Harvard Forest
Long Term Ecological Research Program

Northern Hardwoods
and Spruce - Fir

Transition Hardwoods

HARVARD FOREST

WC

Pitch Pine - Oak
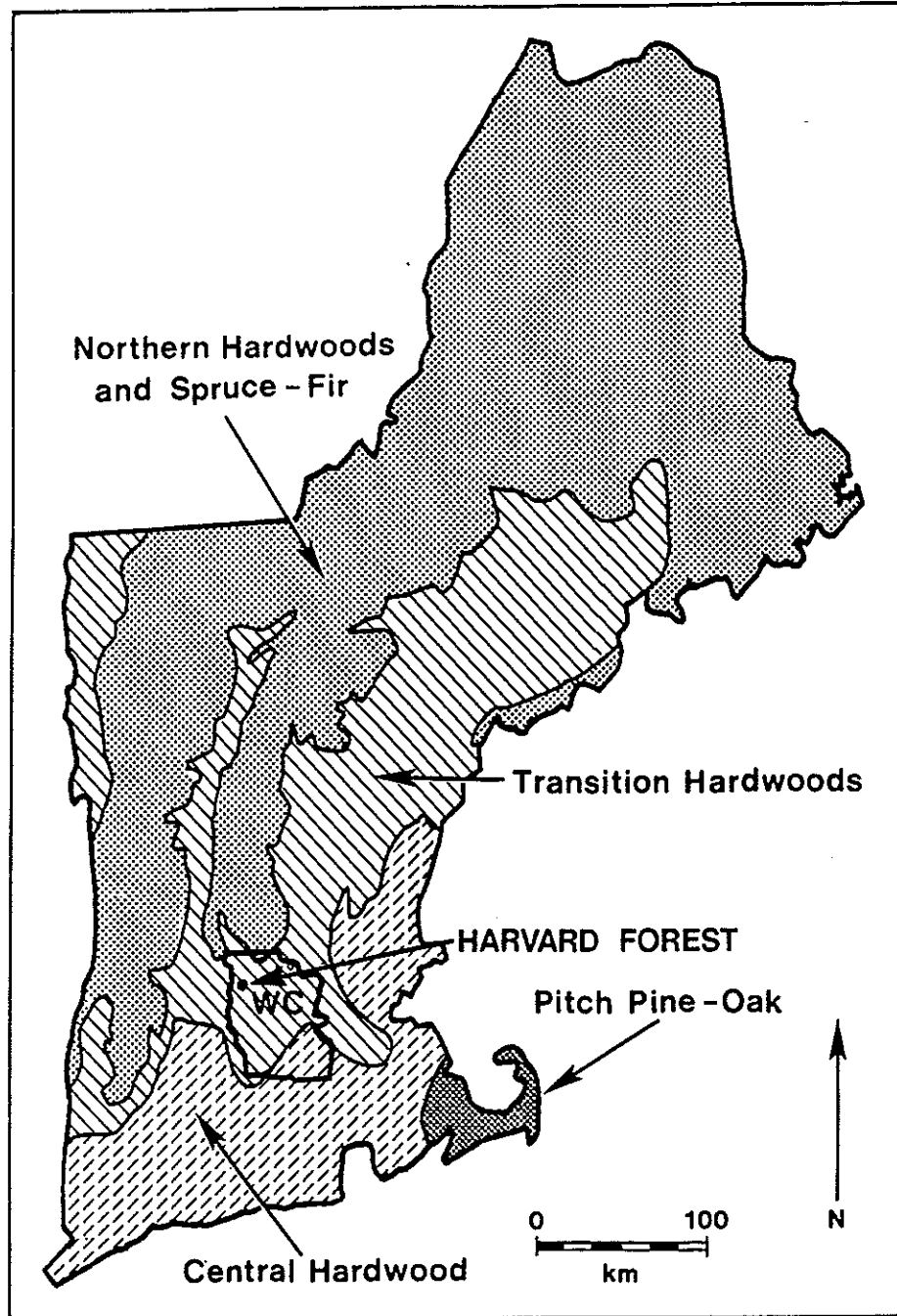
Central Hardwood

0   100

km

N

Figure 1.   The Harvard Forest is located in the northwestern corner of Worcester County,
Massachusetts in the Transition Hardwood forest zone. Map modified from
Westveld (1956).

LONG TERM ECOLOGICAL RESEARCH AT HARVARD FOREST

23 April 2001

Julie S. Pallant and Dottie Recos-Smith, Editors

HARVARD FOREST LONG TERM ECOLOGICAL RESEARCH PROGRAM

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 Zebryk 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). 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, dendrochrono-logical 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

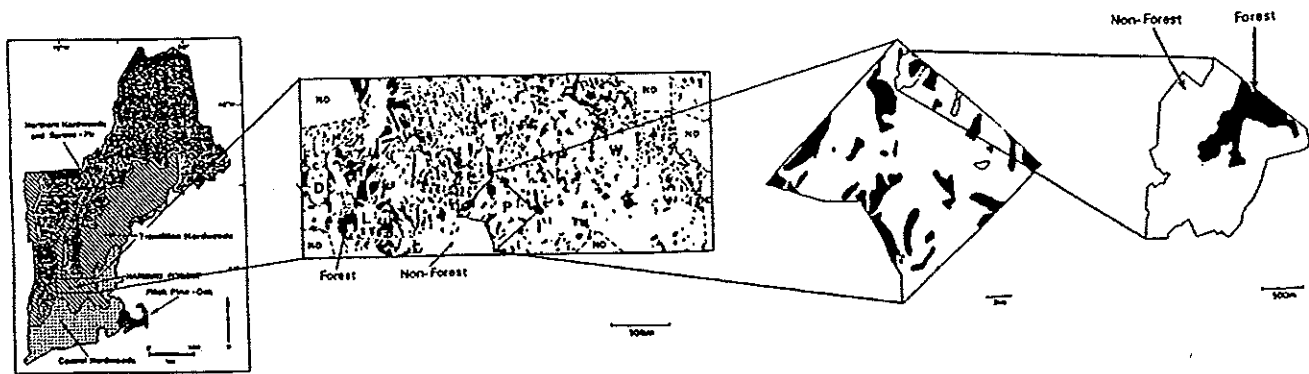| Region	Sub-region	Landscape	Site
New England	Central Massachusetts	Petersham	Harvard Forest
1000 km	100 km	10 km	1 km

Figure 1. Spatial scales of investigation in the Harvard Forest LTER program. Each map depicts the distribution of forest area in the mid 19th century, at the height of agricultural activity and deforestation.
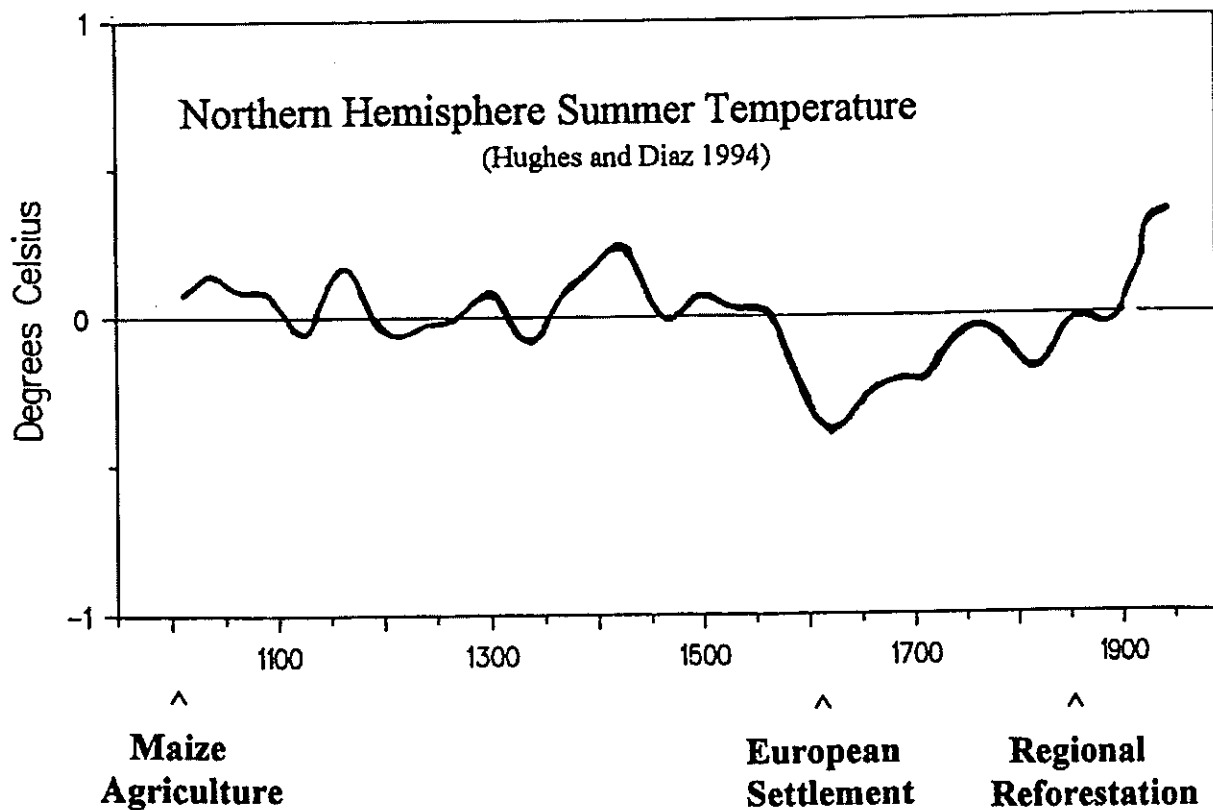
Figure 2. Northern hemisphere summer temperature.

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

	REGION	SUB-REGION	LANDSCAPE	SITE
Area	New England	C Massachusetts	Petersham	Harvard Forest
Size	1000 km	100 km	10 km	1 km
Elevation	0 - 1870 m	30 - 610 m	190 - 425 m	280 - 425 m

RECONSTRUCTION

	REGION	SUB-REGION	LANDSCAPE	SITE
Paleoecology	*	*	*	*
Archaeology		*		
History	*	*	*	*
Dendrochronology			*	*
Hurricane Modeling	*	*	*	*
Ecosystem Modeling	*	*	*	*

MEASUREMENT

	REGION	SUB-REGION	LANDSCAPE	SITE
Vegetation Surveys	*	*	*	*
Soil Surveys	*			*
Fauna/Flora			*	*
AVIRIS/LANDSAT		*	*	*
Atmosphere Exchange				*

EXPERIMENTAL MANIPULATION

	REGION	SUB-REGION	LANDSCAPE	SITE
Hurricane Pulldown				*
Nitrogen Saturation				*
Soil Warming				*
Organic Matter				*
Controlled Environment				*

APPLICATION

	REGION	SUB-REGION	LANDSCAPE	SITE
Atmospheric Deposition	*	*	*	*
Water Management	*	*	*	*
Forest Management		*	*	*
Land Protection		*	*	*
Land Use Planning		*	*	*
Education	*	*	*	*

flux measurements of atmosphere-biosphere exchanges to define current conditions and rates.

3. Experimental manipulations of ecosystems and **controlled environment studies** on individual plants and population 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
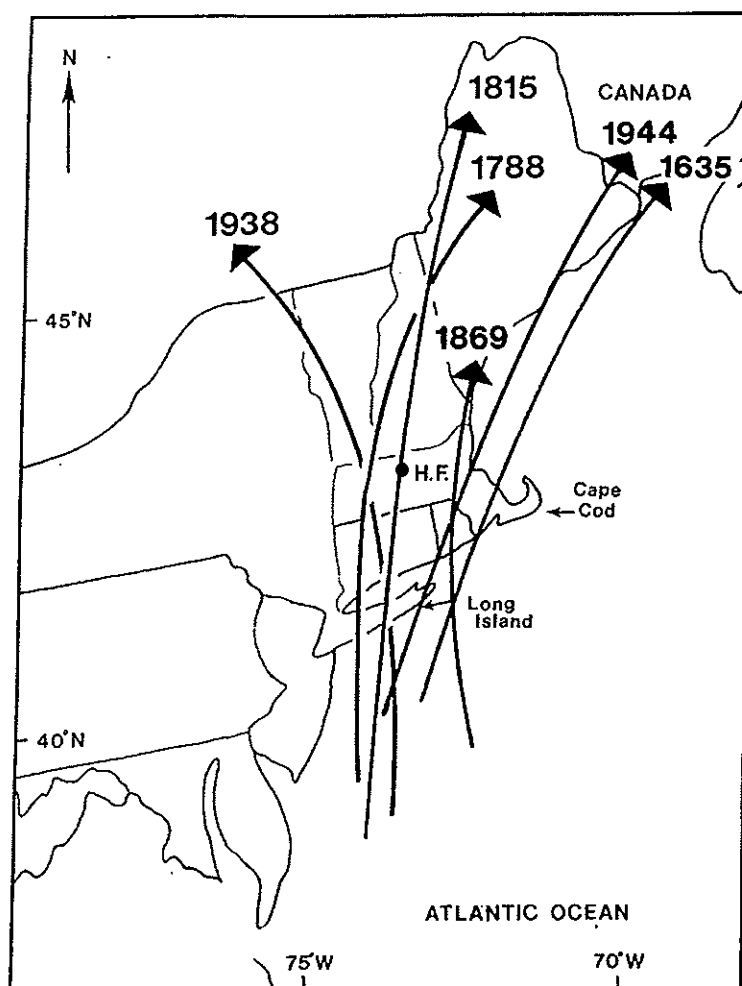
Figure 3. Paths of major hurricanes that have impacted New England and the Harvard Forest during the historical period.
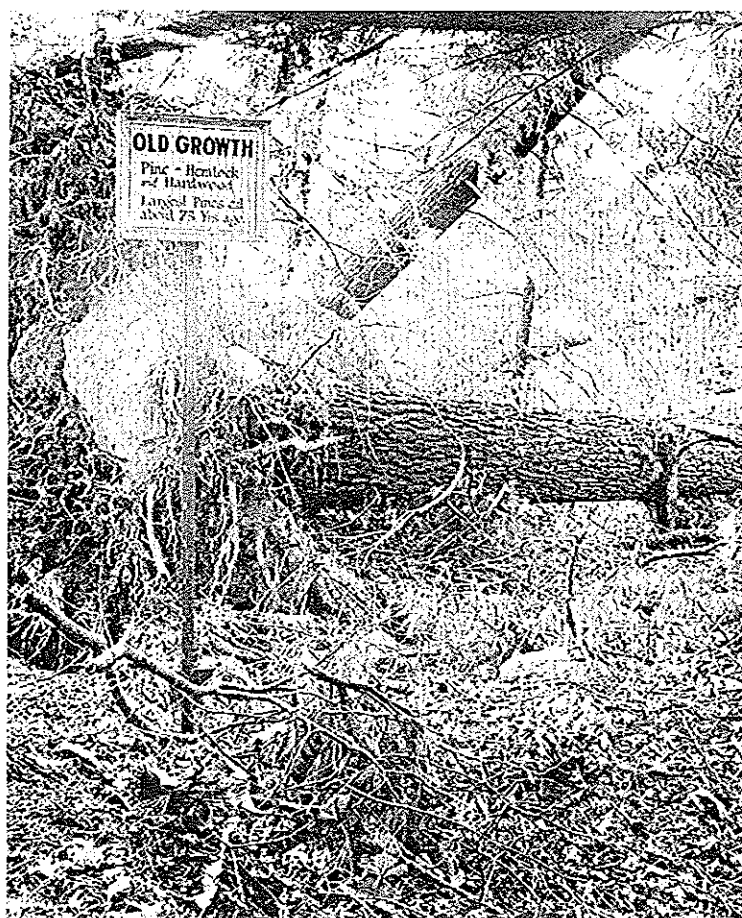

Figure 4. Damage from the 1938 Hurricane was particularly severe for old conifer-dominated forests located on sites exposed to wind such as the old-growth Pisgah Forest in southwestern New Hampshire. Photograph from the Harvard Forest Archives.

physiographic patterns in controlling vegetation structure and composition (Foster and Boose 1995). Long-term records and the ubiquitous presence of mound and pit topography in old forest stands suggest that finer-scale disturbances such as gap dynamics, downbursts and tornadoes have contributed more local patterning to forests over the ages. The relative role of these different types and scales of physical disturbance and their spatial distribution across the landscape and region are largely unknown.

Although infrequent, perhaps occurring as rarely as once every thousand years in some regions and forest types, or ten times as frequently in others, fire has played an uncertain and variable role in New England forests (Fuller et al. 1998). 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). 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, increases in the 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 tropospheric ozone layer that shields the earth from ultraviolet radiation, stagnant circulation patterns during the summer growing season bring damaging ozone episodes up the east coast to interior New England forests (Goulden et al. 1996; Munger et al. 1996). Increases in major greenhouse trace gases - CO_2, CH_4, and N_2O 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,
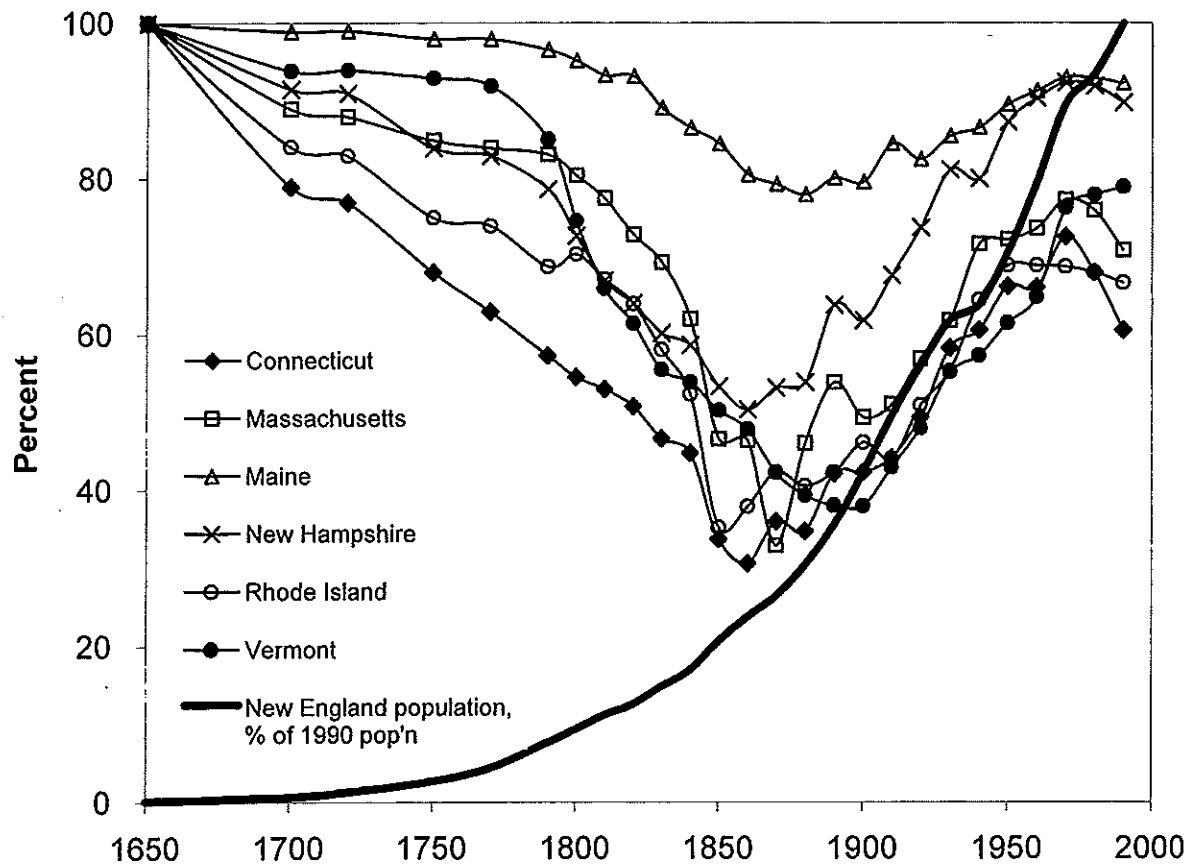
Figure 5. Forest cover and population trends for the New England states.

Massachusetts Landscape of Henry Thoreau (ca. 1830)
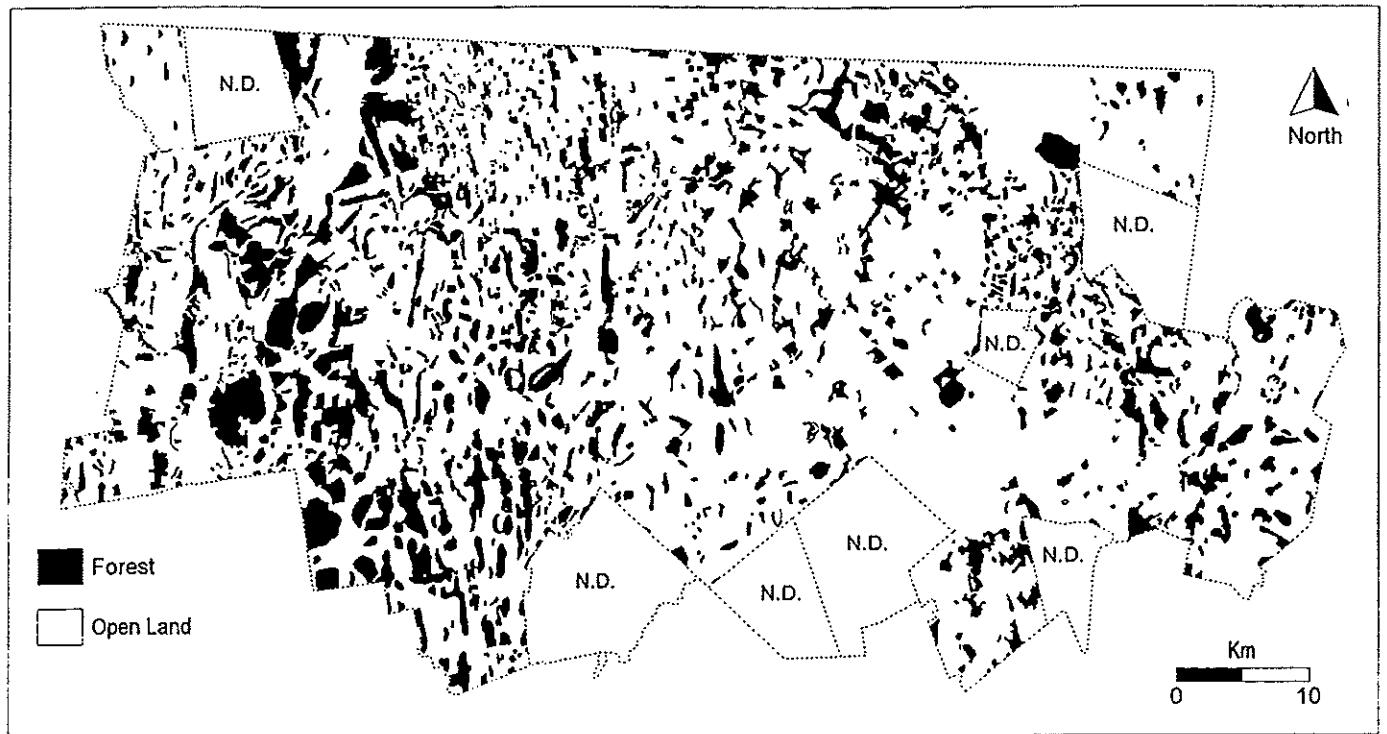
The Modern Massachusetts Landscape (ca. 1985)
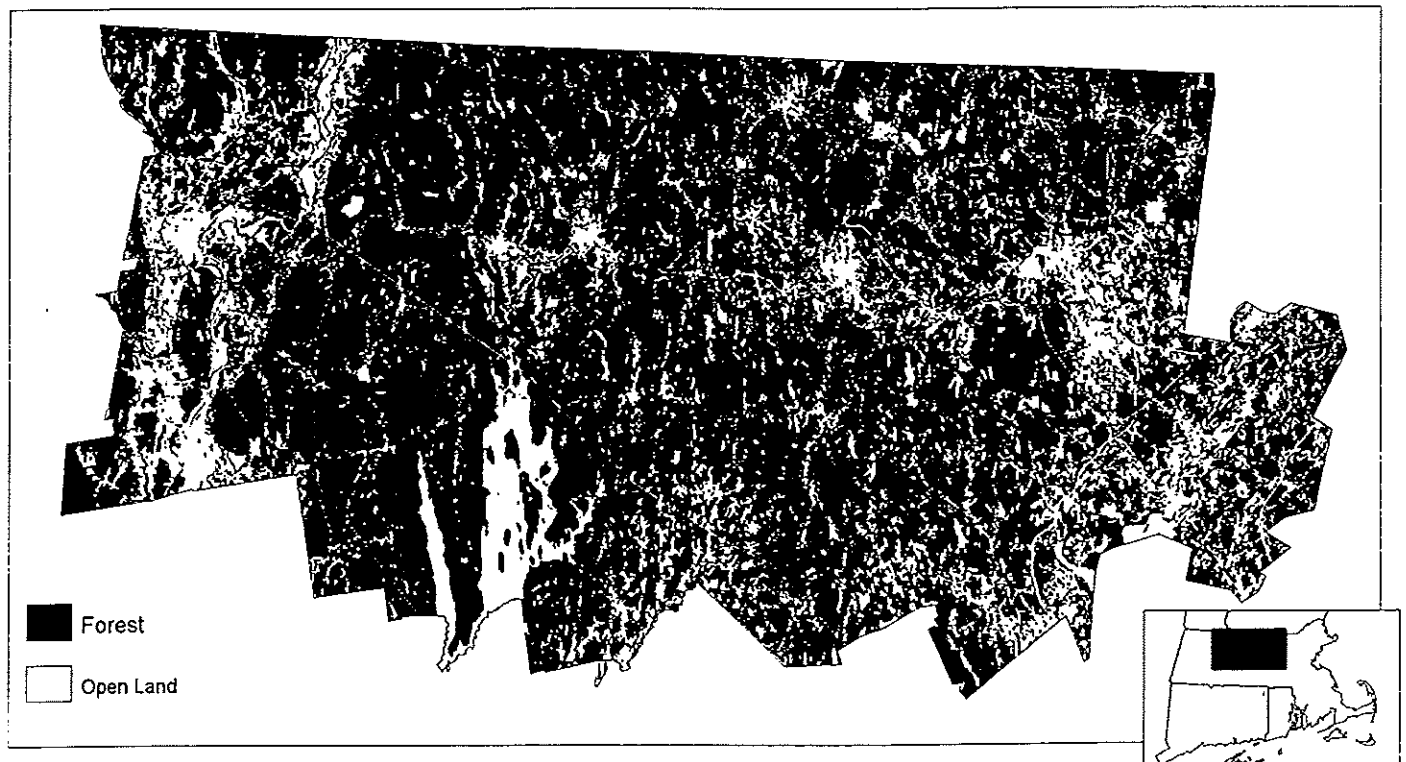
Figure 6. Change in forest cover in the central Massachusetts study region from 1830 to 1985. The town of Petersham is just east of the northern tip of the Quabbin Reservoir.

