands. Any factors that consistently enhance leaf-level carbon gain, even modestly, may have substantial cumulative impacts over longer time frames for many forest plant species, including those that reside permanently in the NEC zone and those that pass through as juveniles. The ubiquitous occurrence of enriched CO\(_2\) in the herbaceous stratum and its likely impacts on carbon gain have been noted for many decades, but no comprehensive effort has been made to measure or model spatial-temporal NEC profile variation or quantify its effects on photosynthesis by co-occurring species, especially under the fluctuating PPF levels typical of the understory environment. Although much has been learned about sunfleck photosynthesis, we know very little about how species differ in photosynthetic response to dynamic PPF environments in the field, or how covariance with other resources such as NEC could alter such responses.

This research expands on previous work during the NSF-CRUI project (1995-99) involving the impacts of land-use legacies on current forest processes at Harvard Forest and will be done in two of the CRUI land-use sites. Our data show that the impacts of enriched CO\(_2\) on leaf-level photosynthesis are substantial during both background shade and sunflecks for three herb species measured in the field. However, we need
to expand the scope of these efforts to more extensive measurements of NEC/irradiance regimes and photosynthesis in order to build predictive models of NEC variation and daily carbon gain. Six species will be used, including three herb species we have already studied (Aralia nudicaulis, Medeola virginiana, Clintonia borealis) and three tree species (Acer saccharum, A. rubrum, A. pensylvanicum). Measurements in summer 2003 will focus on broad spatial-temporal variation in NEC levels and irradiance regimes across the two sites, microclimatic and herbaceous stratum regulators of NEC variation, and the initial phase of photosynthetic measurements aimed at parameterizing a recently developed dynamic photosynthesis model.

Heartwood Formation and Patterns of Cell Death in Woody Stems

R. Spicer

Trees maintain variable amounts of sapwood - the physiologically active part of the xylem - to function in water transport and storage, carbohydrate storage, mechanical support, and in response to stem wounding. In contrast, the central core of most tree stems is gradually converted to heartwood, which no longer conducts water and contains only dead cells. Heartwood is defined by the death of parenchyma cells that, while alive, store carbohydrates and serve as an important route of exchange between xylem and phloem. Shortly before death, these cells synthesize secondary compounds (typically polyphenols) that impart the decay resistance and darker color that often characterize heartwood. As a first step toward understanding the biology of heartwood formation and possible causes of parenchyma cell death, I have been characterizing radial (bark to pith) patterns in cell death in a number of conifers and gymnosperms, and comparing metabolic rates in xylem of different ages (young versus old sapwood).

I have found that the presence or absence of the nucleus (as detected by fluorescence microscopy) serves as a good indicator of cell vitality (Fig. 1a); that is, when parenchyma cells die their nuclei rapidly disappear. Using radial tissue sections to tally the relative proportions of live versus dead cells, I have found variation in the pattern of cell death that suggests conifers show a gradual loss of living tissue, whereas angiosperms have a more abrupt transition (Fig. 1b).

Ongoing work on the metabolic activity in sapwood of different ages suggests that aging parenchyma cells within the 'transition zone' (region between sapwood and heartwood) are able to respire at just as high a rate as younger cells in the outermost xylem. This work, coupled with the existence of abrupt sapwood/heartwood boundaries, suggests that the death of this tissue is likely to be regulated by a tree, forming an important stage in plant development. This is in contrast to previous work suggesting that parenchyma death is simply the end of an aging process in which metabolism gradually slows.

The Impact of Hemlock Woolly Adelgid on Throughfall Chemistry and Microorganism Abundance

B. Stadler, T. Müller, D. Orwig and R. Cobb

In 2002 we began an experiment to study the effects of trophic interactions between hemlock woolly adelgid and epiphytic bacteria and the spatial and temporal variability in flows of energy and matter through the hemlock canopy. At each of three sites varying in HWA infestation level (Harvard Forest = uninfested, Devil's Hopyard = medium infested, Seldon Neck = heavy infested) throughfall solutions were collected underneath four trees, each about 5 m tall. To investigate the within-tree variability in infestation rates, litter production, microorganism abundance/diversity, and throughfall chemistry, three throughfall samplers were placed beneath each tree: one close to the trunk, the second close to the periphery of the canopy, and the third in between. Uninfested hemlock showed a significant decline in canopy biomass from the center of a tree to the periphery, but not so for infested trees, which had significantly less biomass in the canopy and produced less new foliage. Much of the remaining biomass in the canopy of infested trees is wood. On uninfested trees needle litter was positively correlated with the estimated biomass in the canopy but not so for
Figure 1. Fluorescently stained nuclei in ray cells of the outer sapwood of *Acer rubrum* (a). Presence of nuclei indicates parenchyma are alive (verified with vital stain), and is used to generate radial profiles of live versus dead parenchyma (b). Conifers measured (including *Pinus strobus*, *Larix decidua*, and *Picea abies*) show a gradual loss of living parenchyma across the sapwood, whereas 100% of angiosperm ray tissue is alive until an abrupt sapwood/heartwood boundary. Each line represents an individual (e.g., four individuals are shown for *Tsuga*). Species sampled but not yet measured include *Liquidambar styraciflua*, *Liriodendron tulipifera*, and *Prunus serotina*.