Figure 7. Hemlock woolly adelgid infestation and the range distribution of hemlock across the eastern United States
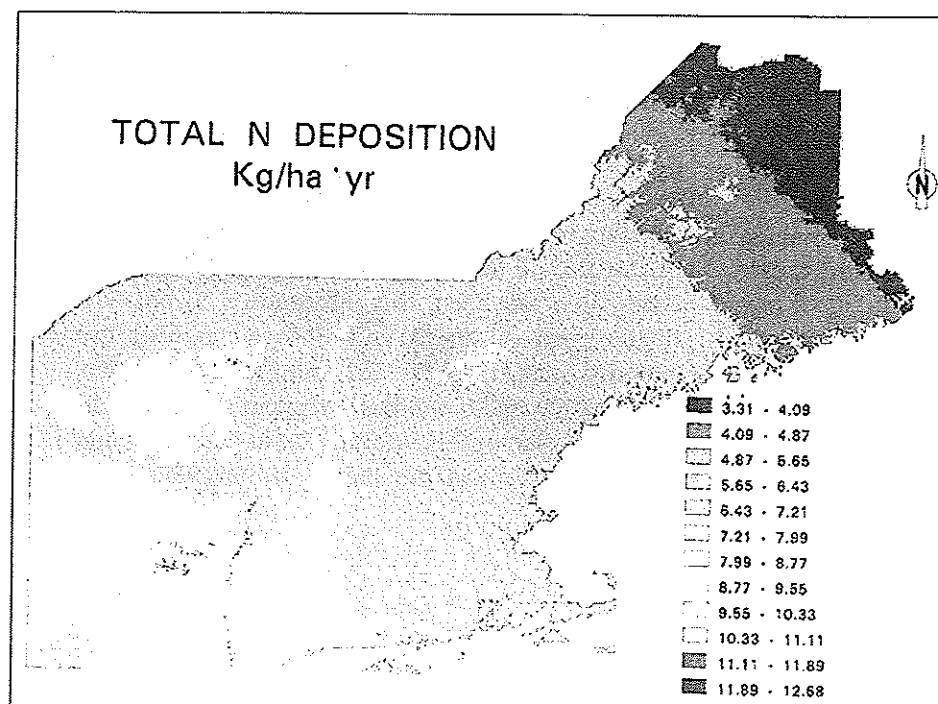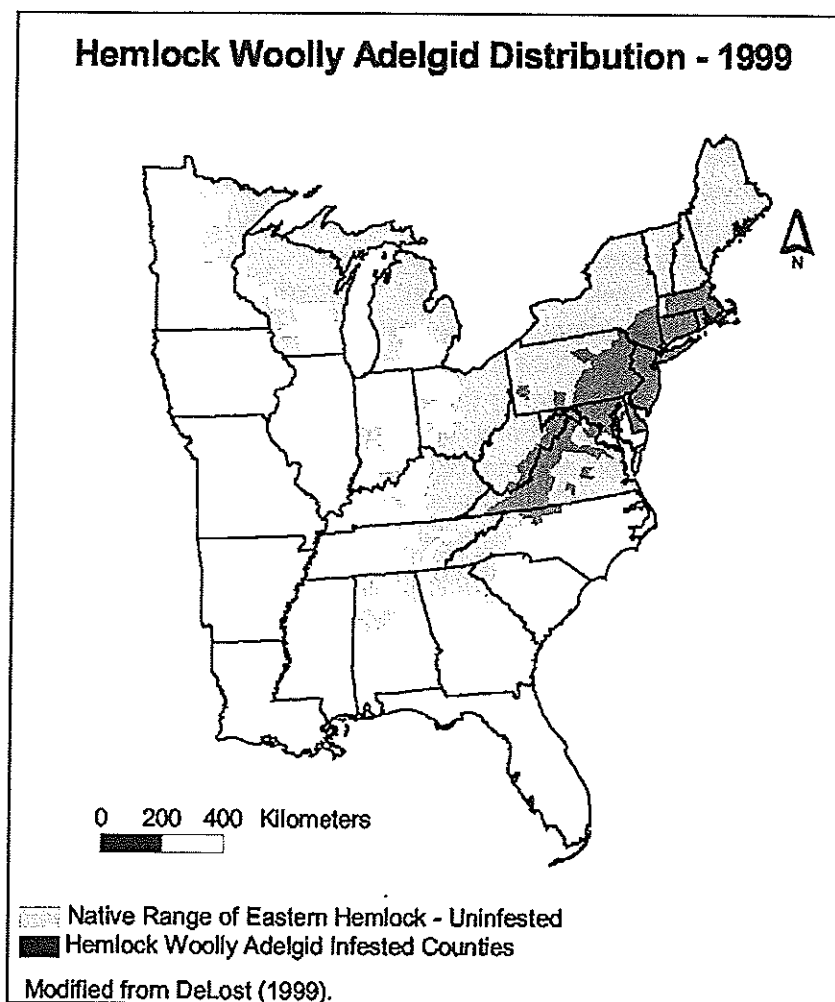
Figure 8. Geographic pattern of atmospheric nitrogen deposition across New England. Concentrations of nitrogen are strongly related to westerly air flow from major sources of human production of nitrogen elevation which controls precipitation that contains nitrogen compounds (Ollinger et al. 1995).

consequences on plant performance and ecosystem processes (Bazzaz and Miao 1993; Bazzaz *et al.* 1996). The interaction and comparative impact of these novel stresses with historically important disturbance processes is a major issue for ecologists and concern for natural resource managers.

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

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., CO_2 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.

4

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 Zebryk 1993).

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 enables 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).

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), 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 CO_2 (Berntson and Bazzaz 1997a, b). The coupling of response measurements under laboratory control with those obtained from field experiments and under natural conditions make 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). Infrastructural 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

6

HARVARD FOREST
Long-Term Study Sites

Prospect Hill
Tract

▲ Prospect Hill

ATHOL
PETERSHAM

NITROGEN
SATURATION

HEMLOCK
HOLLOW

HURRICANE
PULLDOWN

ENVIRONMENTAL
MONITORING
STATION

BLACK GUM
SWAMP

SOIL
WARMING

Riceville
Pond

Shaler
Hall

LYFORD
PLOTS

☒ = CANOPY TOWER

Tom Swamp
Tract

Route 32

Harvard
Pond

Tom Swamp Rd.

Route 122

MAPPED OVERSTORY
PLOTS

HURRICANE
PULLDOWN

Sunset Lane

DIRT
EXPERIMENT

■ The Country Store

▲ Pisgah Tract,
Winchester, NH
35 km

Petersham
Center

N

Slab City Tract
1 km

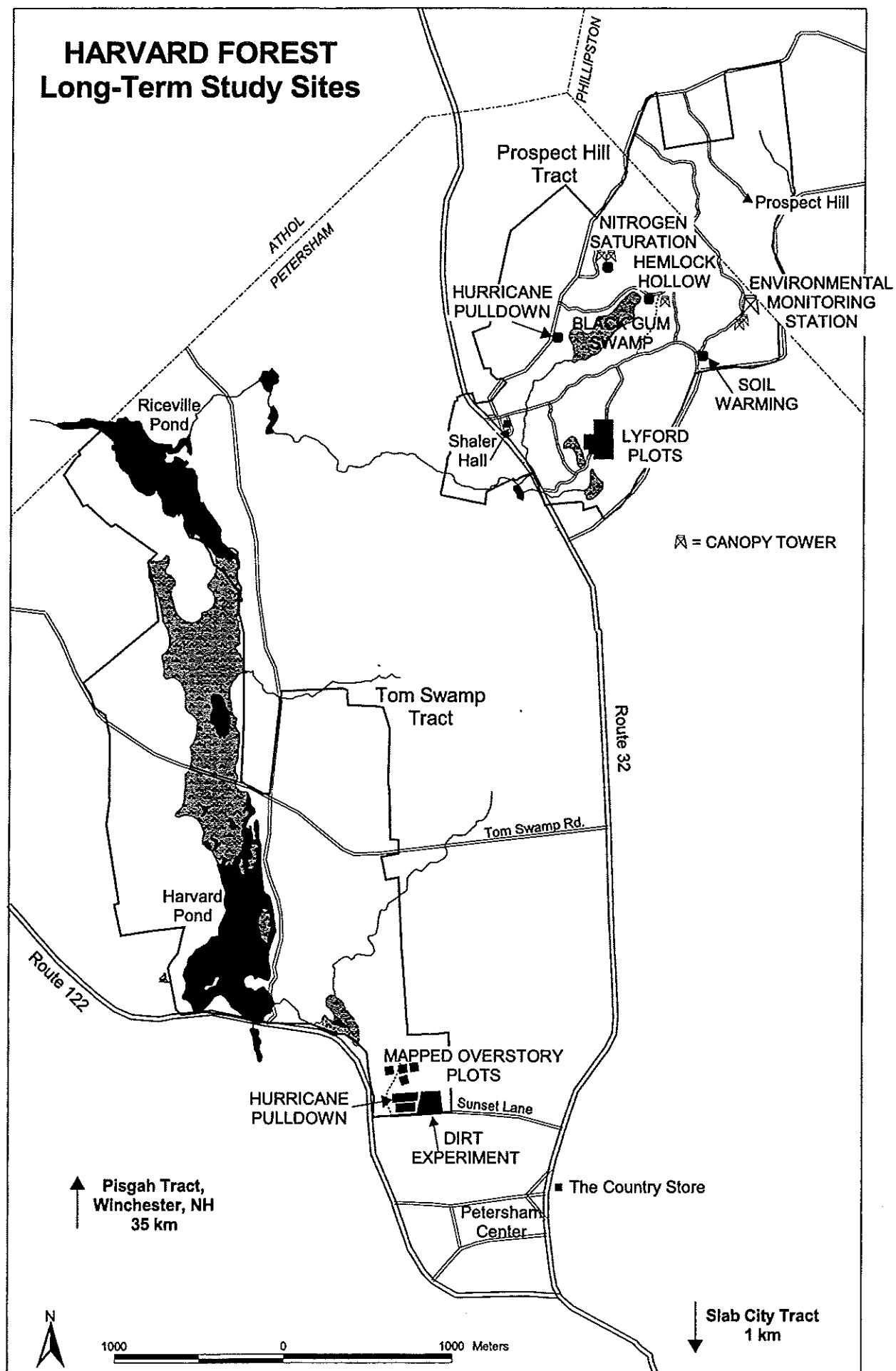1000   0   1000 Meters

Figure 9. The northern part of Petersham, Massachusetts showing major study sites in the Harvard Forest
LTER program.

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 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). Currently, this approach is being extended to the entire state, to develop a comprehensive database of land-cover change in Massachusetts.

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 comprised 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-Plotkin, Boose, Foster, Francis, Hadley, Motzkin, O'Keefe, Orwig, Parshall and Pallant), Department of Earth and Planetary Science (Barford, Munger and Wofsy), Department of Organismic and Evolutionary Biology (Bazzaz), Arnold Arboretum (Del Tredici), the Ecosystems Center at Woods Hole (Melillo, Nadelhoffer and Steudler), the

University of New Hampshire (Aber, Magill and Ollinger), College of the Holy Cross (Langtimm) and the University of Massachusetts (Field, 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 back-hoe, bulldozer, tractor, crawler, dump truck, flat bed truck, pick-up and van, are stored in garages and in a 2400 sq ft pole shed. The staff operates a wood-working shop which serves as the center for building maintenance and a sawmill is operated seasonally.

The University owns five houses and eight

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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, Kittredge *et al.* 2001). Research by investigators from the Marine Biological Laboratory Ecosystems Center (Melillo *et al.* 1983, Melillo and Aber 1984, Nadelhoffer *et al.* 1986, Steudler *et al.* 1986), the Woods Hole Research Center (Davidson *et al.* 2000), and University of New Hampshire (Aber *et al.* 1983, Aber *et al.* 1985) have provided a very strong ecosystem component. Integrated research among the many groups using the Forest has contributed to a strong interdisciplinary understanding of forest processes.

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.

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Development and Lateral Expansion of Peatlands in Central New England

R. Anderson

My project is investigating the developmental history of forested peatlands in central New England by examining two questions: 1. What is the influence of climate and topography on the development of forested peatland? 2. Is lateral expansion across adjacent uplands, i.e. paludification, an important part of this history?

With adequate moisture, peatlands form through the mechanisms of terrestrialization, when a waterbody fills with peat, and paludification, when the peat mass laterally expands onto dry land. The relative importance of these two mechanisms can be distinguished by characterizing the peat deposits and developing detailed chronologies for individual sites. Terrestrialization is identified by the presence of open-water sediments, and paludification is indicated by the progressively younger basal peat sediments towards the peatland edge.

Both climate and topography function as fundamental controls on the development of peatlands and the dynamics of paludification. When climate is a driving force across a region, multiple sites may be expected to have similar dates of peat initiation or lateral spread. Topography influences paludification by directing lateral expansion towards the shallowest slopes.

To address these questions we mapped basin morphometery and sediment stratigraphy in detail. Table 1 presents the field classification scheme utilized and interpretations of the sediments types. In addition, we took basal sediment samples running in transects from the deepest part of the basin to the upland edge and samples at sediment transitions from a core from the deepest basin of each site. These results will help interpret the role of climate in development. We are currently awaiting the AMS radiocarbon dating results.

Basin depth was defined as depth to mineral sediments, either till or glacial clay. Basin shape typically varied gradually, although in some instances there were very abrupt changes. To examine sediment patterns, an average

stratigraphy was determined for three depth zones at each site (Figs. 1, 2, and 3). If a sediment type was not present in over 10% of the sample points in that zone, it was not included in the pictorial representation.

At all three sites, the shallowest area (zone 1) was characterized by woody peat deposited directly on glacial till, which is potential evidence of lateral expansion. Zone 2 was typically composed of woody peat and shrub peat over macrofossil rich algal lake sediments (gyttja). In zone 3, the characteristic stratigraphy was woody and shrub peat over gyttja and limnic clay. There were consistently more sediments preserved in deeper basins. Site 1 Black Gum Swamp, had slightly different patterns. In Zone 2 it did not contain shrub peat and it was the only site where sedge/shrub peat was consistently found.

Overall, there were no apparent large-scale reversals from peat sediments to aquatic sediments. Sediment patterns were consistent across all three sites, suggesting similar developmental pathways.

Eddy Covariance and Biometric Measurements of CO$_2$ Exchange at the Harvard Forest

C. Barford, S. Urbanski, L. Hutyra, E. Pyle, F. Frizzell, S. Heath, J. Munger and S. Wofsy

Forest inventories and atmospheric studies both indicate that forests in northern mid-latitudes have sequestered significant atmospheric CO$_2$ since 1980, although the magnitude and distribution of the sink are the subjects of lively debate. Factors controlling net carbon uptake must be understood in order to predict future growth rates of atmospheric CO$_2$, and to enable management of regional carbon budgets. Recent analyses have attributed net C uptake to land use, fire history, longer growing seasons, and fertilization by anthropogenic CO$_2$ and N. Our carbon exchange studies at Harvard Forest use eddy covariance and biometry, two independent methods, in order to: (1) monitor net ecosystem exchange (NEE) of CO$_2$ over time scales from hours to several years, (2) place CO$_2$ exchange

Table 1 Sediment descriptions

Sediment	Description	Community Source	Source Description
Woody peat	Well-decomposed peat with large wood fragments, scattered shrub and sedge fragments	Swamp forest	Swamp forest with variable amount shrub and herb cover over moss groundlayer
Shrub peat	Abundant shrub fragments and scattered sedge fragments in a matrix of well-decomposed *Spaghnum*	Shrubby bog mat	Shrubby bog mat dominated by *Sphagnum* moss
Sedge/Shrub peat	Well preserved and defined narrow zone with a matrix of abundant sedges and scattered small woody fragments	Bog mat	Sedge dominated bog mat with scattered shrubs
Algal gyttja	Medium brown grading to green stiff fine-grained sediments; macrofossil abundance typically decreasing with depth	Standing water	Standing water with plant communities present in some areas
Limnic clay	Finely textured mineral clay	Open water	Post-glacial lake

R. Anderson

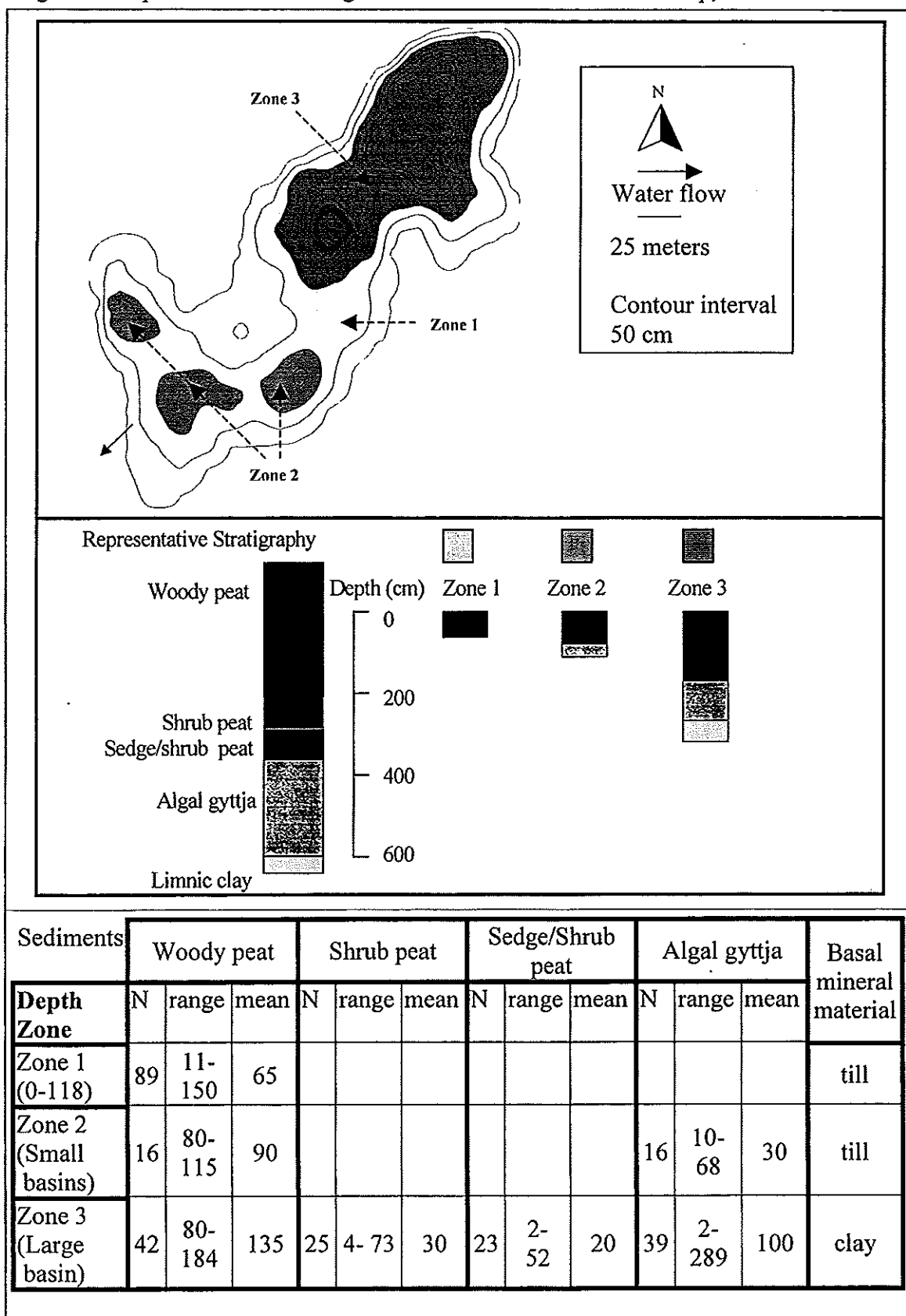# Figure 1 Depth zones and average sediments for Black Gum Swamp, Harvard Forest

Sediments	Woody peat			Shrub peat			Sedge/Shrub peat			Algal gyttja			Basal mineral material
Depth Zone	N	range	mean	N	range	mean	N	range	mean	N	range	mean	
Zone 1 (0-118)	89	11-150	65										till
Zone 2 (Small basins)	16	80-115	90							16	10-68	30	till
Zone 3 (Large basin)	42	80-184	135	25	4- 73	30	23	2-52	20	39	2-289	100	clay

R. Anderson

Figure 2 Depth zones and average sediments for Rindge Bog, NH

Sediment	Woody peat			Shrub peat			Sedge/Shrub peat			Algal gyttja			Basal mineral material
Depth Zone	N	range	mean	N	range	mean	N	range	mean	N	range	mean	
Zone 1 (0-105 cm)	31	15-100	70	1		25	1		24	1		15	till
Zone 2 (105-500 cm)	55	62-217	145	47	4-110	40				37	26-135	55	till
Zone 3 (500-1050 cm)	54	175-325	255	42	30-179	100	5	7-45	20	54	20-370	235	clay

R. Anderson

Figure 3 Depth zones and average sediments for Ellinwood Cemetery Bog, Athol, MA

Figure 3 Depth zones and average sediments for Ellinwood Cemetery Bog, Athol, MA

Sediment	Woody peat			Shrub peat			Sedge/Shrub peat			Algal gyttja			Basal mineral material
Depth Zone	N	range	mean	N	range	mean	N	range	mean	N	range	mean	
Zone 1 (0-100 cm)	46	20-98	55							4	15-30	20	till
Zone 2 (100-300 cm)	65	50-135	110	36	10-80	35	1		75	54	10-150	50	till
Zone 3 (300-600 cm)	31	115-200	155	30	17-115	65	3	10-80	40	30	55-250	175	clay

R. Anderson

measurements in the context of past land use, disturbance and current tree species demography, (3) facilitate comparisons with other forested ecosystems.

Over a seven-year period (1993-2000), annual NEE averaged -1.9 Mg C ha^{-1} yr^{-1}, with ± 50% inter-annual variations. Biometric measurements in the eddy covariance footprint compared well with long-term NEE, with 60-70% of mean NEE attributed to above-ground wood increment (AGWI), and the balance to soils and coarse woody debris. However, the ratio AGWI/(-NEE) for individual years with detailed dendrometry was 1 (1998), 0.6 (1999) and 0.7 (2000). This variation arises from asynchrony between carbon cycle processes, such as lagging respiration of leaf litter in dry years, and use of stored carbohydrate for tree growth. Tree mortality also contributed to inter-annual variation in the carbon budget (mortality = 0.4, 1.0, and 0.3 Mg C ha^{-1} yr^{-1} in 1998-2000, respectively).

Current C sequestration at Harvard Forest may be attributed to ecosystem characteristics, which have been strongly influenced by land-use and disturbance history. The 1938 hurricane and subsequent salvage allowed establishment of fast-growing, shade-intolerant northern red oak (*Quercus rubra* L.). These oaks are now approximately half mature size and constitute half of above-ground woody biomass and AGWI. Their growth rate is relatively slow for the species, which argues against significant fertilization by CO_2 or N deposition. Harvard Forest soils are strongly N-limited, which decreases the potential for CO_2 fertilization at ambient levels. Anthropogenic N deposition rates at Harvard Forest are modest, contributing on the order of 10% of the annual N mineralization rate, but chronic deposition over decades has likely contributed to C storage at the site.

We find that decadal mean C uptake rates were controlled by stand age and composition, the legacies of prior disturbance. Inter-annual fluctuations reflected ecosystem response to climate variations, through changes in litter decay rates and tree mortality. Given the broad spatial cohesion of global climate anomalies and high variability in the atmospheric CO_2 increase rate, it seems likely that year-to-year variations in C sequestration by the terrestrial biosphere are also influenced by climatic factors quite different from the ecological factors regulating long-term sequestration.

Long-Term Forest Monitoring at Harvard Forest

A. Barker Plotkin and D. Foster

Permanent plots are a key component of a long-term ecological research program. They provide direct insight into forest development, complement reconstructive and space-for-time techniques, and serve as controls to experimental areas. Sites in which the trees are mapped provide detail into the mechanisms of forest change and spatial patterns of forest dynamics. Permanent plot studies have been part of the Harvard Forest's mission since it was established.

Since 1909, quantitative forest inventories of the Harvard Forest have been undertaken every 10-30 years. One of these inventories was completed in 1937, fortuitously providing a detailed set of baseline data to compare to the post-1938 hurricane forest. In 1992, establishing permanent plots in the approximate locations of the 1937 inventory plots, and sampling all vascular species and soil chemical and physical properties augmented this inventory. This study helped to elucidate persistent effects of past land-use on current forest structure and function (Motzkin *et al.* 1999, Compton and Boone 2000). Another set of permanent plots (121 20x20m plots and a 4.5 ha stem-mapped area) was established at the Montague Sand Plain for a similar study of the effects of land-use on modern vegetation and ecosystem processes in an environment with little environmental variation (Motzkin *et al.* 1996, Compton and Boone 1998).

Research at the Harvard Tract of the Pisgah Forest, an 8 hectare area of old-growth hemlock-white pine forest in southwestern New Hampshire, has been ongoing since the 1920s. The current set of permanent forest plots (fourteen 20x20m plots) was established in 1984 (Foster 1988) and was most recently remeasured in Fall 2000. This stand was severely damaged by the 1938 hurricane; data from these permanent plots shows continuing forest development with major

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trends of increasing basal area, decreasing stem numbers and a decline in tree species richness as short-lived or light-demanding species become less important over time. At Harvard Forest, fourteen permanent plots (0.025-0.1 ha) were established to document vegetation recovery directly after the 1938 hurricane; these plots illustrate successional trends in both the trees and understory vegetation (Spurr 1956, Hibbs 1983, Mabry and Korsgren 1998).

Walter Lyford, a soil scientist at the Harvard Forest for many years, established a three hectare mapped forest site on the Prospect Hill tract of Harvard Forest. The forest is a typical mixed hardwood site with some variation in soils, particularly drainage. This area has been remeasured decadally since 1969; we plan to remeasure the site in Summer 2001, and translate the hand-drawn maps to a Geographic Information System.

The Mapped Overstory Plots and Hemlock Woodlot Plot were established in 1990 as part of the Harvard Forest Long-Term Ecological Research program. Both sites include large mapped areas. The Mapped Overstory Plots include four 50x50m plots in which all stems >5cm are mapped and measured; this area is due to be revisited soon. The Hemlock Woodlot is a 0.72 ha site dominated by hemlock. This area has been subject to intensive paleoecological reconstructions (Foster *et al.* 1992, Foster and Zebryk 1993). The site was remeasured in 1999 with particular attention paid to evaluating the vigor of the overstory hemlock trees. This should provide valuable baseline data in anticipation of the arrival of the hemlock woolly adelgid to the site. So far, no evidence of adelgid infestation has been found.

These sites help us develop an understanding of the long-term processes that affect forest development and the role of disturbances on these systems (e.g., hurricanes and pathogens). Such studies become ever more valuable over time.

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Motzkin, G., D.R. Foster, A. Allen, J. Harrod and R.D. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecological Monographs 66: 345-365.

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Understory Dynamics in the Experimental Hurricane

A. Barker Plotkin and D. Foster

The hurricane experiment at Harvard Forest was designed to simulate the impacts of a catastrophic storm like the 1938 New England Hurricane to mature hardwood forest. In October 1990, canopy trees were pulled over using a winch, resulting in direct and indirect damage to nearly 70% of the stand. In addition to the dramatic effects on the arboreal layer of the stand, this disturbance altered conditions in the forest understory. More light reached the forest floor for several years, and uprooting of trees resulted in patches of disturbed soil. After the manipulation, pits and mounds covered 8% of the site (Cooper-Ellis *et al.* 1999). We have periodically assessed the shrub and herb layer response to the manipulation for ten years, from 1990 – 2000.

Composition and abundance of understory vegetation was assessed in 1990 (before the manipulation), 1991, 1992, 1995 and 2000 in the experimental and control sites within nested $10m^2$ (shrubs) and $1m^2$ (herbs) plots placed along each of three transects in the 0.8 ha pulldown site and one transect in the 0.6 ha control area. In addition to cover estimates for individual species and total cover of life-form categories, the height of the tallest individual shrub of each species on each plot was recorded and cover of substrates (leaf litter, woody debris, rock, exposed soil, pit and mound) was estimated.

Most species were found in the experimental area both before and after the manipulation, but some species turnover has been observed throughout the ten years (Table 1). Two club moss species dropped out of the experimental site, and a few other species disappeared from the site but have returned. Several new species, many of which tend to colonize disturbed areas, have come in to the site. Some were transients, but others have persisted. Many of these species were found in plots containing a pit or mound (Cooper-Ellis *et al.* 1999). Two exotic and potentially invasive species (*Lonicera morowii* and *Celastrus orbiculatus*) have been found in one part of the experimental site in recent years; this area will be monitored closely but since the forest canopy is

re-establishing well, these species are not expected to greatly increase.

A few species showed changes in abundance after the manipulation. *Rubus* species appeared in the experimental site, probably from buried seed; by 2000, they had begun to decline (Fig. 1). Hay-scented fern (*Dennstaedtia punctilobula*) and starflower (*Trientalis borealis*) increased markedly after the manipulation, but are also now declining, indicating that after 10 years, understory conditions in the experimental site may be more similar to pre-disturbance conditions. However, two abundant shrub species, *Amelanchier* spp. and *Corylus cornuta*, continue to increase. When species are grouped more broadly in life-form classes, tall shrubs and saplings show higher abundance in the experimental site versus the control (Fig. 2).

Overall, changes in understory flora in the hurricane experiment are relatively modest and concentrated in areas with disturbed soil. The landscape context of the site, which is surrounded by intact forest, and rapid recovery of the forest canopy via advance regeneration and sprouting, contribute to this stability.

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Forest Development Ten Years after an Experimental Hurricane

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The hurricane experiment at Harvard Forest was designed to simulate the impacts of a catastrophic storm like the 1938 New England Hurricane to mature hardwood forest. In October 1990, canopy trees were pulled over using a winch, resulting in direct and indirect damage to nearly 70% of the stand. One goal of the experiment is to study regeneration mechanisms and changes in species composition. In summer 2000, we surveyed all stems that had grown above

Table 1. Understory composition in the experimental area by year before (1990) and af (1991, 1992, 1995, 2000) the manipulation. Most graminoids are not included. _ _ _ inc that species was probably present but missed in sampling. Species present in all years ᐧ *Amelanchier cf. canadensis, Amphicarpa bracteata, Aralia nudicaulis, Ariseama atrorut Aster acuminatus, Aster divaricatus, Athyrium felix-femina, Berberis thunbergii, Brachy erectum, Clintonia borealis, Corylus cornuta, Crataegus* spp., *Dennstaedtia punctilobula lonicera, Dryopteris carthusiana / intermedia, Gaultheria procumbens, Ilex verticillata, L canadensis, Lycopodium obscurum, Lysimachia quadrifolia, Maianthemum canadense, ; virginiana, Mitchella repens, Onoclea sensibilis, Osmunda cinnamomea, Osmunda clayt Prenanthes* spp.,*Rhododendron nudiflorum, Rubus hispidus, Smilacina racemosa, Smil Thelypteris novaboracensis, Trientalis borealis, Uvularia sessilifolia, Vaccinium angusti Vaccinium corymbosum, Viburnum acerifolium, Viburnum cassinoides, Viburnum recog; Viola blanda.*

|	1990	1991	1992	1995	2000
Lycopodium clavatum	—				
Lycopodium lucidulum	—				
Monotropa uniflora	—			—	—
Polygonatum pubescens	—	—			—
Vitis spp.	—	—			—
Celastrus scandens		—			
Cirsium spp.		—			
Houstonia caerulea		—			
Hypericum punctatum		—			
Pycnanthemum spp.		—			
Erechtites hieracifolia		—	—		
Eupatorium spp.		—	—		
Hydrocotyle americana		—	—		
Lobelia inflata		—	—		
Luzula multiflora		—	—		
Epilobium coloratum / ciliatum		—	—	—	
Potentilla simplex		—	– – – –	—	—
Rhus radicans		—	—	—	—
Rhus typina		—	—	—	—
Rubus allegheniensis		—	—	—	—
Rubus idaeus		—	—	—	—
Rubus odoratus		—	– – – –	—	—
Solidago caesia		—	– – – –	—	—
Pteridium aquilinum			—	—	—
Sambucus pubens			—	– – – –	—
Lonicera morrowii				—	—
Apocynum androsaemifolium				—	—
Solidago rugosa				—	—
Celastrus orbiculatus					—

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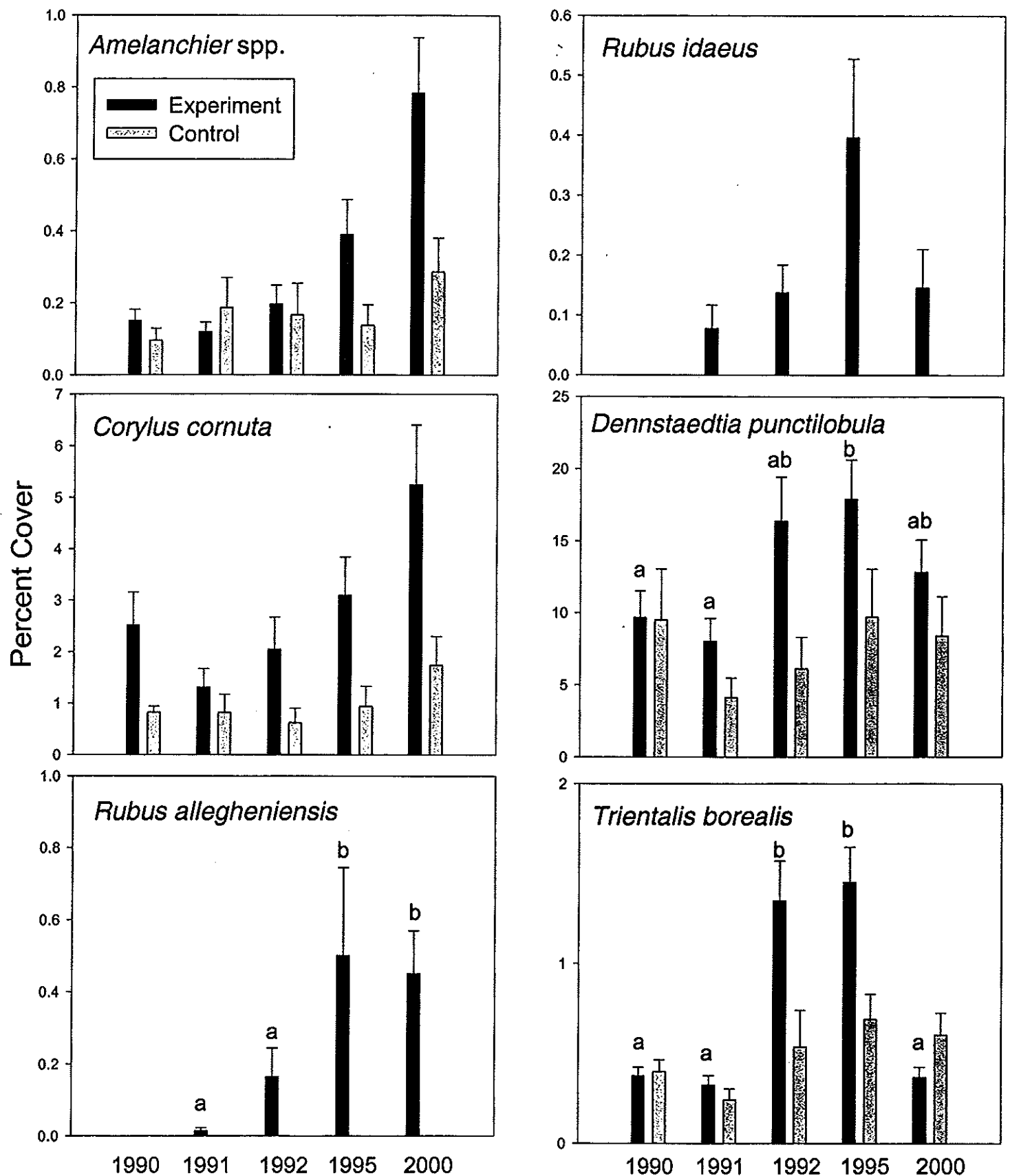
Figure 1. Changes in average percent cover of major shrub and herb species. Error bars are +1 S.E. Within each panel, experiment means (solid bars) that do not share the same lowercase letter differ significantly (p < 0.05).
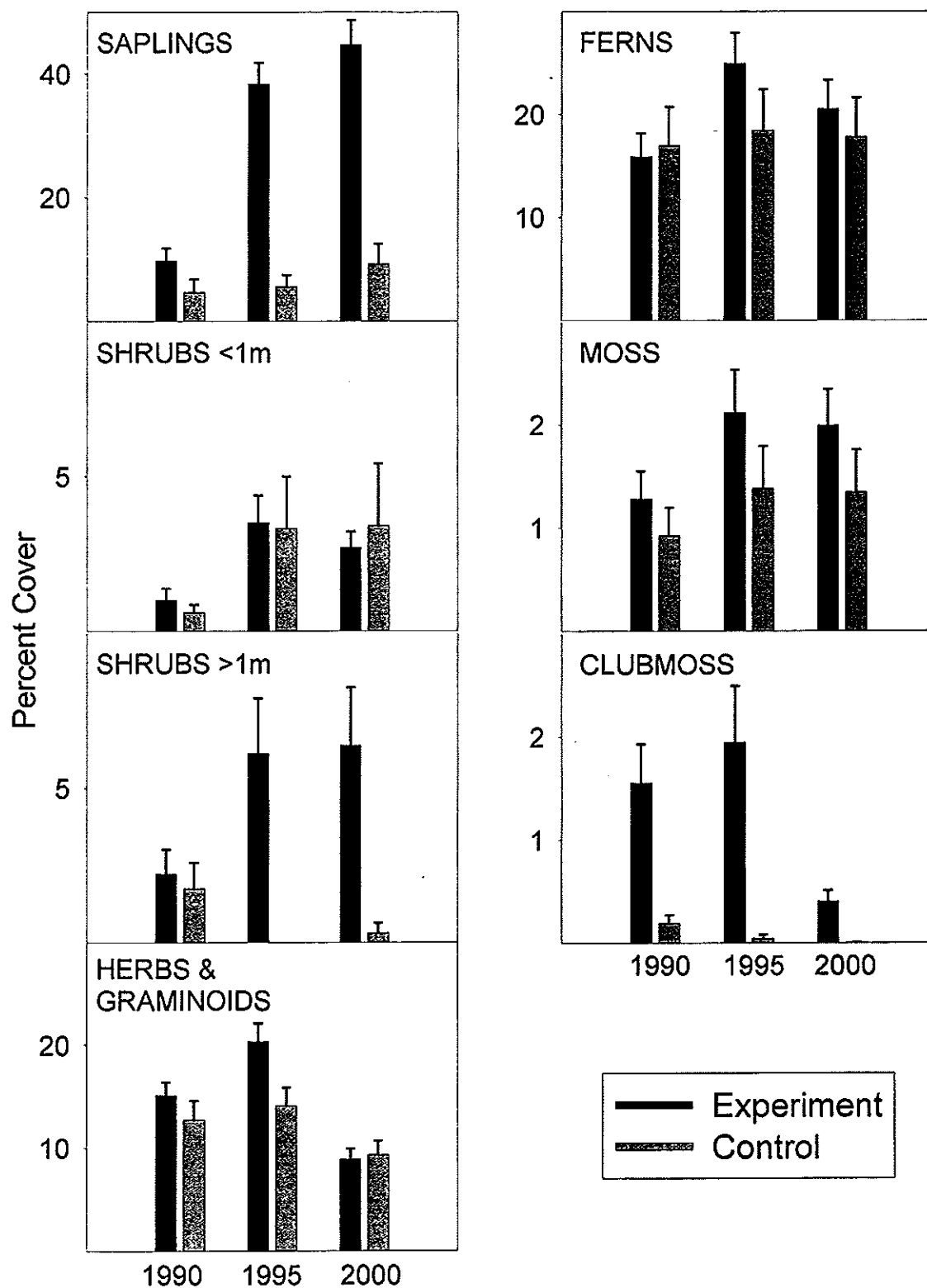
Figure 2. Changes in cover of life forms over time. Saplings and shrubs >1m increased significantly in the experimental site compared to the control. Error bars are +1 S.E.

Table 1. Tree density and basal area over time in the experimental hurricane and control plots.

	Experiment		Control	
	Density (stems/ha)	Basal area (m²/ha)	Density (stems/ha)	Basal area (m²/ha)
1990	920	27.8	1053	29.4
1993	489	12.4	982	28.9
1996	823	11.2	937	31.6
2000	980	Not available	829	Not available
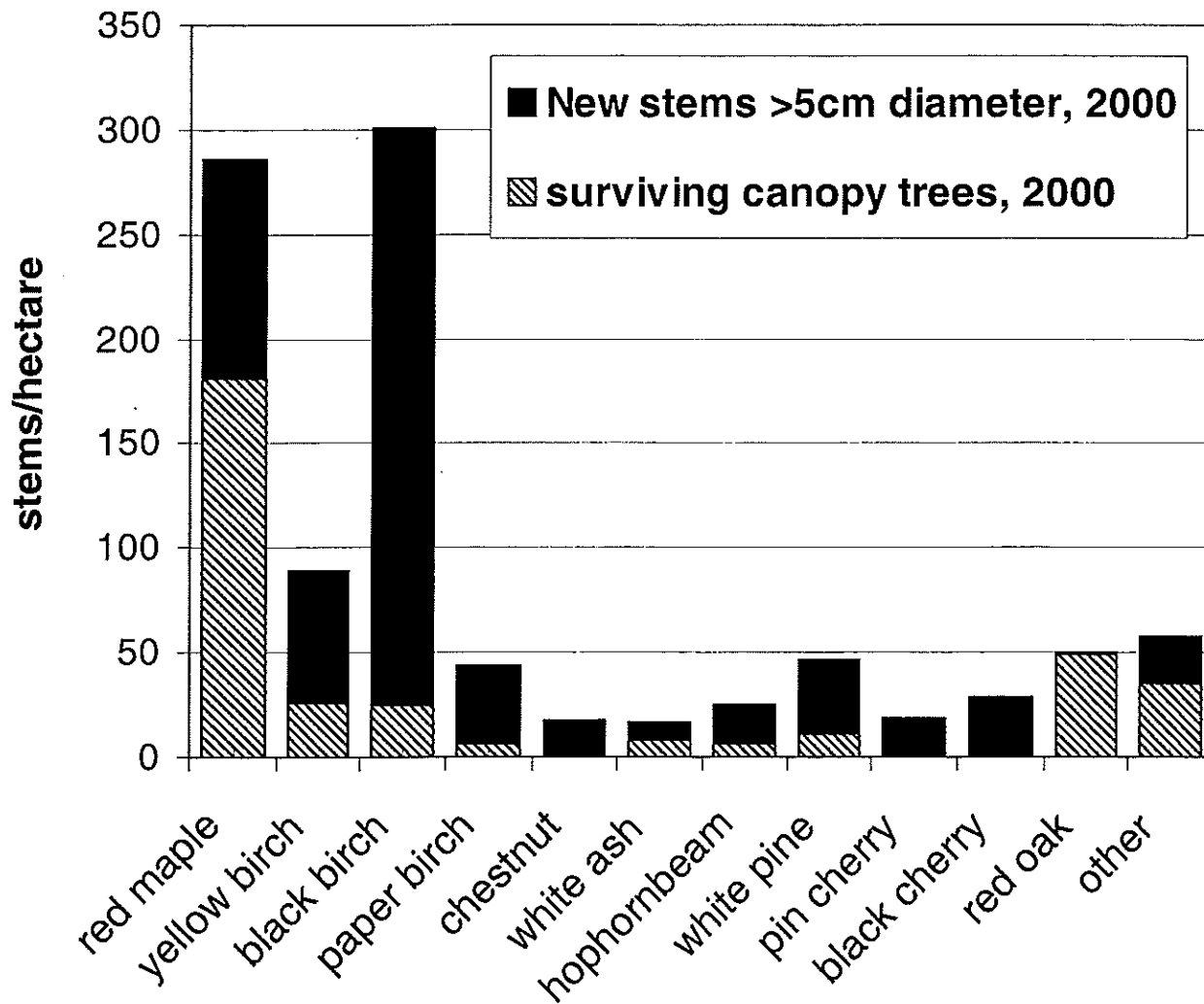
Figure 1. New stems that have grown above 5 cm diameter since the manipulation, and surviving canopy trees in 2000. Other species include striped maple, sugar maple, hickory species, American beech, American mountain-ash and eastern hemlock.