Spicer
infested trees. Foliar % N was strongly influenced by needle age and level of infestation. Infested trees had significantly higher foliar %N, while foliar %C was not affected by HWA or foliar age. %N was highest in young foliage where HWA was found in the highest density. Epiphytic microorganisms showed little differences in abundance on needles growing in different parts within the canopy of hemlock, but bacteria, yeasts and filamentous fungi thrived significantly better on medium and heavy infested compared to uninfested trees. The amount of rain collected in throughfall strongly depended on the position of the throughfall samplers beneath uninfested trees, with most throughfall passing in the periphery of the canopy and least close to the trunk. No such gradient was found for the canopies of infested trees through which relatively more precipitation was percolating. Throughfall chemistry was strongly affected by HWA infestation. From infested canopies higher concentrations of different nitrogenous compounds and carbon as well as different ion species were leaching. Therefore, beneath infested canopies relatively more precipitation and nutrients reach the forest floor. We intend to continue these investigations in the future to help identify and understand the chain of mechanisms that lead to changes in decomposition and nutrient availability as forests respond to invasive pests.

Does Selection on Ecophysiological Traits Facilitate Invasion of Alliaria petiolata?

K. A. Stinson And F. A. Bazzaz

The Eurasian invasive plant Alliaria petiolata, or garlic mustard, establishes in North America in disturbed sites, and aggressively invades adjacent forest communities and threatens native understory flora. Our study examines the role of genetic variation and phenotypic plasticity in driving aggressive invasions in this species. The spread of this species from open, disturbed sites into the intact forest understory is likely to require a high degree of flexibility in ecophysiological response to light and other environmental variables. Evolutionary changes in water use efficiency, photosynthetic rates, and partitioning of nitrogen may all contribute to this species' spread into forested habitat. Using comprehensive environmental measurements in the field and reciprocal transplanting techniques, we aim to identify which traits facilitate invasion into the understory in different geographical locations. In order to measure divergence among latitudinal populations, we also compare forest edge and canopy populations at Harvard Forest and three other sites in central-western Massachusetts to more southerly and northerly populations. Quantitative genetics experiments using Harvard Forest populations are also underway to determine whether or not selection on these traits will drive further invasion. Our results should elucidate the role of selection within divergent habitat types for this species' rapid spread.

Carbon Sequestration at Harvard Forest in 2001: A Banner Year?

S. Urbanski, J. Munger and S. Wofsy

Eddy co-variance measurements of the net ecosystem exchange of CO₂ (NEE) at Harvard Forest indicate the ecosystem sequestered over 4 tonsC ha⁻¹ in 2001. NEE of (-4.4) tonC ha⁻¹ measured in the ecological year 2001 (Oct 27, 2000 – Oct 27, 2001) was more than twice the mean net uptake observed in the previous 9 years (-2.0 tonC ha⁻¹) and 1.7 tonC ha⁻¹ greater than the previous high sequestration year of 1995 (see Fig. 1). Estimates of gross ecosystem exchange of CO₂ (GEE) and ecosystem respiration (R) indicate the anomalous NEE observed in 2001 results from increased photosynthetic uptake of CO₂ (Fig. 1). Because the NEE measured in 2001 was 4σ below the 1992-2000 mean NEE, the 2001 data set was investigated extensively in an attempt to uncover any error(s) in the data set. Prime suspects for error include data processing (i.e. gap filling), sonic anemometer malfunction, LiCor malfunction, and the calibration and flow system.

The results of four different gap filling methods, (bivariate interpolation, mean diurnal variation, look-up tables, and non-linear regression) agreed within 7% for ecological year 2001, demonstrating that the estimated annual sum of NEE was not an artifact of gap filling.
Figure 1. Ecological year sums of NEE, R, and GEE

Urbanski et al.
The hourly measurements of NEE were NOT anomalous during the dormant or the nighttime growing season. The 2001 anomaly in NEE is a daytime-growing season phenomena, an observation not consistent with a systematic error that simply makes NEE large (or less positive). An extensive statistical examination of the 1992-2001 growing season sonic anemometer data, at various time scales, (variance of the vertical wind, rotation angle, friction velocity, smearing ratio, sensible and latent heat fluxes) indicated the sonic anemometer was functioning as normal in 2001. An assessment of water vapor flux, calibration, and sampling system data failed to reveal any errors in the LiCor instrument or the calibration and sampling flow systems.