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5 cm dbh across the experimental and control sites.

The number of new stems is far greater in the experimental site (630 stems/ha) than in the control (27 stems/ha). The importance of sprouts (72 stems/ha; 12%) is less than that of saplings (558 stems/ha; 88%). Most of these saplings are advance regeneration, stems that were present in the understory of the stand before the manipulation. The greatest number of new stems was found in the center of the site with fewer to the north and south, possibly an edge effect.

Stem density has recovered to original levels (Table 1), but species composition has shifted in the experimental site from red oak – red maple to a black birch - red maple forest. Regeneration in the manipulation is dominated by black birch (*Betula lenta*), followed by red maple (*Acer rubrum*) and yellow birch (*Betula alleghaniensis*) (Fig. 1). Red oak (*Quercus rubra*) was a dominant species in the pre-manipulation forest, but only one red oak has grown into the 5 cm size class since 1990. This compositional shift is dampened somewhat by the component of the original canopy that has survived the manipulation. Surviving canopy trees form the new stand along with stems recruited since the manipulation. Currently, more than one-third of trees ≥ 5 cm dbh are survivors from the original overstory. These survivors include a few low-vigor prostrate stems, bent and leaning trees that are rebuilding their crowns, and vigorous undamaged trees. The largest trees in the stand are undamaged red oaks (46 stems/ha), and many smaller red maples have persisted as well. The current forest stand has a multi-layered structure, with dense new stems forming a lower stratum below a middle stratum of small surviving and recovering trees and scattered large emergent stems from the original stand.

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

D. Barnes and S. Wofsy

The Montreal Protocol on Substances that Deplete the Ozone Layer in 1987 and its subsequent London (1990) and Copenhagen (1992) Amendments mandated control measures on the production and consumption of ozone-depleting substances (UNEP, 1985-1997). The majority of the substances, including CFC11, CFC12, CFC113, Halon-1211, CCl_4, and CH_3CCl_3, were scheduled for 100 percent reductions in production and sales by 1 January 1996 in developed countries. The success of the Protocol in the U.S. has thus far been determined by inventory estimates only. Given that today emissions violate international agreements, they may not be reported willingly. The quality of these inventories and the recent urban pollution history has yet to be independently established for the post-1996 ban years.

To address this deficiency, this study provides an independent measure of emissions from a major emitting region of ozone-depleting species for the years 1996 through 1998, the first three years after the full implementation of the Montreal Protocol. The measurements were taken every 24 minutes at Harvard Forest, MA, downwind of the Northeast urban-industrial corridor, including the greater metropolitan region of New York City. Using the well-documented EPA carbon monoxide emissions, which are reported on a per county basis, and a composite PCE inventory, derived from the EPA/TRI records and the McCulloch and Midgley sales-based country-level tallies (McCulloch *et. al.* 1996 and P. Midgley, pers. comm.), we estimate the annual and seasonal urban/industrial emissions of CFC11 (CCl_3F), CFC12 (CCl_2F_2), CFC113 ($C_2Cl_3F_3$), methyl chloroform (CH_3CCl_3), and halon-1211 ($CBrClF_2$) all on a per capita basis. The results of this study have confirmed the accuracy of the above listed inventories for the New York City – Washington, D.C. corridor (Barnes 2000).

The annual urban pollution emissions for each species indicate that a number of the species exhibit distinct inter-annual trends. Our data indicate that, following the full Montreal Protocol ban in 1996, emissions of CFC12, CFC113, and CH_3CCl_3 have continued to decline, as expected. Halon-1211, a fire-extinguishant for which no adequate replacement has yet been found, does not exhibit any distinguishable pattern. For CFC11, the trend is positive, which is a surprise especially given the ban on its production by the

Montreal Protocol, the decline in its atmospheric growth rate witnessed as early as 1989 (Elkins *et. al.*, 1993), and its close seasonal correspondence to CFC12 whose emissions are decreasing, not increasing.

Also measured over the three year experiment was molecular hydrogen, a major trace gas with an ambient concentration of around 530 ppb. Although a major by-product of combustion that is involved in a range of processes that directly impact on the levels of OH and O_3 in the troposphere and stratosphere, it is not itself deleterious to the atmosphere and has received little attention in the literature.

With a number of field stations reporting a correlation between observed H_2 enhancements and local traffic flow (Schmidt *et. al.* 1970; Scranton *et. al.* 1980; Novelli *et. al.* 1999), the focus of anthropogenic H_2 source studies has centered almost entirely on automobiles, with little reference to other technological processes. Remarkably, the only direct evidence of the presence of H_2 in automobile exhaust dates back to a motor emission study by the Society of Automotive Engineers in 1965 (*Starkman et. al.* 1965), before the era of emission standards, fuel additives, catalytic converters, and other automotive changes. At that time, *Starkman et al.* attributed the hydrogen they observed to the well-known water-gas equilibrium reaction found in engines, with a H_2/CO yield of about 40% (Penner *et. al.* 1977).

We use here our three years of continuous H_2 and CO measurements, taken downwind of the major urban/industrial region of the New York City–Washington, D. C. corridor, to provide robust estimates for H_2/CO ratios by season for polluted air in the late 1990s. Despite changes in the automotive industry and advances in our understanding of the intricacies of tropospheric chemistry, the average H_2/CO value of 0.403 ppb/ppb (or 0.0290 kg/kg) observed at Harvard Forest for winds issuing from the southwest is entirely in harmony with that predicted by Starkman *et. al.* (1965) from the water-gas reaction.

On the basis of the EPA CO emissions inventory for 1996 (www.epa.gov/ceis), we can create county-level maps of H_2 fossil fuel releases for the Northeastern U.S. in 1996 (Fig. A). As with CO, for which the anthropogenic emissions

are likewise dominated by road transportation and combustion, those counties which contain or neighbor large cities are responsible for the bulk of the H_2 anthropogenic output. The largely rural counties in Virginia and West Virginia have the lowest absolute H_2 fossil fuel emissions. On a per capita basis (Fig. B), New York City and environs have the lowest emission rates and are surrounded by counties whose values increase slowly with distance from New York City. The greatest per capita emitters are at the furthest distances from New York City, predominantly in Virginia and West Virginia. That such a pattern should emerge between H_2 and population is not unexpected given that cars are a major source of anthropogenic emissions for both gases. The low per capita H_2 emissions for New York City in particular may be explained by the high population density and the greater reliance on public transportation in that area.

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H2 Emissions
(kg/km^2)

13 to 306
306 to 985
985 to 3516
3516 to 6150
6150 to 81352

H2 Emissions
(kg/person)

1.9 to 4.8
4.8 to 8.1
8.1 to 12.3
12.3 to 17.3
17.3 to 87.6
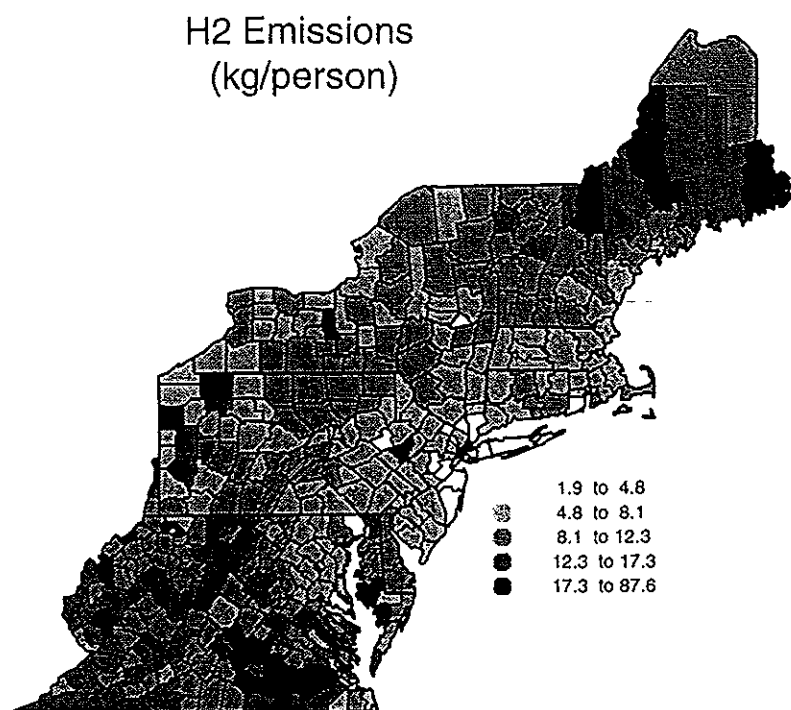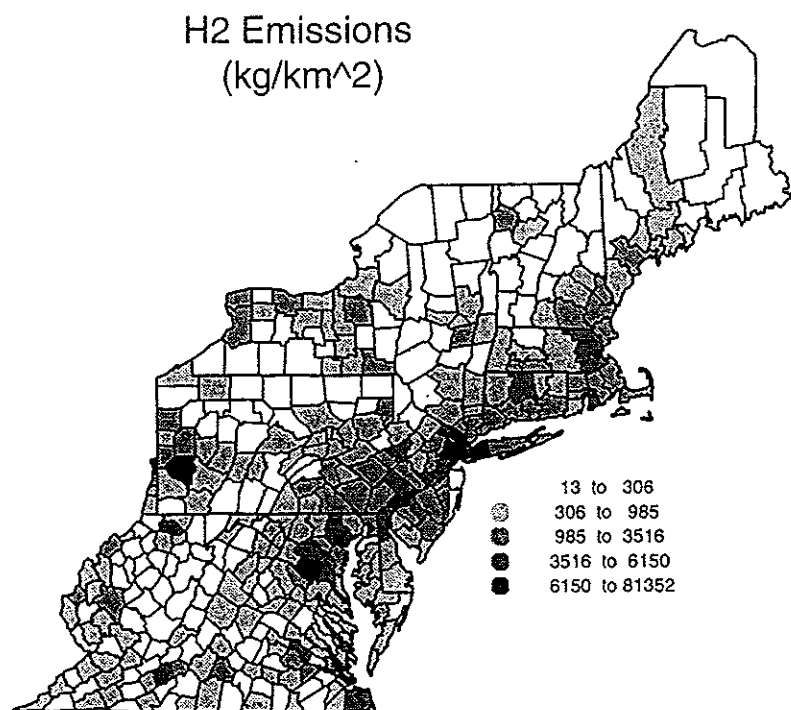
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Is Increased Nitrogen Availability Predictive for Long-term Forest Carbon Sequestration?

G.A. Bauer, R. Minocha, G. Berntson, J. Aber and F. Bazzaz

Temperate forests are predicted to play a key role as important sinks for atmospheric carbon dioxide. This sink could be enhanced by atmospheric nitrogen (N) deposition. However, the predicted response may vary for deciduous and coniferous trees due to differences in photosynthetic nitrogen use efficiency. Experimental evidence to suggest 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 Chronic N Experiment, where a 12-year 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 decoupling 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. Gas exchange measurements confirmed this observation, showing that trees from the high N treatment had significantly lower photosynthetic capacity than the control trees. These results indicate that the increase in leaf N is not accompanied by a greater capacity for carbon assimilation in the high N treatment.

Investigating the Role of History in the Modern Distribution and Species Composition of the Rich Mesic Forest Community in Western Massachusetts

J. Bellemare, G. Motzkin and D. Foster

The effects of historical factors, such as past land-use, on modern plant species distributions in eastern North America has proved difficult to document, due in part to a lack of records detailing historical land-use. Despite this difficulty, the importance of understanding the long-term impacts of human disturbance on cannot be overstated. Our research has focused on a single upland community type, rich mesic forests (RMF), which are known for their diverse assemblage of woodland herbs, including numerous species with limited dispersal ability. The RMF community is considered to be a northern variant of the Mixed Mesophytic Forest Type of the southern Appalachian Mountains as described by Braun (1950). In Massachusetts, RMF sites are most common in the western portion of the state, where their distribution largely coincides with the occurrence of calcareous bedrock.

The RMF community has been the subject of previous speculation as to the effects of past human land-use on woodland herb species,

however the absence of detailed land-use records throughout much of the eastern United States has precluded an accurate assessment of these effects. Unlike other regions, land-use maps of our study area in western Massachusetts do exist and allow for the spatial reconstruction of forest cover during the past two centuries. As in much of southern New England, forest cover in the study area decreased rapidly following European settlement, reaching a low of 15-30% in the early 19th century. During the past century forest cover has come to dominate the landscape as numerous farms have been abandoned.

Vegetation sampling on sites with differing histories has enabled us to document varied species responses to past land-use. These responses appear to result from species specific life history traits, including dispersal mode, growth form and tolerance to exposure. Herb species with seeds lacking adaptations for dispersal and those with ant-dispersed seeds tend to be strongly associated with primary forest and bedrock outcrop refugia in secondary forest, whereas endozoochorous and wind dispersed species tend to be present in both primary and secondary stands. Notable exceptions to this pattern do exist: *Sanguinaria canadensis*, an ant-dispersed species often considered an indicator of RMF, has persisted and thrived in hedgerows allowing for its successful re-colonization of many secondary stands. The species is now significantly more frequent in secondary forest and hedgerows than in primary forest. Spatial data from the study area stresses the long-term significance of small-scale refugia, such as bedrock outcrops and hedgerows, which have allowed for the persistence *in situ* of certain woodland plant species in otherwise heavily modified agricultural landscapes.

Meteorological Station

E. Boose

The new Harvard Forest Meteorological Station became operational on 11 Feb 2001. The new station records air temperature, relative humidity, dew point, precipitation (water equivalent of snow), global solar radiation, barometric pressure (corrected for elevation = 340m), horizontal scalar wind speed, vector wind speed, peak gust speed (1-second), vector wind direction, standard deviation of wind direction (wind measurements at 10m height), and soil temperature (10cm depth). Instruments are scanned once per second, and hourly and daily values are calculated and stored by a datalogger.

The station is connected to Shaler Hall via underground conduit, which contains 110VAC (for power supply and heated rain gage) and category 5 data cable (for communication with computer via short-haul modem). Hourly and daily data are posted on the Harvard Forest web page. Recent data are updated hourly but are not checked. Older data are checked and missing, questionable, or estimated values are flagged (following methods of LTER ClimbDB project). A log of events affecting station measurements (e.g., instrument repair and calibration, ice storms, lightning) is also posted.

The new station is located in the pasture north of the Community House, about 200m north of the old station next to Shaler Hall. The new site was chosen to minimize the angle of surrounding trees above the horizon for solar radiation and wind measurements (currently 15-25 degrees from the station at breast height). The old station, which measures daily minimum and maximum temperature and daily precipitation (8am-8am observation period), will be run in parallel with the new station for a full year and then discontinued.

Response of CO$_2$ Release from O-horizon During Drying and Wetting Cycles

W. Borken, E. Davidson, K. Savage and K. Angeloni

The water content of O-horizons in temperate forests varies widely during summer droughts and rainfall events, and this temporal variation in water content may affect microbial decomposition of organic matter and release of CO$_2$. Low water content can limit the growth rate and activity of microorganisms, as well as the

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diffusion of nutrients and carbon substrates in water films. It is well known that wetting of dry mineral soil can cause a pulse of CO_2 release due to altered availability of carbon and microbial activity. However, little attention has been paid to the short-term response of microorganisms in O-horizons to drying and wetting cycles.

In a laboratory study, we measured CO_2 release of dry O-horizon from the mixed hardwood stand at Harvard Forest following wetting. The amounts of added water were 0,5, 1.0, 2.0, 4.0 and 8.0 mm and were sprayed onto the surface in less than 5 min. Only the 8.0 mm wetting treatment required two wetting events that were applied within 1 hour. Air temperature was constant (17 ±1°C) during the entire experimental period. Soil moisture (g g^{-1}) was semi-quantitatively measured in the litter layer at 2 cm and 5 cm depths using DC-halfbridges.

The CO_2 release of the dry O-horizon was less than 10 mg C m^{-2} hr^{-1}. Surprisingly, a pulse of CO_2 release peaked in less than 5 min after the water was added to the dry O-horizon (Fig. 1). Similar peak CO_2 fluxes were observed at water additions of 0.5 mm (32 mg C m^{-2} hr^{-1}), 1.0 mm (44 mg C m^{-2} hr^{-1}), and 2.0 mm (35 mg C m^{-2} hr^{-1}). Larger peak CO_2 fluxes were observed at 4mm (50 mg C m^{-2} hr^{-1}) and 8mm (68 mg C m^{-2} hr^{-1}) water additions. The rate of CO_2 release dropped with decreasing water content to pre-wetting levels in 1-10 days, depending on the amount of water that had been added. The rather short-term CO_2-peak observed after small water additions indicates a certain amount of easily decomposable carbon that becomes available for microorganisms after the O-horizon is wetted. Because of the relatively strong response at only 0.5 mm water addition, which mostly wetted only the surface layer of intact leaf litter, it is likely that much of the easily decomposable carbon mineralized after wetting resides in this surface litter layer. Pulses of CO_2 emissions in the range of 30-70 mg C m^{-2} hr^{-1} represent 10-30% of average summertime emissions. Our results indicate that even small rainfall amounts significantly increase the CO_2 emissions of dry forest soils.

The Historical Landscape of Southern New England in Early Records

J. Burk, G. Motzkin and D. Foster

In order to determine forest composition across southern New England at the time of European settlement, we have been gathering data from a variety of early references. The majority of towns in the region cited "witness" trees as reference points in early land division (proprietor), deed, town boundary, and road surveys. The most useful and detailed sources are proprietor and deed records, which usually have more citations and cover a greater geographic area than road and boundary surveys. Records were located at a variety of sources including town halls, libraries, historical societies, registries of deeds, state archives and libraries, and individual residences.

In general, tree citations were more common in towns settled during the eighteenth century and less so in the coastal and valley areas which were settled earlier. Settlement and town division histories were compiled for all three states, and several historical town maps were added to the archives.

Near-complete proprietor coverage was gathered in Massachusetts for the North and South Shore communities. Road and boundary surveys were tallied in the greater Boston area, where proprietor records did not cite trees or were missing. For coastal towns such as Boston and Gloucester, records dated as far back as the 1620s. In all, nearly 58,000 trees were tallied from 292 of the 351 current towns (84 %). Eight books had over 2,000 trees, with the largest total 3,155 in Andover.

In Connecticut, 138 of 186 (74 %) towns had useful records totaling 44000 citations. Three surveys had over 3,000 trees, with 4,500 recorded in Killingworth alone. Near complete coverage was found east of the Connecticut River and the northwest hills, with gaps in Hartford and Fairfield Counties, where trees were not used as reference markers in early surveys. Dates ranged from mid-1630s for coast and Connecticut Valley towns to 1830s for some hill towns. Coverage was also found for the majority of Rhode Island, with the only gap in the southeast coast region
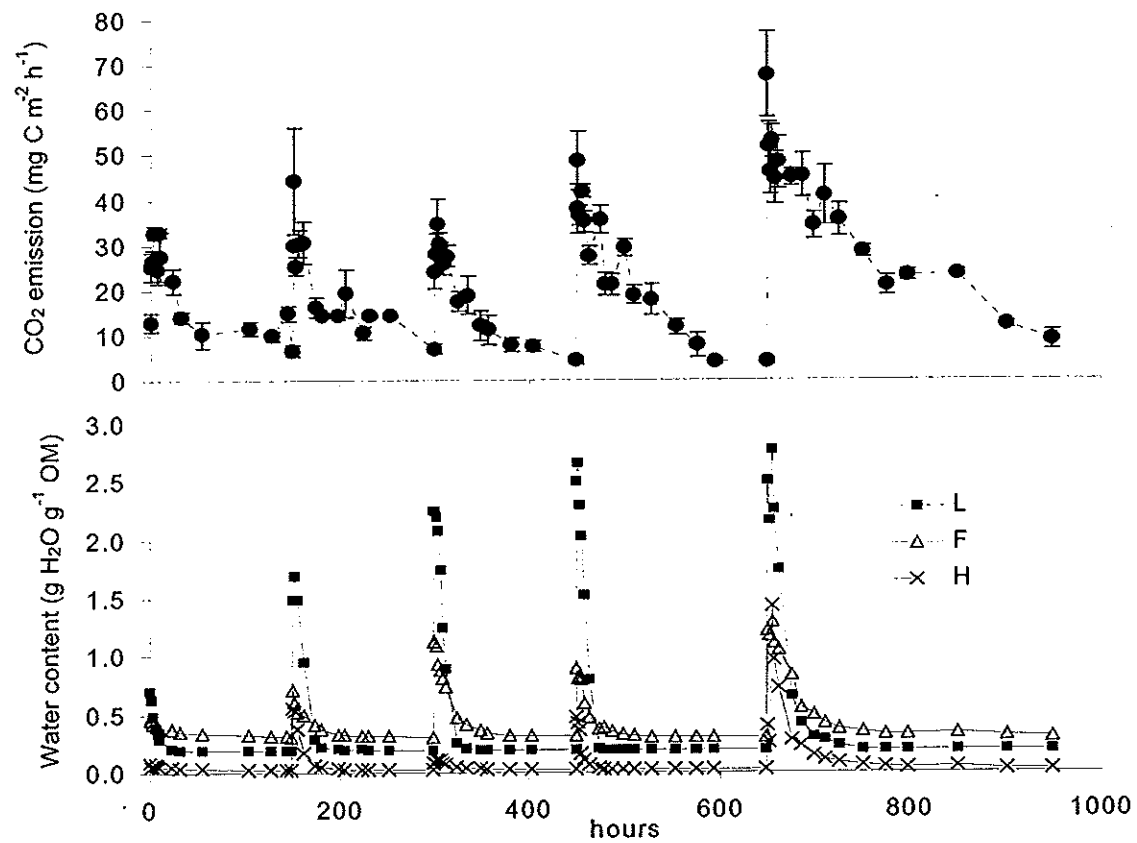
Figure 1: CO_2 release of the total O-horizon and water content in the L, F and H layer from Harvard Forest during drying and wetting cycles.

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including Newport, Jamestown, and Block Island. Large data sets were compiled from the Providence, Little Compton, and Tiverton records. Data from southeast Massachusetts records were used for several towns annexed to Rhode Island in the eighteenth century. In Rhode Island surveys, 33 of 39 (85 %) had large data sets, totaling 2,700 trees.

In addition to the witness tree project, in order to facilitate analysis of Massachusetts historical information, a number of databases were created from 19th and early 20th C historical records. These data represent an unusual data source and provide the first opportunity to evaluate controls on vegetation composition in the early period. Census data for every town from 1801 and 1845-1905, which included agricultural land-use and woodland acreage, were summarized in a large table. A separate database was created for forest cutting data by species from information in the 1885 census. Summary tables were created for the early 1900s county forest surveys, the 1907 state forester's report, and the Umass/MaConnell data books.

Archives Development, 2000-2001

John Burk

While the majority of time spent on archival work was devoted to active research, several projects and additions continued the development of the facility, which is entering its fifth year of operation.

Harvard Forest's information about the Sanderson family, which farmed portions of Prospect Hill in the 18th and 19th C, was strengthened by the purchase of an original account book from a local rare book dealer, providing a firsthand account of early agricultural activity in the area. In addition, Kathleen Hunter, a descendant of the Sanderson family, made several visits and donated a copy of her family genealogy research to the archives.

All Harvard Forest property records including deed, correspondence, and buildings and grounds records were researched for land-use citations in order to help develop a long-term plan for the tracts. An enlarged and simplified property file was created, combining related documents from the various sources.

As part of an ongoing effort to create a unified database, all archive databases, including maps, samples, photos and slides, aerial photos, research files, and rare books, were converted to ProCite bibliographic format. The enhanced features of Procite have facilitated data entry and research. During this process all related collections were inventoried and updated, with new paper listings printed.

Additions to the map collection included comprehensive coverage of the coast from New York to Cape Cod in 19th C Coast and Geodetic surveys, and 20th century USGS topographic quadrangles. Copies of the final maps from the 1830s Massachusetts series were acquired, giving Harvard Forest a complete set of this valuable resource.

Over fifty boxes of soils and tree cores were added to the soil and sample archive, mainly from the Cape and Islands project. Other material included soils from MBL and the adelgid studies, and tree cookies and soils from the ancient Gribben Forest in Michigan.

Historical and current slides and photographs were used to create a photo gallery on the Harvard Forest web page. The lantern slides were sorted and cataloged, and several successful enlargements were produced from the glass originals, enhancing the collection's value as an archival resource. A series of 1938 Cape Cod images was added to the aerial photo collection.

The archive facilities were used daily by staff researchers on projects such as the 1830s mapping effort, and regularly by students, planners, and historians from outside institutions including Mount Wachusett Community College, the University of Massachusetts, Harvard University, the Trustees of Reservations, and the towns of Petersham, Hardwick and New Braintree.

The Effects of Hemlock Woolly Adelgid Infestation on Foliar Decomposition in Eastern Hemlock Forests of Southern New England

R. Cobb, D. Orwig and S. Currie

Forests dominated by eastern hemlock (*Tsuga canadensis*) are cool and deeply shaded ecosystems found throughout the New England landscape. Due to favorable climate and lack of effective native predators, the Hemlock Woolly Adelgid (*Adelges tsugae*, HWA) is spreading throughout southern New England's hemlock forests with little impediment. Eastern hemlock has no natural resistance to this insect and tree mortality typically occurs within 5 to 10 years after infestation. In a recent study, Jenkins *et al.* (1999) demonstrated a strong linkage between HWA related canopy damage and altered community structure and ecosystem function. These authors hypothesize that changes in decomposition dynamics may be contributing to functional changes in HWA damaged stands. Insect attack can effect decomposition indirectly by altering microclimate and directly by altering foliar quality. The objectives of this study are (i) to compare relative rates of foliar decomposition in eastern hemlock forests with varying stages of adelgid caused damage and (ii) examine how HWA herbivory influences this functional process.

We studied surface decomposition for 18 months in hemlock forests ranging from uninfested controls to stands with significant HWA related canopy damage. Hemlock foliage was collected from 8 study sites where we have developed a detailed 3 year database of soil temperature, soil moisture, and N dynamics (see Orwig *et al.*, this volume). These stands include 2 sites with canopy damage, four sites with little damage but with large HWA populations, and 2 sites without adelgid (control). At each site, we distributed foliage from each respective stand and uninfested foliage from Harvard Forest.

Sites with severe damage tended to have lower rates of mass loss and lower rates of %C and %N accumulation relative to low damage and control sites (Fig. 1). This trend was associated with dryer forest floors suggesting that reduced soil moisture in the surface soils of infested stands

may be limiting fungal hyphae establishment and thereby inhibiting decomposition. Foliage type also influenced the dynamics of decomposition however, these effects were most pronounced at control sites where both sets of foliage were uninfested by HWA. This suggests that site factors have a greater influence on foliar quality than HWA herbivory alone.

Reduced decomposition at damaged sites is counter to the dynamics hypothesized by Jenkins *et al.* (1999) and our own expectations. Soil N mineralization has been greatly increased at these damaged sites relative to the controls, a pattern opposite of surface decomposition. However, reduced soil moisture is most pronounced in the forest floor, suggesting that subterranean processes may not be limited by moisture status and may be responding to increased soil temperature also associated with damaged stands. To better understand functional changes associated with this insect, we are preparing to make relative comparisons of surface and subsurface decomposition at a larger subset of hemlock dominated sites.

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Decadal Scale Recovery of [15]N Tracers in Bolewood at the Harvard Forest Chronic N Study

B. Colman, K. Nadelhoffer and W. Currie

Wood is posited to be an important carbon sink in the North Temperate Zone, and elevated nitrogen deposition on temperate forests could contribute to carbon storage by stimulating wood production. This hypothesized fertilization effect is dependent on the uptake of nitrogen deposition by trees and allocation to bolewood growth.

In order to determine the fate of elevated nitrogen inputs in temperate forest ecosystems, ^{15}N-tracers were added to Control (ambient
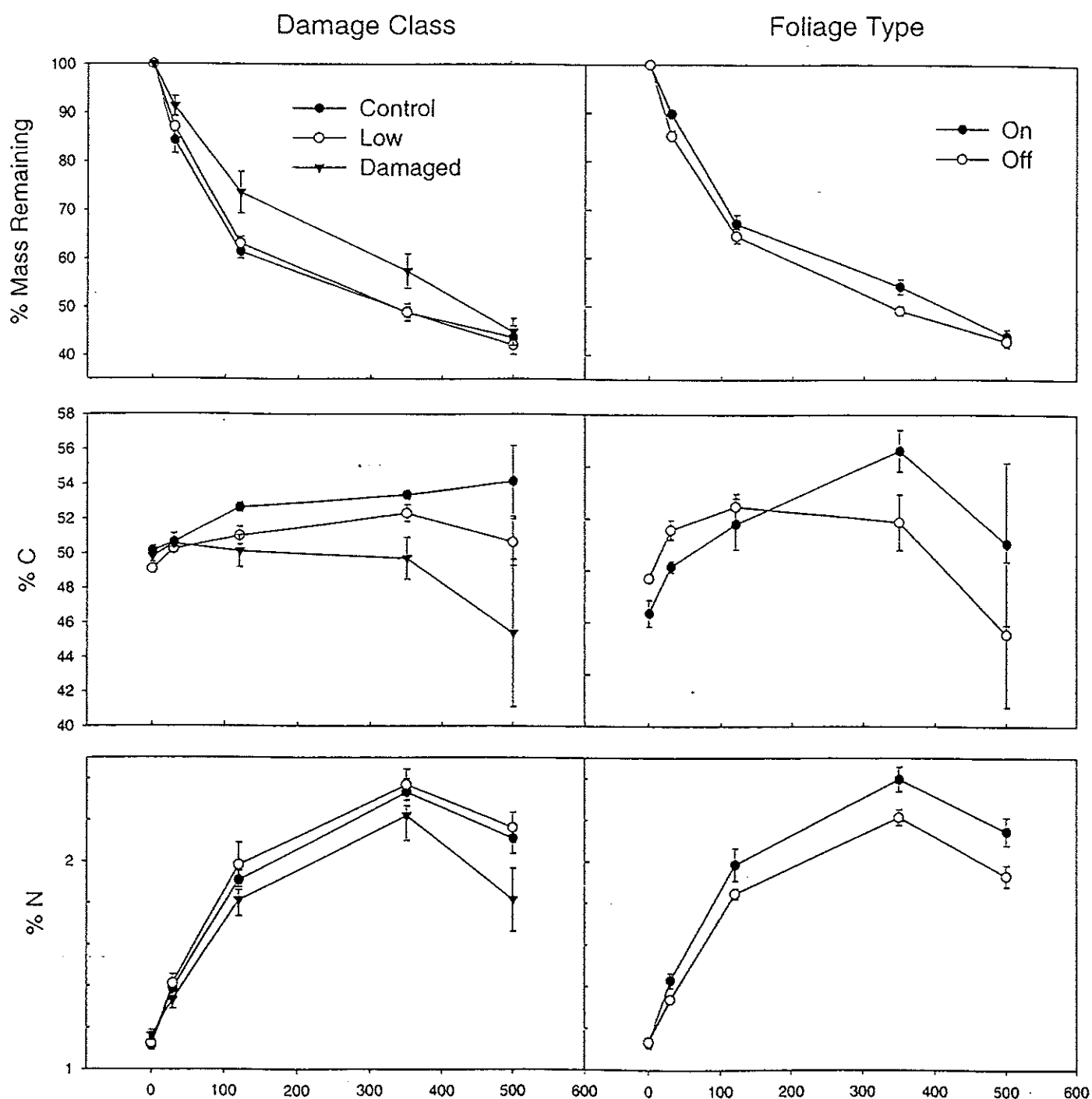
Figure 1. Damage class and foliage type effects on % mass remaining, C, and N. Damage class values are biased on infested and uninfested foliage incubated at each of eight study sites. Foliage type values are relative dynamics of infested (on, including two controls) and uninfested (off) foliage at each study site. Study sites are distributed throughout Connecticut. Error bars are on standard error of the mean.

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deposition) and Low-N addition (50kg N ha^{-1}yr^{-1} since 1988) plots in 1991 and 1992 at the Harvard Forest LTER Chronic N Amendment Study. In both forest types studied (oak and red pine) ambient and fertilized plots received NH$_4$^{15}NO$_3$ tracer on one half and ^{15}NH$_4$NO$_3$ on the other. Recovery and redistribution of ^{15}N tracers in the first few years following labeling was reported previously (Nadelhoffer *et al.* 1999). Bole wood, green foliage, soil, roots, woody debris, and understory-canopy foliage were sampled again, 8 years following the mid-point of ^{15}N labeling (in 1999) in order to assess decadal scale patterns of ^{15}N movements and C / N interactions.

The measured recoveries from all pools will be compared to modeled recoveries as predicted by the TRACE model. TRACE combines the vegetation production and allocation of PnET (Aber and Federer 1992) with a detailed model of decomposition, humification, and production of dissolved organics, with an emphasis on C and N interactions and an ability to predict ^{15}N tracer redistributions in vegetation and soils (Currie *et al.* 1999). Direct model-data comparisons of ^{15}N redistributions help to test and refine the model (Currie and Nadelhoffer 1999). Previous work showed that ^{15}N tracer recovery in bolewood at the end of the two-year tracer addition ranged from 0.1% to 4.4% when averaged across tracer forms (Fig. 1). Tracer recovery varied with forest type, N-input rate, and ionic form of ^{15}N added (Fig. 2). Overall, more ^{15}N accumulated in wood when ^{15}NO$_3$$^-$ was applied, oaks accumulated more tracer than pines, and the percent recoveries increased with N input rate.

In 1999, seven years after the end of tracer application, recoveries were larger in bolewood than at the end of the two-year tracer addition, ranging from 0.8% to 5.1% averaged across tracer forms. The overall trend from 1992 still holds, with tracer recovery depending on forest type, rate of N-input, and form of tracer addition.

Tracers have continued to accumulate in wood for almost a decade after being added to the plots, as was predicted by TRACE before these data were obtained (Currie and Nadelhoffer 1999). At the same time, the low ^{15}N recoveries in bolewood show that N deposition may be

having a small influence on wood production in these forests.

Next steps in this project include working up a complete budget for C and ^{15}N in these forests over decadal time scales, as well as incorporating lessons learned in model-data comparisons to refine and revise TRACE to apply the model across other sites. TRACE will be used to predict ^{15}N redistributions at other intensive-study sites including Klosterhede, Denmark, and Bear Brooks Watershed, Maine. The model will also be used to scale up C and N interactions to landscape scales in the northeastern U.S.

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Nadelhoffer, K. J., M. Downs and B. Fry. 1999. Sinks for 15N-enriched additions to an oak forest and a red pine plantation. Ecol. Appl. 9L 72-86.

Woody Detritus, Land-use History, and Long-term C and N Interactions

W. Currie, K. Nadelhoffer, and B. Colman

Depending on the particulars of forest management and disturbance, wood in varying size classes and amounts enters detrital pools in soil where it contributes to energy flow, C (carbon) storage, N (nitrogen) storage, and N cycling. Two key questions in the study of large-scale C and N cycling in temperate forests are how N cycling in soil detritus controls ecosystem-level retention of elevated N deposition, and whether elevated N deposition is likely to cause
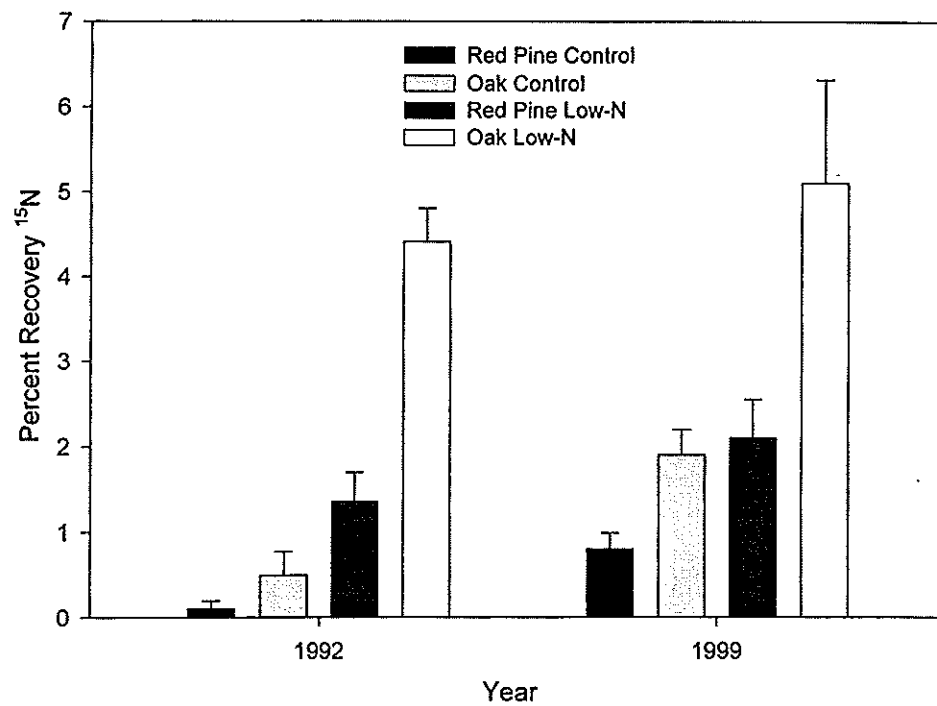
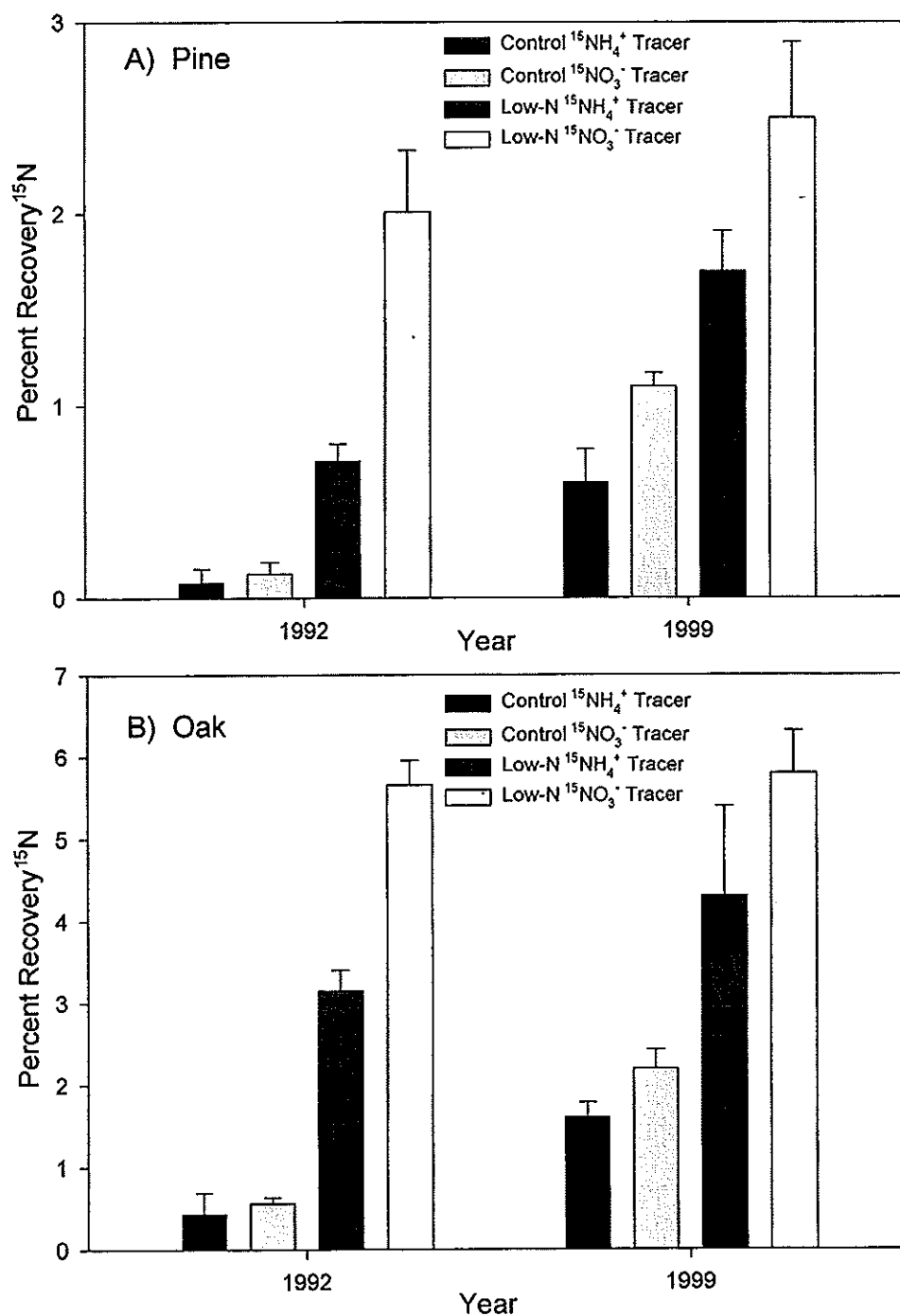**Figure 1.** Percent Recovery ^{15}N in Bolewood as measured in 1992 and 1999, averaged over tracer forms.

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Figure 2. Percent Recovery ^{15}N in bolewood of Pine and Oak forests by treatment and tracer form.

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increases in C pools. The large C:N ratios in woody detritus make it a potentially important contributor to N retention, if N immobilization increases, and a potentially important contributor to C sequestration, if pool sizes increase.

Both fine woody debris (FWD) and coarse woody debris (CWD) are often excluded from ecosystem-level studies of C and N dynamics, because these are difficult to sample methodically and they comprise relatively small fractions of C and N stocks. High variabilities across size classes, across decay classes, and in spatial distributions create challenges for the measurement of pool sizes. However, producing a complete C or N budget at a particular site requires the measurement of woody pools at that site. Pools of woody detritus are difficult to generalize to any given site from elsewhere because inputs are heterogeneous in space and time, and pool sizes reflect the particulars of disturbance and land use history at any site.

Long-term movement of ^{15}N tracers into fine woody debris

The contribution woody debris makes to N retention in the forest floor under elevated N inputs is unknown. Two very different mechanisms are plausible for increased N retention in this material under increased N inputs. First, N immobilization would provide a direct mechanism for increased N retention in the forest floor. Woody debris has higher C:N ratios than other litter, but the extent to which woody debris can be expected to immobilize N as it decays is a matter of current debate. Second, any increase in N uptake and the flux of N in woody litter could provide an ecosystem-level mechanism of N retention.

We studied N concentrations, C:N ratios, and pool sizes of N and biomass in fine woody debris (FWD < 5 cm diam.) 12 years into the Chronic N Study (Aber *et al.* 1993, Magill *et al.* 2000), a long-term N-amendment study in two contrasting forests: a naturally-regenerated forest dominated by *Quercus* spp., and a 63-yr old plantation of *Pinus resinosa*. We also quantitatively recovered ^{15}N tracers (originally applied as $^{15}NH_4$ and $^{15}NO_3$) in FWD, eight years following their application in the same study, in both ambient and N-amended plots. We used

these data to test predictions of tracer redistributions made by TRACE, a biogeochemical process model incorporating the vegetation processes of PnET (Aber and Federer 1992), and predicting redistributions of ^{15}N (Currie *et al.* 1999).

Results from the N pool-size analysis and the ^{15}N tracer-recovery analysis indicated that under elevated N inputs of 5 g N m^{-2} yr^{-1} (as NH_4NO_3) over the decadal time period, only 0.15% to 0.76% of the elevated N inputs were recovered in FWD of N-amended plots relative to ambient. Any increase in N immobilization in wood appeared to be minimal, in agreement with predictions made by the TRACE model (Currie and Nadelhoffer 1999). Under N amendments, pool sizes of C in FWD were not significantly different from ambient, whereas pool sizes of N were marginally higher. Patterns of $^{15}NH_4$ vs. $^{15}NO_3$ recovery, treatment differences, and forest-type differences suggested that plant uptake, rather than detrital immobilization, was the dominant mechanism of ^{15}N tracer movement into FWD. This result indicates that plant-soil cycling operating over a decadal time scale or longer controls C:N ratios and N pool sizes in woody debris.

Land Use History: Contrasting Patterns of C and N Stocks in Woody Detritus

Data on C and N cycling from the Harvard Forest have played a key role in the development of numerous models with a wide range of purposes. In addition, some models of generalized processes across types of terrestrial ecosystems have used data from Harvard Forest to parameterize temperate forest regions. Ecosystem budgets and synthetic models applied at the Harvard Forest have relied on woody detrital measurements from other temperate forests. In 1999, by combining quadrat-sampling methods with line-intercept methods on long transects, we completed quantitative measurements of pool sizes of mass, C, and N in downed fine and coarse woody debris in two forest types in the Prospect Hill tract: the two forest stands containing the Chronic N Study. Given the knowledge of long-term management and disturbance history of land at the Harvard Forest (Foster and Boose 1992, Foster et al. 1992), we also sought to quantify

relationships between site history and current ecosystem structure in the woody detrital pools.

One of the most striking patterns in our data was the difference, between these two forest stands, in the patterns of size and decay classes in coarse woody debris (CWD) (Fig. 1). In the oak forest, detritus was distributed across all size categories, and nearly all of the CWD mass was in the most advanced decay classes. Patterns of CWD mass in the pine stand stood in direct contrast to this in two ways. First, all of the CWD mass in the pine stand was in the smallest size class (< 25 cm). Second, the material was distributed across all five stages of decay, including the two most sound (least-decayed) categories.

Most of the differences we observed between stands can be attributed to differences in land use and disturbance histories. The even-aged nature of the pine stand is evident in the large masses of rotten woody debris in the largest size class of FWD and smallest size class of CWD; these are highly decayed stems that fell during the stem exclusion phase of forest development. The lack of any debris in larger categories corresponds in a clear way to the fact that this stand was pastured into the 20th century, became a pine plantation in 1926, experienced little damage from the 1938 hurricane, and is still in its first episode of forest growth after reversion from agriculture. There are numerous living trees and some snags present in larger sizes, but since the trees have attained that size there has been no disturbance severe enough to cause extensive mortality or windthrow.

The oak forest, in contrast, was one of the first patches of the Prospect Hill tract to revert to forest following agriculture. Over a 150-yr period this hardwood stand has experienced numerous disturbances; it was lightly logged at the turn of the century, suffered extensive damage from the 1938 hurricane, and experienced mortality from the Chestnut blight (Foster and Boose 1992, Foster et al. 1992). The forest has naturally regenerated following these disturbances. The patterns of CWD that we observed (Fig. 1) show that with such a history, large well-decayed pieces of woody debris are present; it is this debris that contains the bulk of the N in woody detritus (data not shown) because of the narrow C:N ratio of this highly decayed material.