We have been unable to demonstrate a measurement error in 2001. The measurements appear to be free of a systematic error in 2001; however, the measured anomalous uptake may reflect interference from the timber harvest site located 500m S of the eddy flux tower. A wind direction based analysis of the 10-year data set by wind sector shows that the relative uptake enhancement observed in 2001 is similar across the four wind direction quadrants. This suggests the anomalous uptake measured in 2001 is not a result of interference from the timber harvest site.

If the measured NEE is “real,” why did the forest sequester so much carbon in 2001 and where did the carbon go? The 2001 NEE anomaly is driven by growing season activity. The 2001 growing season was 18 days longer than the 9 year mean growing season (see Fig. 2). If these extra 18 days are typical of mid growing days of 1992-2000, a rough estimate for increased in C sequestration attributable to the longer growing season is 0.8 tonC/ha, one third of the anomaly. The bulk of the remaining 2001 anomaly is attributable to enhanced photosynthetic activity during the growing season.

Disturbance Histories as a Predictor of Habitat Invasibility in a Mosaic Landscape: Cape Cod National Seashore

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

Landscape spatial pattern is being paired with historical, environmental and biotic properties of Cape Cod National Seashore to determine habitat invasibility. Using a large, spatially explicit dataset, the anthropogenic and natural disturbances that are most associated with exotic species presence and distribution are being assessed. We are employing a multi-scale technique, where we are determining landscape-level influences on exotic species invasion. The influence of landscape structure on connectivity of exotic species, and thus invasibility of habitats, will be determined with various landscape ecological metrics. This study attempts to separate out the various contributions that historical natural and anthropogenic disturbances have on exotic species presence and abundance in the mosaic landscape of Cape Cod National Seashore.

The most influential factors resulting from the landscape-scale analyses will be further investigated by B. Von Holle, with patch-scale analyses. The thresholds of anthropogenic and natural disturbances that enhance or inhibit exotic and native species richness and cover will be investigated using field methods to determine disturbance frequencies and intensities. The various disturbance levels and frequencies will be determined for 80 Cape Cod plots using historical methods. Seral stage of the patch will be assessed as a factor of habitat invasibility. Linking complex environmental and historical factors in a spatially explicit manner will guide the greater understanding of invasibility of ecosystems.
Figure 2. Cumulative sum of NEE at Harvard Forest for ecological year 2001 and the 1992-2000 mean. NEE gaps filled using the look-up table method.


Berntson, G. 96. Root growth and nitrogen cycling in temperate deciduous forests in an elevated
Boose, E. R., K. E. Chamberlin, and D. R. Foster.


Identifying mechanisms of seasonal cueing of germination using *Arabidopsis* mutants. Heredity.


Foster, D., B. Hall, S. Barry, S. Clayden, and T. Parshall. 2002. Cultural, environmental, and historical controls of vegetation patterns and the modern conservation setting on the island of Martha's Vineyard. Journal of
Biogeography 29: 1381-1400.
Foster, D. R. 1993. Land-use history and forest transformations in central New England. Pp. 91-110 In S. Pickett and M. McDonald (Eds.), Humans as Components of Ecosystems. Springer-Verlag, NY.


George, L. and F. A. Bazzaz. 2002. The herbaceous layer as a filter determining spatial patterns in forest regeneration. In K. Jensen (Eds.), Oxford University Press, U. K.


Lawrence, D. and D. Foster. 2001. Determinants of regional variability in litter production of forests in the Southern Yucatan: environmental gradients or human legacy? EOS. Trans. AGU 82 (20), Spring Meeting Suppl.


Mack, R. N., D. Simberloff, W. M. Lonsdale, H.


Elsevier, Amsterdam, The Netherlands.
Moore, K. E., D. R. Fitzjarrald, R. K. Sakai, M. L.


Orwig, D. A., R. C. Cobb, M. L. Kizlinski, S. J.


Schulze, E.-D., F. A. Bazzaz, K. Nadelhoffer, T.


Wayne, P. M., A. L. Carnelli, J. Connolly, and F. A. Bazzaz. 1999. The density dependence of


ACKNOWLEDGEMENT OF SUPPORT

Research activities described in this booklet are supported in part by funds provided by the following sources:

Friends of the Harvard Forest
Anonymous donor
Fund for Protection of Wildlife and Natural Areas
John and Edith Downs Memorial Trust
Massachusetts Environmental Trust
Massachusetts Natural Heritage and Endangered Species Program
A. W. Mellon Foundation
Mount Everett Research and Protection Fund of the Southern Taconics Research and Conservation Center
National Park Foundation
National Science Foundation, Programs in
  Digital Government
  Ecology
  Ecosystems
  Long Term Ecological Research
  Research Experience for Undergraduates
The Nature Conservancy
Sweetwater Trust
U. S. Department of Agriculture, Northeastern Area Federal Focus Funding
U. S. Department of Energy
  National Institutes for Global Environmental Change
U. S. National Park Service