These results have important implications for the use of Harvard Forest C and N data in models that are used to extrapolate across landscapes. It is well known that climate and litter quality control decay rates, and thus pool sizes, of detritus; for woody debris, more so than for other types of litter inputs, it is also true that input rates and pool sizes depend on particulars of disturbance and forest history over long time periods. To scale results from intensive-study sites up to a grid cell or region, models could include links between land use history and woody pools, and apply those links across landscapes with data layers representing patches of history and disturbance. In any case, history should not be neglected in modeling pool sizes of C and N in woody detritus.

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Currie, W. S., K. J. Nadelhoffer and J. D. Aber. 1999. Soil detrital processes controlling the movement of 15N tracers to forest vegetation. Ecol. Appl. 9: 87-102.

Currie, W. S., K. J. Nadelhoffer and B. Colman. Long-term movement of ^{15}N tracers into fine woody debris: increased N sinks under chronically elevated inputs. Plant Soil (In Review).

Foster, D. R. and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. J. Ecol. 80: 79-98.

Foster, D. R., T. Zebryk, P. Schoonmaker and A. Lezberg. 1992. Post-settlement history of human land-use and vegetation dynamics of a Tsuga candensis (hemlock)
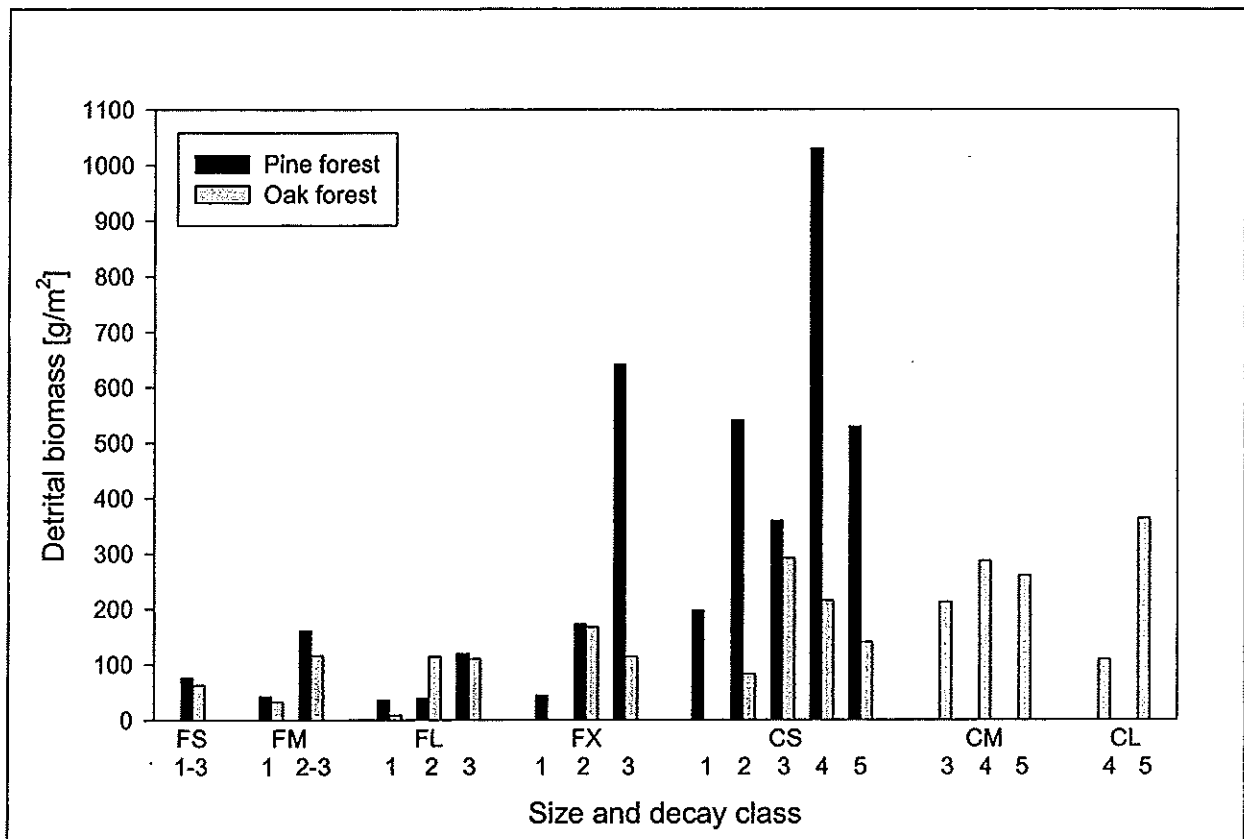
Fig. 1. Pool sizes of mass of downed woody detritus, by size class and decay class, in the red pine and mixed-oak forests in the Prospect Hill tract at the Harvard Forest. Size classes FS, FM, FL, and FX are finer to coarser sizes of fine woody debris (FWD) < 10 cm diam; size classes of CWD are CS (10 to 25 cm diam), CM (25 to 50 cm diam.), and CL (> 50 cm diam.). Decay classes range from 1 (sound) to 3 (rotten) for FWD, and from 1 (sound) to 5 (rotten) for CWD. Reproduced from Currie and Nadelhoffer *in review*.

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woodlot in central New England. J. Ecol. 80: 773-786.

temperate forest soils. Soil Biol. Biochem. 32: 151-156.

Rapid abiotic transformation of nitrate in an acid forest soil

D. Dail, E. Davidson, J. Chorover, K. Dria and P. Hatcher

Nitrate immobilization into organic matter is thought to require catalysis by the enzymes of soil microorganisms. However, recent studies at the Harvard Forest suggest that nitrate added to soil is immobilized rapidly and this process may include abiotic pathways (Berntson and Aber, 2000). We amended living and sterilized soil with ^{15}N-labeled nitrate and nitrite to investigate biotic and abiotic immobilization. We report rapid transformation of nitrate in incubations of the O layer of forest soils that have been sterilized to prevent microbial activity and to denature microbial enzymes. Approximately 30, 40, and 60% of the ^{15}N-labeled nitrate added to live, irradiated, or autoclaved organic horizon soil disappeared from the extractable inorganic-N pool in less than 15 minutes. About 5% or less of the nitrate was recovered as insoluble organic N in live and sterilized soil, and the remainder was determined to be soluble organic N (DON) (Fig. 1). Added ^{15}N-nitrite, however, was either lost to gaseous N or incorporated into an insoluble organic N form in both live and sterile organic soils (Fig 2). Hence, the fate and pathway of apparent abiotic nitrate immobilization differs from the better-known mechanisms of nitrite reactions with soil organic matter. Nitrate and nitrite added to live A-horizon soil was largely recovered in the form added, suggesting that rapid conversion of nitrate to soluble organic-N may be limited to C-rich organic horizons. The processes by which this temperate forest soil transforms added nitrate to soluble organic-N cannot be explained by established mechanisms, but appears to be due to abiotic processes in the organic horizon.

Berntson G. M. & J. J. D. Aber. 2000. Fast nitrate immobilization in N saturated

Interannual Variation of CO$_2$ Production within the O Horizon and Its Implications for Annual Net Ecosystem Productivity

E. Davidson, K. Savage and S. Trumbore

Carbon in the litter layer of the Harvard Forest is probably no longer accumulating significantly from one decade to the next, but there may be important variation from year to year that could affect annual estimates of net ecosystem productivity (NEP). Goulden *et al.* (1996) reported surprising high values of NEP during years with dry summers, apparently because summer drought suppressed respiration more than photosynthesis, causing above average annual net storage of ecosystem C. Savage and Davidson (2001) have reported significantly lower rates of soil respiration during the dry summers of 1995, 1997, and 1999 compared to the wet years of 1996, 1998, and 2000 (Fig. 1a). If low rates of respiration during dry years contribute to interannual variation of NEP, then it is important to know where within the soil/forest floor system respiration is most variable annually. We hypothesize that the forest floor (the O horizon) is most susceptible to drought-induced suppression of decomposition, resulting in transient C sinks in this horizon. The objective of this study is to estimate interannual variation of CO_2 production within the O horizon.

In addition to chamber measurements of soil respiration during the last six years, we have also measured profiles of CO_2 concentrations, water content, and temperature within the soil on a weekly basis during the growing season and less frequently during the other seasons (Fig. 1b,c,d). We estimate effective diffusivity of CO_2 within the soil as a function of water content, temperature, and porosity. Applying Fick's first law, we estimate CO_2 flux at various soil depths from estimates of diffusivity and CO_2 concentration gradients. Production of CO_2 within each mineral soil horizon is then estimated from the difference between the upward flux
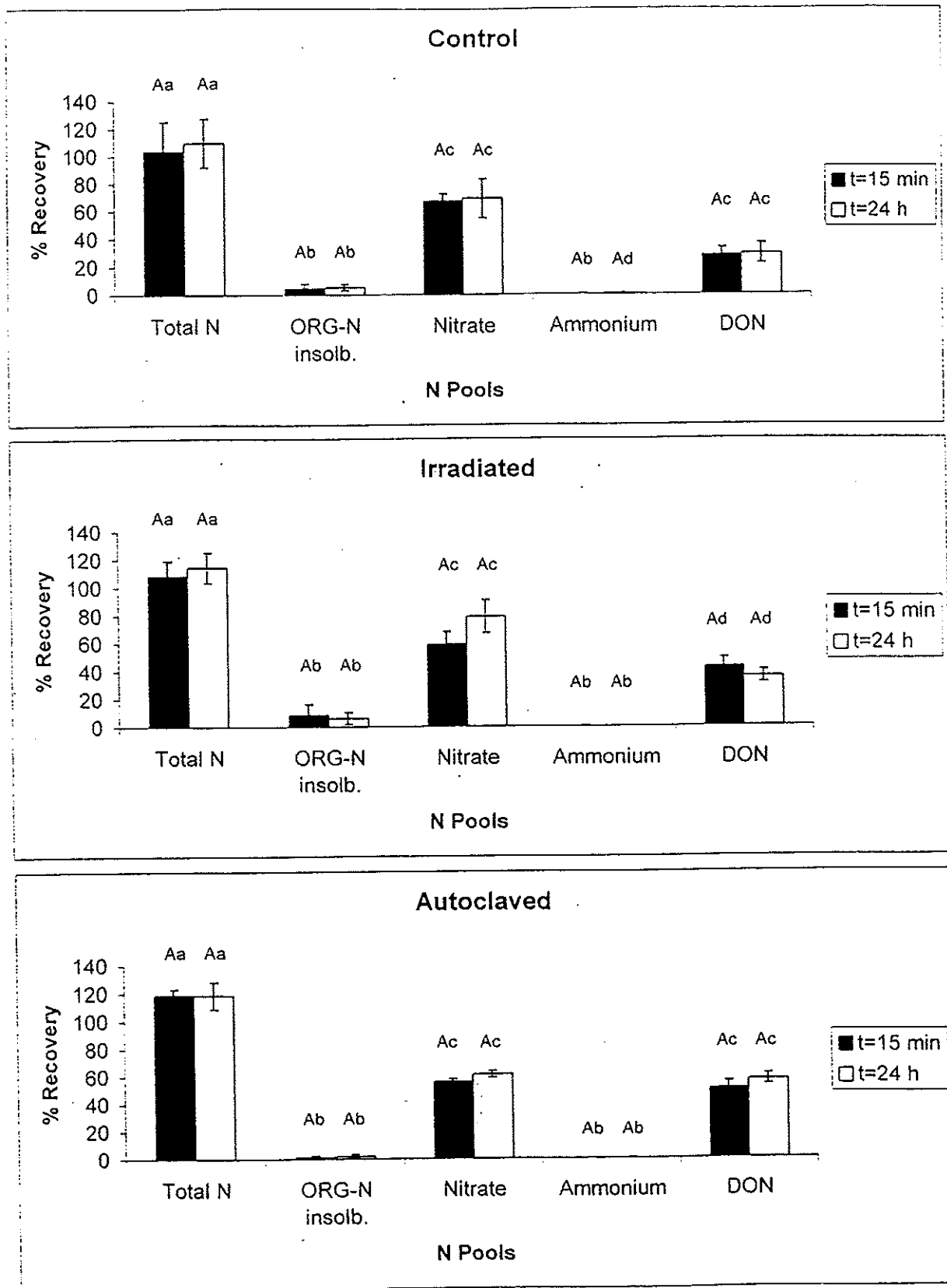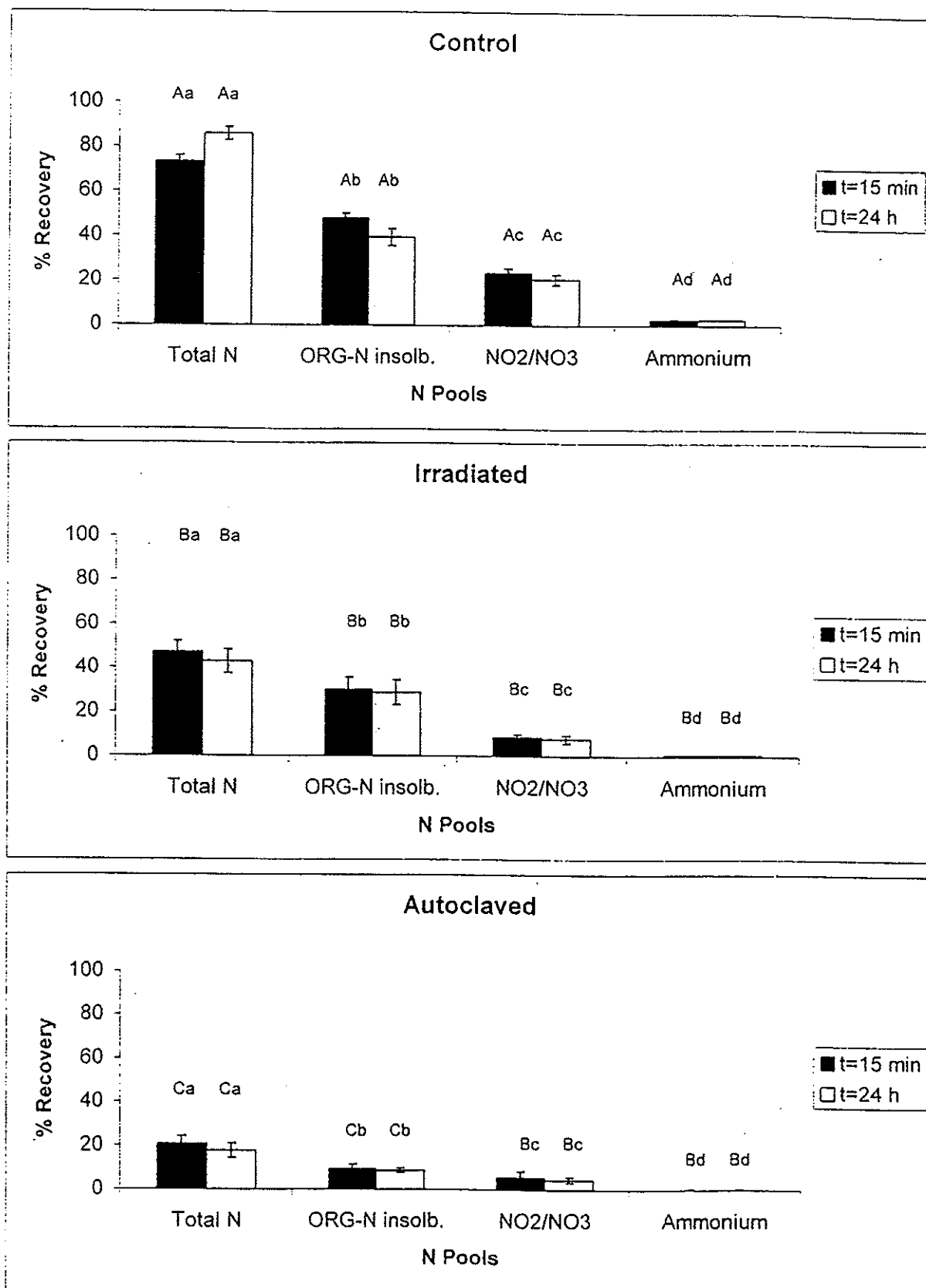
Figure 1. Percent recovery of ^{15}N in O-horizon soil N pools reported for (a) control, (b) gamma irradiated and (c) autoclaved soils amended with [15]NO₃⁻ at the rate of 5 μg ^{15}N per gram soil dry mass (n=3; ±SD). Total N = soil ^{15}N recovered in direct mass spec analysis of non-extracted soil;. Org-N Insolb. = [15]N remaining in soil pellet after K₂SO₄ extraction; DON =[15]N recovered after persulfate oxidation of K₂SO₄ extracts. Columns with different upper case letters indicate significant difference within pool, between soil treatments at α=0.05 level. Columns with different lower case letters indicate significant

Figure 2. Percent recovery of ^{15}N in O-horizon soil N pools reported for (a) control, (b) gamma irradiated and (c) autoclaved soils amended with $^{15}NO_2^-$ at the rate of 5 µg ^{15}N per gram soil dry mass (n=3; ±SD). Total N = soil ^{15}N recovered in direct mass spec analysis of non-extracted soil;. Org-N Insolb. = ^{15}N remaining in soil pellet after K_2SO_4 extraction. . Columns with different upper case letters indicate significant difference within-pool, between soil treatments at α=0.05 level. Columns with different lower case letters indicate significant difference between soil N pools within a soil treatment at α=0.05 level.
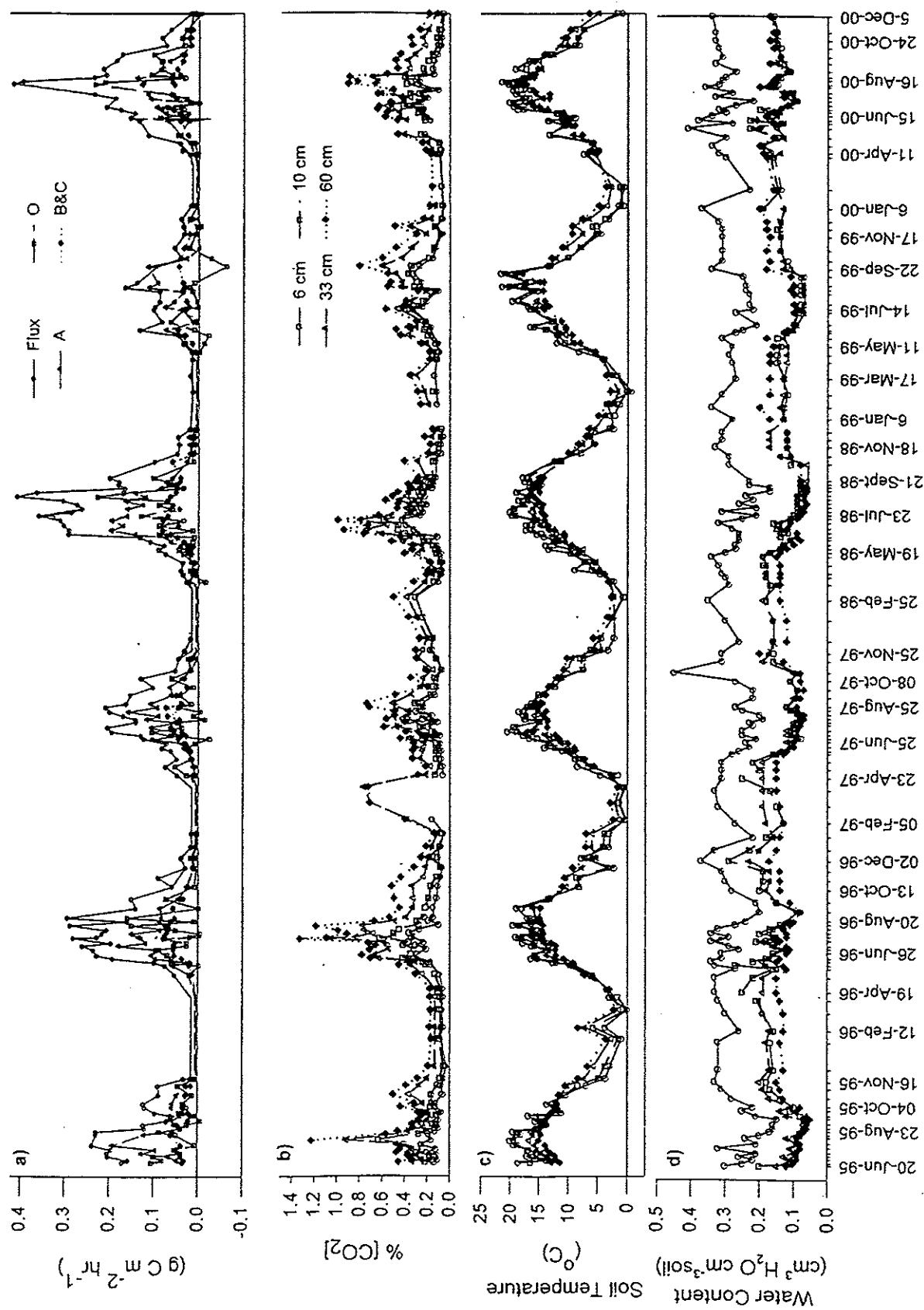
Figure 1. Seasonal and interannual variation at the Harvard Forest tower site of a) CO_2 flux from the soil surface and CO_2 production by soil horizon; b) CO_2 concentration by soil depth; c) temperature by soil depth; and d) volumetric water content by soil depth.

moving out of that horizon and the flux from the horizon below. For the O horizon, CO_2 production is estimated from the difference between mean CO_2 emissions for the site measured with chambers and the CO_2 flux out of the top of the mineral soil estimated from diffusivity and the concentration gradient.

Our estimates of CO_2 production within the O horizon are 2.1, 1.6, 3.1, 0.4, and 3.2 Mg C ha^{-1} yr^{-1} for the successive years from 1996 through 2000. In contrast, litterfall-C has a much smaller interannual range: 1.7, 2.0, 2.2, and 2.0 Mg C ha^{-1} yr^{-1} for the years 1996 through 1999. Although variable root respiration may contribute to interannual variation in soil respiration, the large interannual variation of CO_2 production within the O horizon implies that decomposition of leaf litter is inhibited by summer drought, resulting in a sink of C in the forest floor that could be on the order of 1 Mg C ha^{-1} for the year. This sink is probably transient because the litter layer produces above average CO_2 release during wet years when some of the decomposable material from the previous drought year is decomposed under favorable conditions.

Goulden, M.L., J.W. Munger, S.-M. Fan, B.C. Daube, and S.C. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271: 1576-1578.

Savage, K.E., and E.A. Davidson. 2001. Interannual variation of soil respiration in two New England forests. Global Biogeochemical Cycles, in press.

Changes Observed by NMR and Pyrolysis GC/MS of Harvard Forest Soils and Their Associated Plant Components Caused by Ten Years of Heavy Nitrogen Fertilization

K. Dria, D. Dail, J. Chorover, E. Davidson, and P. Hatcher

Samples from canopy-to-soil stratigraphic profiles, containing leaf, fine root and organic and mineral soil samples, were collected from the Harvard Forest Chronic N plots during 1989, 1996

and 1999 by Nadelhoffer and coworkers and Aber and coworkers. DOM from 1997 leachate samples, obtained from these plots using zero tension lysimeters (ZTL), is currently being characterized to evaluate the changes in DOM content and composition that results from varying levels of N fertilization. All samples were analyzed for chemical structural information by solid-state ^{13}C NMR and molecular level detail by pyrolysis GC/MS. Select samples were analyzed by solid-state ^{15}N NMR and liquid-state ^{13}C NMR. Samples from the 1989 profile were used as a control for comparison with samples from 1996 and 1999 to determine compositional changes caused by N fertilization over time. Additionally, samples were compared across the treatment plots of control, low N and high N to differentiate changes associated with forest changes and N fertilization.

^{13}C NMR spectra from all solid samples contain predominantly signals associated with paraffinic (0-45ppm) and carbohydrate (60-90 ppm) structures and low amounts of aromatic (90-160 ppm) structures. ^{15}N NMR spectra reveal signals associated with amide structures. The mineral soil samples exhibit minor amounts of aromatic structures, suggesting little contribution of lignin structures to the organic matter. Lignin added to the soil by plant inputs may have been oxidized, degraded and/or leached from the soil profile. Primary changes observed in each set of the canopy-to-soil profiles were a loss of carbohydrates and a persistence of the paraffinic carbon regions of the NMR spectra (Fig. 1).

Of particular interest are the effects of N fertilization on the types of leaf carbon and litter decomposition in the various soil horizons. Increased levels of methylene structures (30 and 32 ppm) are observed in the NMR spectra of black oak green leaf samples with increased fertilization in 1999 and to less of an extent in 1996. Spectra of 1999 soil samples collected from both hardwood and pine high N plots from the Oe and Oa horizons reveal greater amounts of carbohydrate, lignin and aliphatic amide carbons relative to paraffinic carbons (Pine shown, Fig. 2). This carbohydrate and lignin increase suggests that the rate of decomposition has decreased with increased N fertilization, and this conclusion is supported by results of a litter decomposition study performed by Magill and Aber (1998).

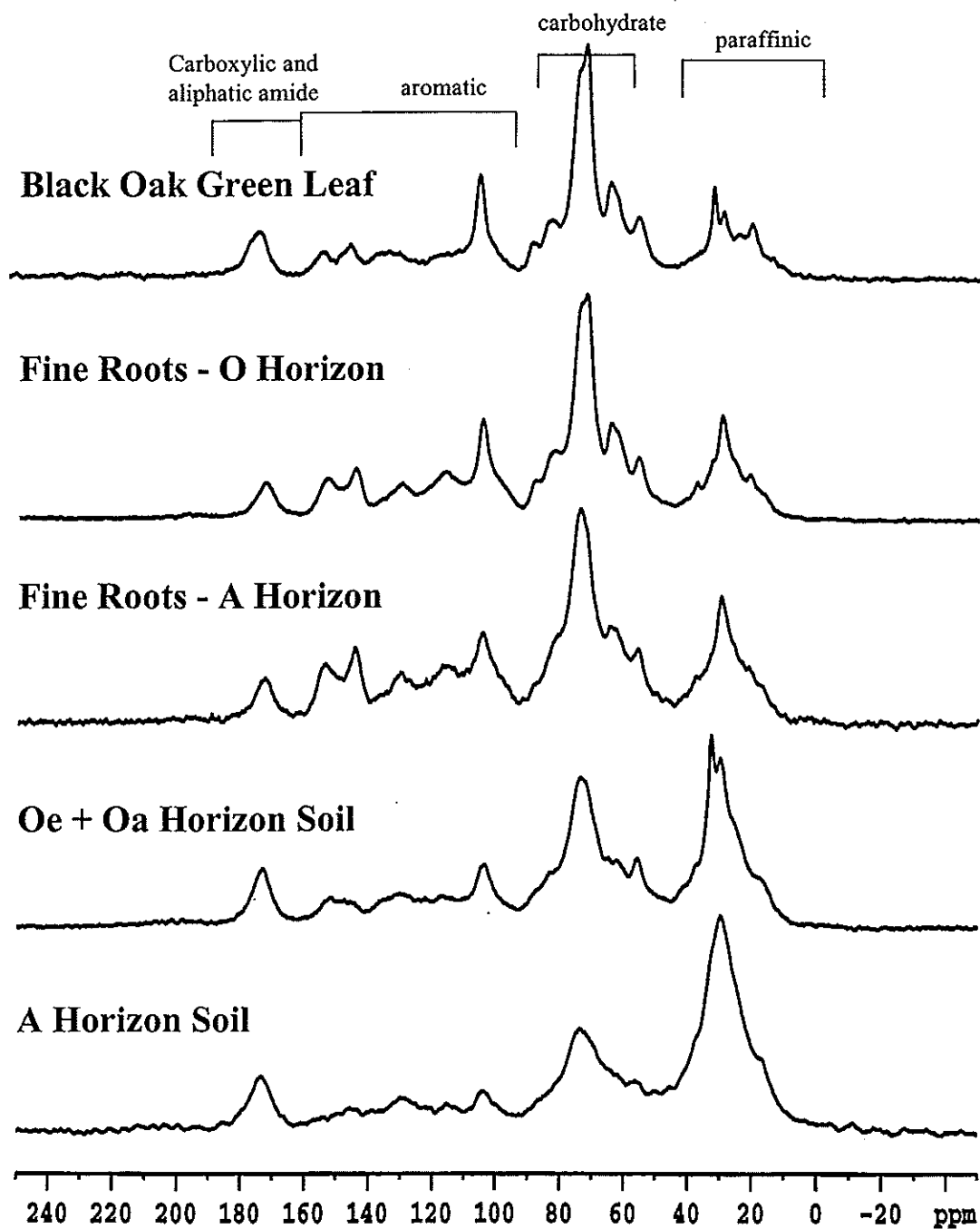# Hardwood Profile Control Plot 1989

Figure 1. Hardwood profile from 1989

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Pine Soils 1999

High N Oe Horizon

Control Oe Horizon

High N Oa Horizon

Control Oa Horizon

High N A Horizon

Control A Horizon

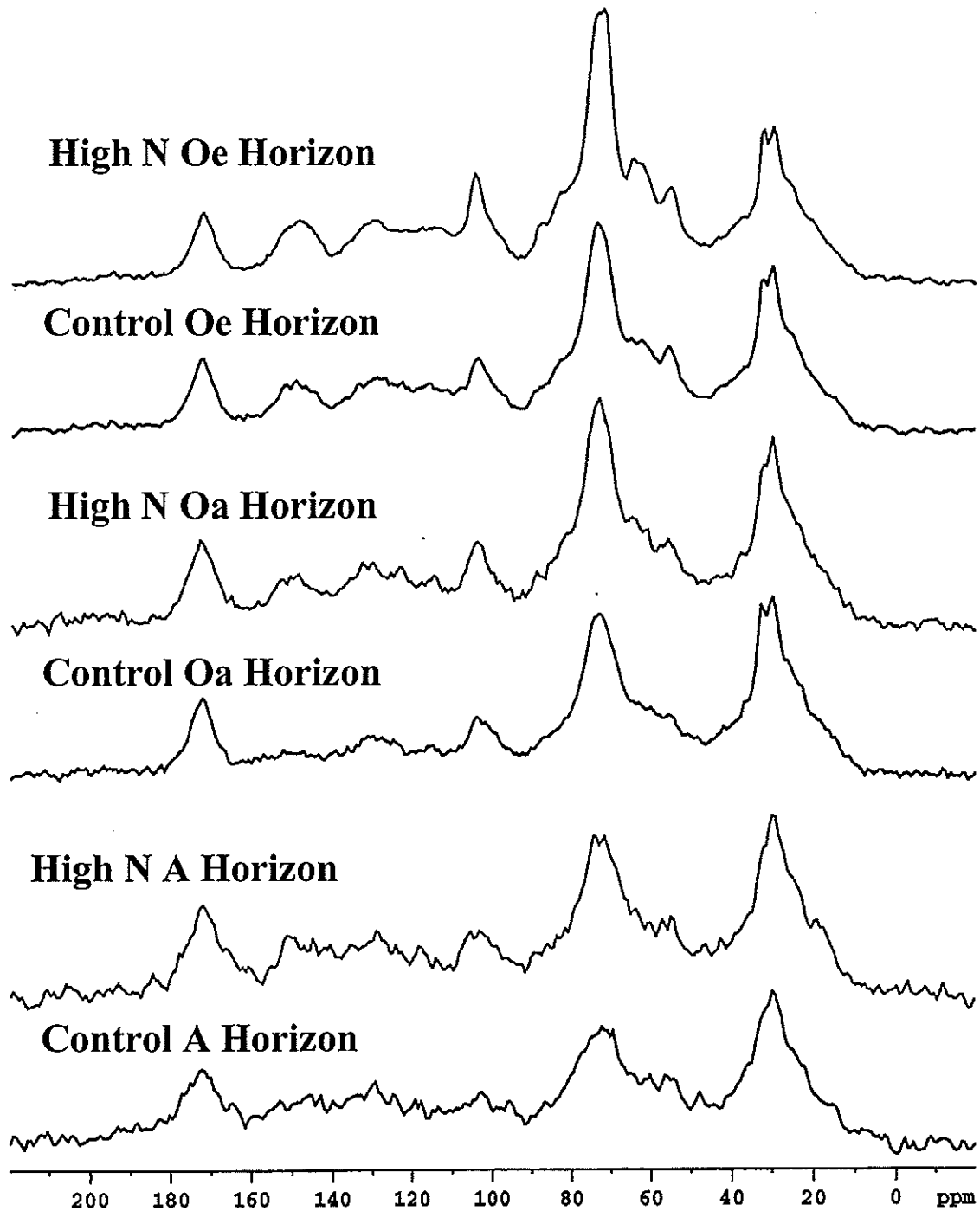200 180 160 140 120 100 80 60 40 20 0 ppm

Figure 2. Soils collected in 1999 from Pine plots

Pyrolysis GC/MS data support the NMR results. Preliminary ZTL analyses indicate a DOM composition that is predominantly aromatic- and carbohydrate-type carbons.

Magill, A.H. and Aber, J.D. 1998. Plant and Soil 203: 301-311.

Land-Use Legacies in the Sand Plain Vegetation of Cape Cod National Seashore

R. Eberhardt, D. Foster, G. Motkzin, and B. Hall

Despite increased reliance in conservation planning on an understanding of landscape dynamics in response to natural disturbance, the pervasive impact of historical land-use is often under appreciated in the management and restoration of conservation areas and natural resources. We used historical and ecological approaches to determine the relative roles of past land-use, fire, and site conditions on woodland vegetation patterns in Cape Cod National Seashore (CCNS), the largest protected area of sand plain vegetation in the New England-New York region. Coastal sand plains are the focus of intense conservation activity since they support uncommon plant and animal assemblages that are dynamic as a result of past disturbance and ongoing human impacts. The study evaluated established theories underlying the interpretation and management of sand plain landscapes that emphasize fire as a controlling process.

Although predominantly wooded at European settlement, the towns of Eastham, Wellfleet, and Truro were extensively settled and 80% open at the peak of New England agriculture in the mid-19th C. Historical maps and modern soil profiles indicate that the 5000 ha of sandplain woodlands in CCNS experienced varied land-use before agricultural abandonment and natural reforestation. Approximately 44% was plowed for crops or pasture, 42% logged repeatedly but never cleared, and 14% open and subjected to diverse uses. Relationships between modern vegetation and 19th C land use are striking and largely independent of site conditions. Continuously wooded areas support pine-oak woodlands with abundant ericaceous shrubs, whereas previously plowed sites have less canopy oak, more pine, few ericaceous shrubs, and a distinct understory including the grass *Deschampsia flexuosa* and the shade-intolerant shrub *Arctostaphylos uva-ursi* (Fig. 1). Current composition and historical sources suggest that past agriculture generated extensive heathland and grassland habitats, much of which has subsequently reforested. In contrast to many interpretations and management guidelines, the persistent influence of fire is principally in the canopy composition and structure of former woodlots. The results highlight a need (1) to integrate an understanding of past land-use into ecological models underlying the management of biological reserves; and (2) to consider the use of management approaches that mimic past agricultural practices in order to maintain and restore important sand plain habitats.

Forest-Atmosphere Exchange Processes: Report on activities 2000-2001

D. R. Fitzjarrald, K. E. Moore, R. K. Sakai, O. C. Acevedo, R. Staebler, G. Wocjik and M. Czikowsky

We investigate mass and energy exchanges between the forest and the atmosphere. We place particular emphasis on a) understanding how turbulent flux convergence affects microclimate and b) how local site characteristics may introduce local bias into flux observation. In our climatological studies, we treat the spring transition as a land use "experiment", to study what changes occur in the environment accompany leaf emergence. A second "experiment" is identified with the evaporative effects of long-term land-use change in the Northeast.

Subcanopy flows. Correctly under-standing subcanopy motions is important to lending credibility to tower-based estimates of ecosystem respiration. R. Staebler has led our effort to understand how subcanopy motions might lead to horizontal CO_2 flux divergence. Detailed studies (DRAINO) were conducted
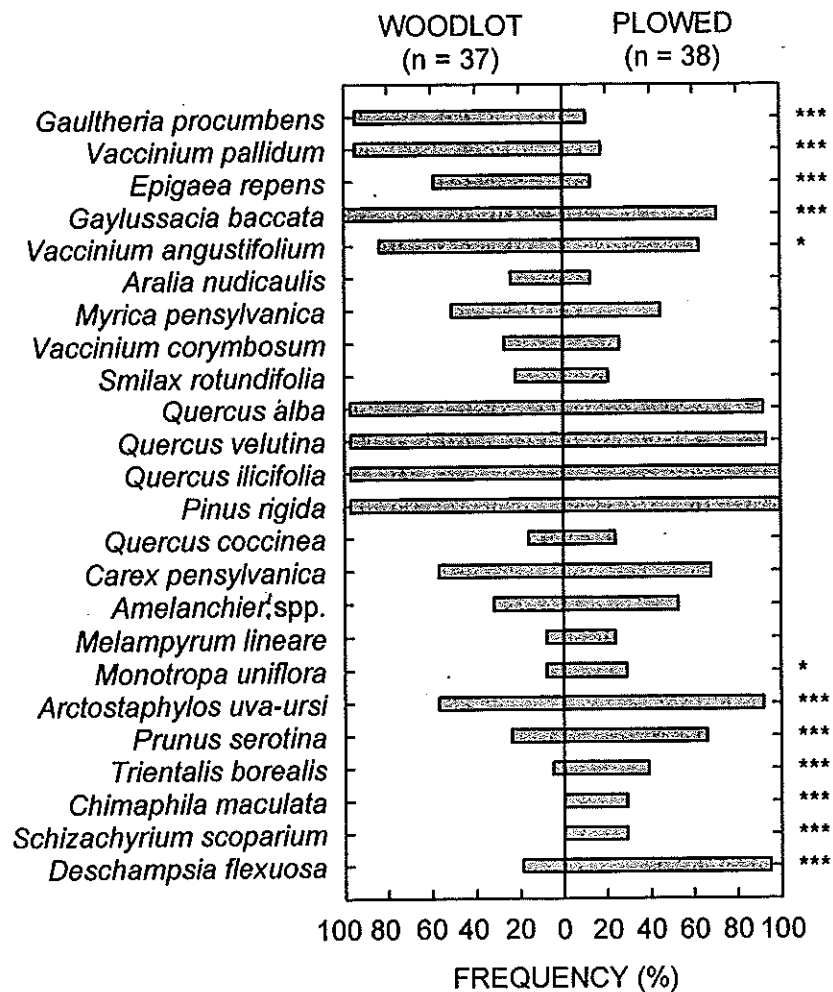
Figure 7. Distribution of common species in woodlands of Cape Cod National Seashore with different land-use histories. G-test results for species that occur in 13-87% of plowed and woodlot plots: *** = $p < 0.001$, * = $p < 0.05$. Tests with $p < 0.01$ are significant after accounting for multiple comparisons.

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during the last two growing seasons. A network of four 2-D and 1 3-D sonic anemometers was installed near the forest floor at the EMS (Fig. 1). In 1999, we found nocturnal drainage winds come preferentially from the north, from Prospect Hill. In 2000, a minor east-west axis and a central auxiliary tower with sonic anemometers at the heights of 1.5, 3 and 5m were added. The winds at 1.5 are usually disconnected from the winds above the forest, while those at 3, 5 and 11m are progressively more often (but intermittently) coupled with flows aloft.

In autumn 2000, a pilot study was begun to determine the horizontal gradient of the CO_2 concentration along the north-south axis. Large gradients (≈ 0.25 ppm/m, south minus north) were found to coincide with periods of low wind speeds (< 0.3 m/s). These conditions allow either for local pooling. The horizontal CO_2 gradient vanishes with increasing wind speed (Fig. 2). Certain inconsistencies appeared in the data from the initial pilot study. Hourly averages indicate convergence at night, but averaged nocturnal vertical velocities are negative, the opposite of what is required for consistency. We are aware of the large potential for error in this approach, but anticipate that longer observation periods planned during the coming growing season will resolve the issue.

To assess horizontal variability of subcanopy microclimate, we (in association with G. Parker at the Smithsonian Inst.) have been developing a balloon-borne sensor package. A small six-channel datalogger has been added to the package. In a frame atop the balloon a registers the angle from the horizontal of the plane of the sensor. Below the balloon hangs a temperature and humidity sensor. A second datalogger at the winch on the ground records line out, which reads out height above ground. Results from a field test of this system (Fig. 3) indicated that the data acquisition system worked smoothly, but that a faster-responding temperature sensor was required. A small thermistor has since been added to remedy this problem.

Local effects on flows and fluxes. The particular features near flux towers can also affect measurements. Airflow around Prospect Hill, for example, can locally deform the streamline near a flux tower. For the last two growing seasons, we have deployed an acoustic radar (sodar) device at the EMS. There have been some difficulties. A comparison study (one sodar near Shaler Hall, one at EMS) showed good agreement. Wind direction observations from sodar compare well with the tower results, but wind speed is underestimated by sodar. Continuing work will identify the thickness of the nocturnal inversion from sodar measurements.

Inhomogeneities in the forest canopy affect airflow and mass exchange between the forest floor and the atmosphere. O. Acevedo has led our modeling effort to understand the effect of canopy gaps on fluxes. Large-eddy simulations were made to study the fate of a scalar emitted uniformly at the surface, taken as a surrogate for CO_2 resulting from soil respiration. Results indicate that a canopy gap can lead to local overestimates in the flux by as much as a factor of 3 (Fig. 4).

Climatological studies. Terrain and land use type variation make significant differences in microclimate over a region. We analyzed the normalized range ("spread factor") of nocturnal temperatures in the moderately complex terrain near Albany NY, taking advantage of data from a dense network of automatic weather stations. We found that the range of temperature as well as the minimum temperature is more strongly dependent on the terrain in the surrounding 3 km, rather than on absolute elevation alone (Fig. 5).

Previously we showed how spring could be detected in climate station records. A noticeable shift in the daily warming and moistening rate can be identified with leaf emergence. M. Czikowski is leading our effort to extend this work, asking whether runoff exhibits a detectable change at the time of leaf emergence, when one would expect enhanced evapotranspiration to compete for available soil moisture.

A second part of this effort is to identify shifts in runoff characteristics that may have accompanied reforestation of abandoned pastureland in New York State. A case study of the Wappinger's creek watershed (near Poughkeepsie, NY) has begun. Black (1963) initially reported that the presence of trees actually increased annual runoff. We have returned to this region to see what occurred in the intervening forty years. Agricultural fields were abandoned in the early 1950's. Since that time,
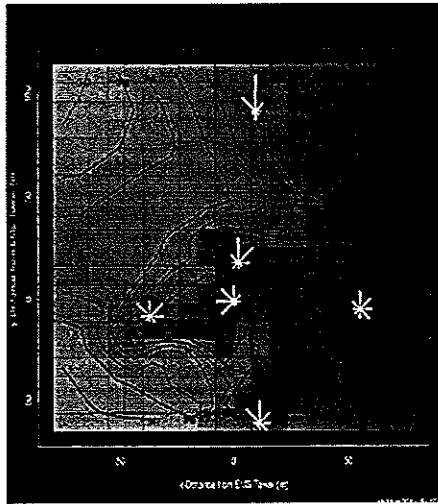
Fig. 1. Location of the five wind observations along the forest floor, DRAINO-2000. Average wind roses for nocturnal conditions at 1.5 m are shown (summer 2000, Harvard Forest EMS). CO_2 gradient inlets were located at the most northern and southern sites.
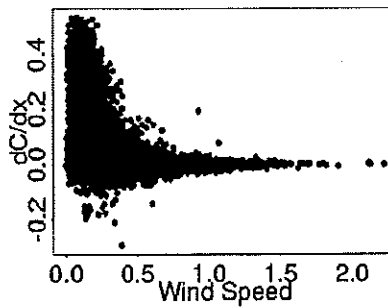

Fig. 2 Horizontal CO_2 gradient (ppm/m) at 1.5 m above the forest floor vs. wind speed (autumn, 2000).
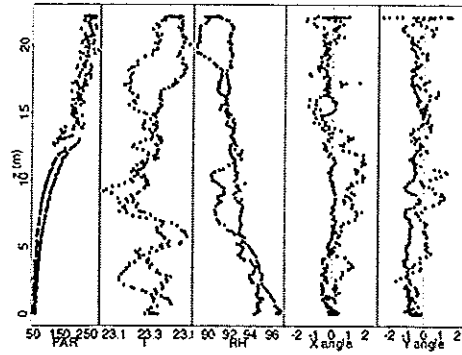
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Figure 3. From left to right are profiles of PAR (μmoles m^{-2} s^{-1}), temperature (°C) and relative humidity (%) collected at Harvard Forest on the overcast mid-afternoon of July 19, 1999, using the balloon system. The rightmost panels show two components of tilt (in degrees) of the balloon, indicating acceptably small shifts from the vertical for the PAR measurement. Both ascent and descent are shown for each parameter. The top of the canopy is at about 20m.
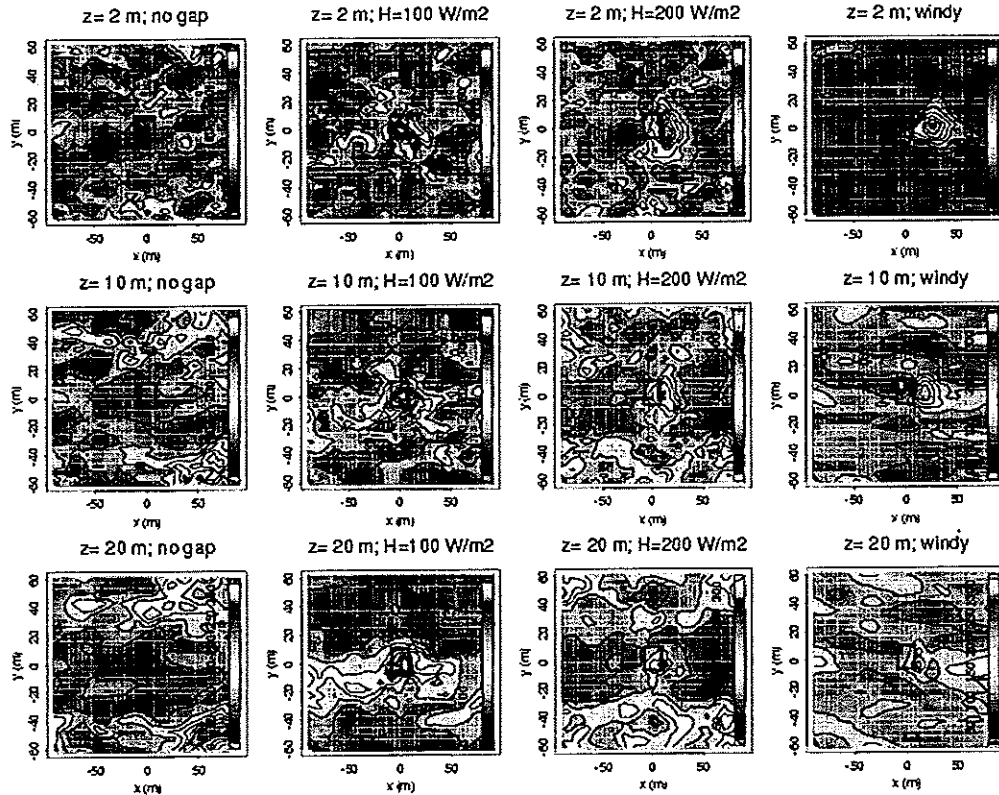
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Fig. 4. Results of large eddy simulations. A uniform scalar is emitted (100 W/m² in these units) at the surface. Canopy thickness is 20 m. Labels indicate height of horizontal cross section. Gap is indicated by thick rectangle near center of the domain. Sensible heat flux at canopy top is 80 W/m² at canopy top. Heating rate at base of canopy given in caption. Horizontal wind speed is 2 m/s (windy case: 5 m/s). Details in Acevedo (2001).
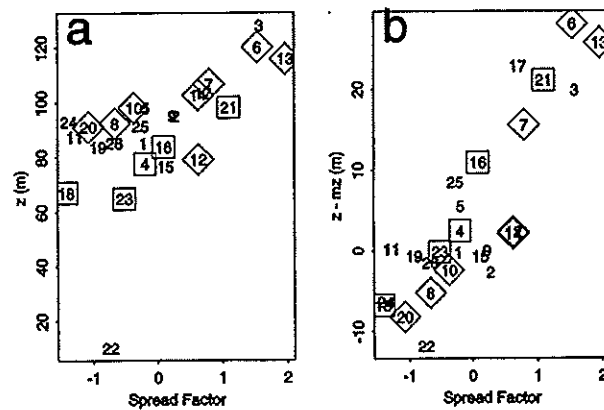

Fig. 5 Normalized spatial temperature spread normalized by the spatial standard deviation for the Albany weather station network. a SF vs. absolute elevation. b.: SF vs. *relative* elevation, the difference between station elevation and the mean elevation within three km. Squares indicate rural stations, diamonds are urban stations (from Acevedo and Fitzjarrald, 2001).

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the area has naturally reforested. Preliminary results (Fig.6) indicate that the watershed effects of reforestation on the fraction of precipitation that runs off are subtle. Current work aims to quantify land cover type and fraction, and then exercise a model that couples the partition of precipitation into evapotranspiration and runoff.

Acevedo, O., C., 2001. Effects of temporal and spatial transitions on surface-atmosphere exchanges, Ph. D. dissertation, Dept. of Earth and Atmospheric Sciences, Univ. at Albany, SUNY, 205pp.

Acevedo, O. C., and D. R. Fitzjarrald, 2001. The early evening surface layer transition: temporal and spatial variability. J. Atmos. Sci. (In Press).

Black, P. E., 1968. Streamflow increases following farm abandonment on eastern New York watershed, Water Resources Res. 4: 1171-1178.

Late Holocene Climate Change in New England as Inferred from Chironomid Remains in Lake Sediments

*D. Francis, J. Fuller, D. Foster, S. Barry and E. Doughty*

Paleoecological studies in central Massachusetts have indicated that changes in some tree species abundances began approximately 500-600 yrs BP, predating European settlement by about 250-350 years (Fuller *et al.* 1998). In order to investigate the factors that could be driving these changes, a multiproxy paleoecological study of vegetation, climate, and human impacts over the last 1000 years has been undertaken (See also Fuller *et al.*, this volume). Climate is potentially an important factor driving the observed vegetation changes, thus local climate change is being investigated using stable oxygen isotope studies, geochemistry, diatoms, and chironomid remains. In particular, the cold interval known as the Little Ice Age (approx. AD 1450 to 1850) coincides with the timing of the observed vegetation changes.

The Chironomidae are a family of insects (order *Diptera*) which have an aquatic larval stage, are extremely abundant, produce identifiable fossil remains in the form of head capsules that result from larval molting, and thus provide an ideal tool for paleoenvironmental reconstructions. Water temperature has proven to be one of the most important factors determining the distribution of chironomid species. We can exploit this relationship in order to hindcast both lake-water and air temperatures, and hence gain an understanding of past climate regimes. The use of chironomid remains and transfer functions to infer past temperatures has been shown to be an effective tool in the study of late-glacial and early Holocene climate change in Atlantic Canada and Europe. In this study, we use fossil chironomids from New England lake sediments to study the more recent and more subtle climate changes of the Little Ice Age period.

To produce quantitative estimates of past temperatures, a temperature inference model is constructed using modern species and environmental data from a transect of sites with a temperature gradient. Surficial sediments from the suite of sites are analyzed for chironomid remains and weighted averaging regression is then used to estimate the temperature optimum for each taxon in the "training set", based on their abundance at each site. These optima are then used to reconstruct past temperatures from down-core species data. For this study, we are using a training set of sites spanning the Atlantic coast region from Baffin Island to Maine. Much of the data is provided by Dr. Ian R. Walker (Walker *et al.* 1997). We are adding additional modern surface sites from New England.

The new inference model for summer surface water temperatures using weighted averaging regression results in an r^2 value of 0.9357 and a root mean square error of prediction of 2.26 °C (Fig. 1). This model was used to calibrate the down-core data from the six sites for which we have chironomid analyses completed (Fig. 2). In four of the six sites, there is a distinct decrease in chironomid-inferred temperatures at times corresponding to the Little Ice Age period (Fig. 2). Although the change is subtle (average of 1.3 °C), the timing and magnitude of the shift is consistent with other evidence for this cool interval (Bradley and Jones 1993). Statistically,

Wappinger Creek Watershed: annual runoff and precip
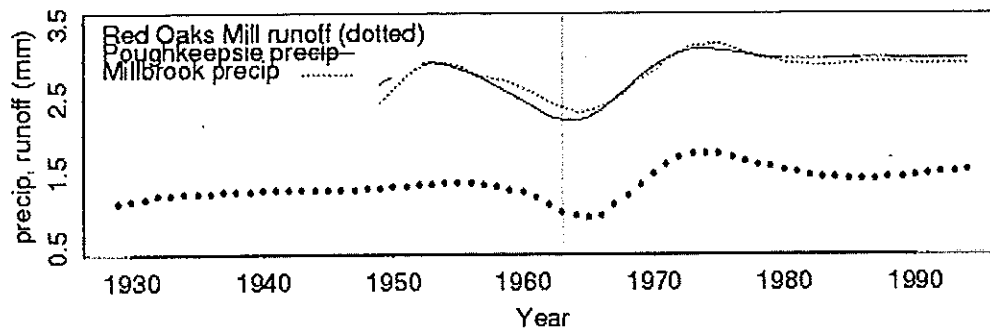
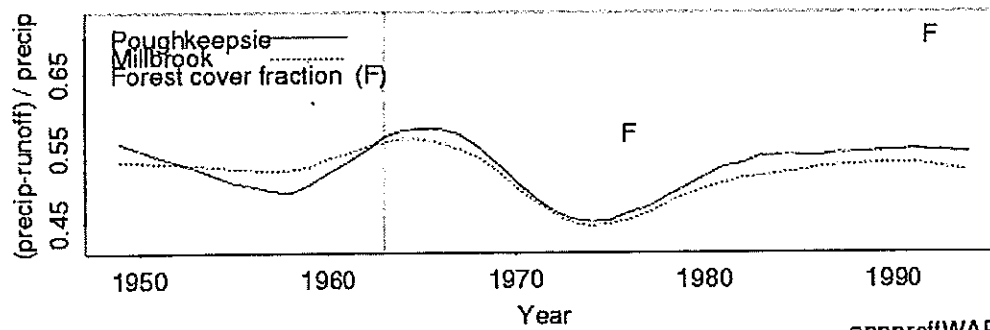## Wappinger Creek Watershed: Normalized precip - runoff

annproffWAP1()

Fig. 6. Top: Average runoff (R, Wappinger's Creek, NY, dots) and precipitation (P, Poughkeepsie and Millbrook NY) or the years shown. Bottom: (P-R)/P and forest cover fraction as determined from satellite images indicated by "F". Vertical line indicates last date analyzed by Black (19??).
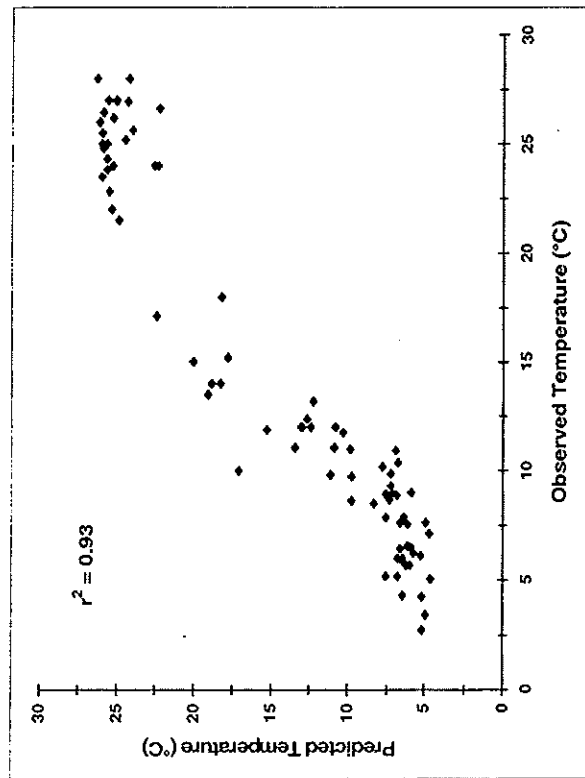
Fitzjarrald et al.

Figure 1. Results of weighted averaging regression model of the Atlantic coast training set, observed water temperatures at each site plotted against the temperature predicted by the model. The root mean square error of prediction is 2.26 °C.
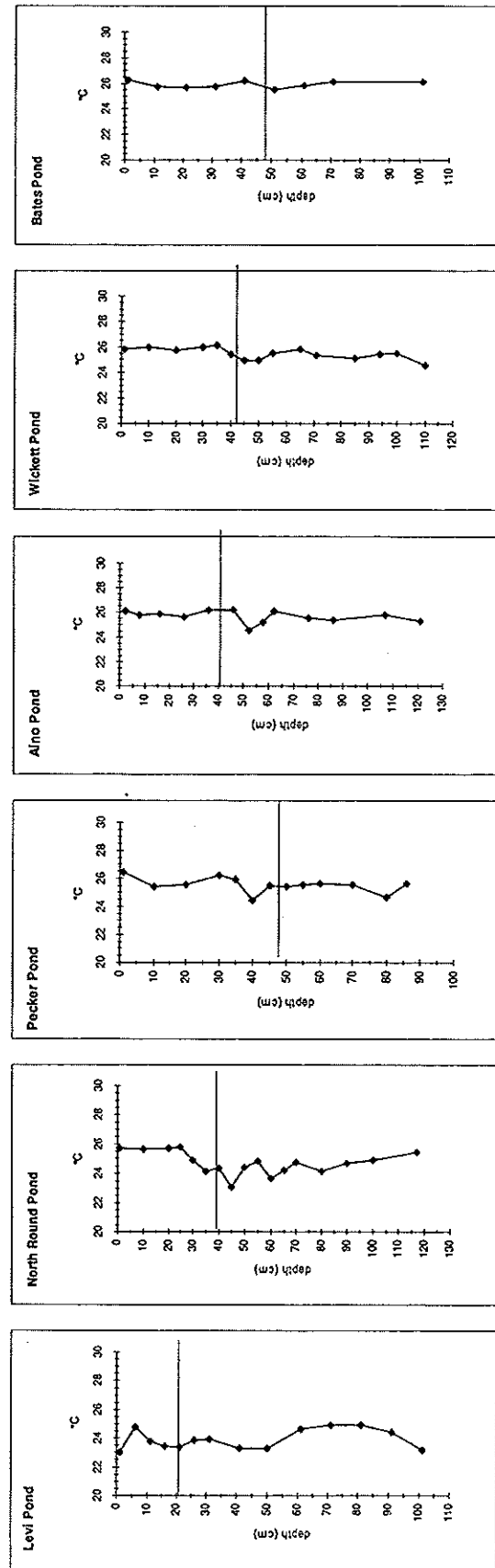

Figure 2. Chironomid-inferred summer surface water temperatures for six New England sites (see Fuller et al., Fig. 1, this volume). The dotted line in each profile is the approximate level of European settlement. The Little Ice Age period lasted from approximately 1450 to 1850 AD, and European settlement in the area was about 1750 to 1800 AD.

Francis et al.

the inferred temperature shifts are problematic since they are smaller in magnitude that the error statistic on the inference model. However, the fact that the temperature signal is manifest at several sites around the region provides more confidence in a Little Ice Age interpretation. Bates Pond, our southernmost site, shows no change in chironomid-inferred temperatures. Perhaps its location nearer to the coast provided it with a more oceanic climate, with less influence of the Little Ice Age cooling.

Future plans include adding more New England surface sites to the inference model, and refining the model to decrease the error estimate; increasing the resolution of chironomid analyses at the existing core sites, and adding three additional core sites, as well as combining the chironomid-inferred temperatures with the other climate proxies and vegetation studies for a complete interpretation of landscape dynamics during the period.

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Walker, I.R., A.J. Levesque, L.C. Cwynar and A.F. Lotter. 1997. An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada. J. Paleolimnol. 18:165-178.

Recent Climate Reconstruction in New England Forests

J. Fuller, D. Francis, D. Foster, S. Barry, D. Köester, R. Pienitz, B. Wolfe, E. Doughty, D. MacDonald, S. Clayden and N. Drake

Preliminary results from a multi-proxy study designed to characterize recent climate history in New England indicate that the vegetation of Northeastern North America was undergoing pronounced changes for 300-500 years before European arrival. Many of the forest dynamics ascribed to human land-use were actually continuations or modifications of trends initiated centuries earlier by climate change that seem to be coincident with the Little Ice Age, a globally-recognized climatic period characterized by cooler temperatures and highly variable growing season length and precipitation. We employ paleoecological, paleolimnological and historical approaches to reconstruct climate, vegetation, and cultural dynamics over the past 1500 years at sites arrayed across a north-south climatic and forest gradient (Fig. 1).

A geochronology has been established for six ponds using Pb-210, calibrated AMS radiocarbon dates, and the emergence of agricultural settlement indicators: grass (*Poaceae*), ragweed (*Ambrosia*), and sorrel (*Rumex*). High-resolution records using pollen assemblages, temperature inference models from chironomids (see Francis *et al.*, this volume) diatoms, stable isotopes, geochemistry (carbon and nitrogen flux), and charcoal abundance allow us to compare the pre- and post- European forest dynamics in light of independent data on climate history and human activity. Fossil pollen data from central Massachusetts record a long-term decline in the abundance of beech (*Fagus*) and hemlock (*Tsuga*) beginning around 500-600 years BP (Fig. 2), along with a general pre-settlement increase in % organic matter.

Regional forest dynamics in New England over the past 2000 years are also being examined using the North American Pollen Database as the main source of data on past tree abundances. To date 130 sites have been selected for analysis of the regional context of vegetation change during the Little Ice Age. Many of these sites record similar changes in pollen composition to those observed in fossil pollen data from central Massachusetts, however, there are considerable variations in the dynamics observed that appear to be correlated with elevation and latitude. While some sites show no evidence of significant vegetation change, the forested ecosystems across New England appear on the whole to have been highly dynamic during the past 1000 years, including the period prior to European settlement.
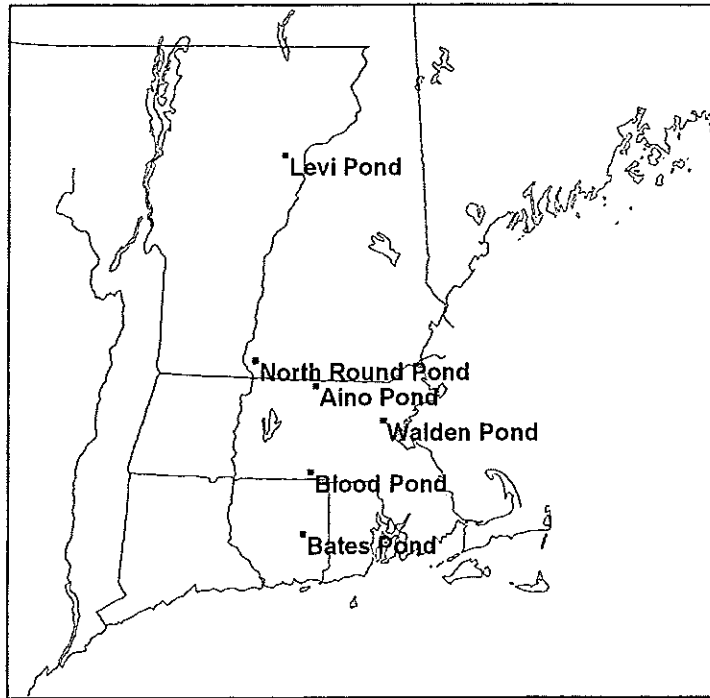
Figure 1: Core site locations along a north-south climatic and forest gradient in New England.
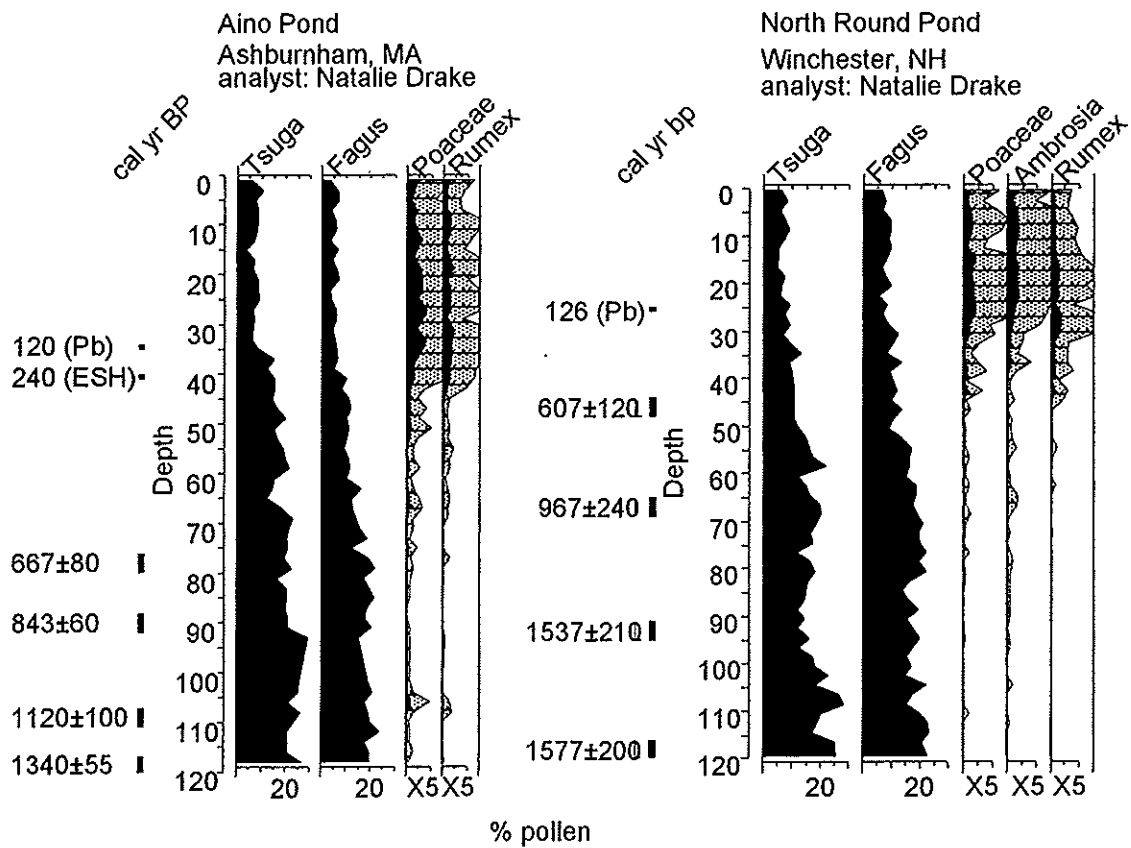

Figure 2: Fossil pollen assemblages for two ponds show a decline in hemlock (*Tsuga*) and beech (*Fagus*), beginning at about 600yBP. European settlement is indicated by the arrival of the agricultural weeds grass (*Poaceae*), ragweed (*Ambrosia*) and sorrel (*Rumex*).

Ecosystem Carbon Exchange in an Old-growth Hemlock Forest During Fall and Winter

J. Hadley and J. Schedlbauer

Carbon exchange above the hemlock stand near the Black Gum swamp at Harvard Forest has been measured by an eddy flux system since mid-October 2000. Because of the position of the eddy flux system, when wind is from the SW the system measures a forest dominated by hemlock (over 80% of basal area within 200 m) with trees up to 200 years old. To the NW, hemlock is only about 40% of basal area within 200 m, but hemlock and white pine form over half the basal area. To the NE and SE of the tower are hardwood-dominated areas, with hemlock and pine only 20 to 40% of the basal area.

Net carbon uptake up to 200 mmol m^{-2} day^{-1} (2.4 g m^{-2} day^{-1}) was measured in October and early November, but net carbon fixation nearly ceased in the second half of November, at the time of the first frost to reach -5 °C (Fig. 1). During this autumn period, simple two-factor regression models including either daily average air temperature, daily minimum air temperature, or soil temperature plus total daily photosynthetically active radiation (PAR) explained 75 to 77% of the variation in daily carbon exchange.

Carbon exchange was strongly affected by wind direction in October and November. During the day, carbon uptake was greatest with SW or NW winds, reaching up to about 10 µmol m^{-2} s^{-1}. During this period, maximum C uptake with NE winds was about 7 µmol m^{-2} s^{-1}. SE winds during the day were very rare. The pattern of carbon uptake was consistent with more photosynthetically active conifers to the SW and NW, and a majority of leafless deciduous trees to the NE. Carbon release at night was highest with SW winds, when the eddy covariance system was measuring hemlock-dominated forest. The Black Gum Swamp, beginning about 200 m from the eddy flux tower to the SW, may also have contributed to higher carbon release with SW wind at night. However, in spite of this, carbon release with SW winds averaged only about 75% of soil respiration in the hemlock stand, as estimated from soil temperature and chamber measurements of soil respiration. This suggests that either soil respiration was overestimated by chamber measurements, or a substantial fraction of CO_2 released from soil at night bypassed the eddy flux system when entering the atmosphere.

The data clearly shows that conifers at Harvard Forest can take up significant quantities of carbon after leaf-fall of deciduous trees. We were able to measure carbon uptake for only 10 complete days between mid-October and mid-November, but at the average rate measured for these days, carbon fixation for the 30-day period would be 58 g m^{-2} or almost 0.6 Mg ha^{-1}. Allowing for much lower carbon uptake during cloudy and rainy weather, monthly uptake might be half has much (0.3 Mg ha^{-1}). These numbers are a significant fraction of the average annual carbon uptake from 1992 to 1999 (≈ 2.0 Mg ha^{-1}) measured in a deciduous forest at the EMS tower at Harvard Forest, and suggest that the autumn can be an important period for carbon storage in conifer forests in central New England. Our preliminary data for the winter of 2000-2001 show that very little carbon was stored from December through March; however, this winter was colder than average with no significant midwinter thaw.

Atmospheric Reactive Nitrogen Partitioning and Fluxes at Harvard Forest

C. Volpe Horii, J. Munger, S. Wofsy and M. Zahniser

From August 1999 through November 2000, measurements of nitric acid (HNO_3), nitrogen dioxide (NO_2), and NO_2 eddy covariance fluxes were added to the extensive suite of trace gas measurements at the Harvard Forest Long Term Ecological Research site. These time-resolved, sensitive (50-200 ppt detection limit) measurements allow the roles of HNO_3 and NO_2 in total reactive nitrogen (NO_y) speciation and deposition to be specifically investigated, whereas past studies have largely inferred or estimated their relative contributions (Munger *et al.*, 1996). Because NO_2 is the precursor to ozone (O_3), the
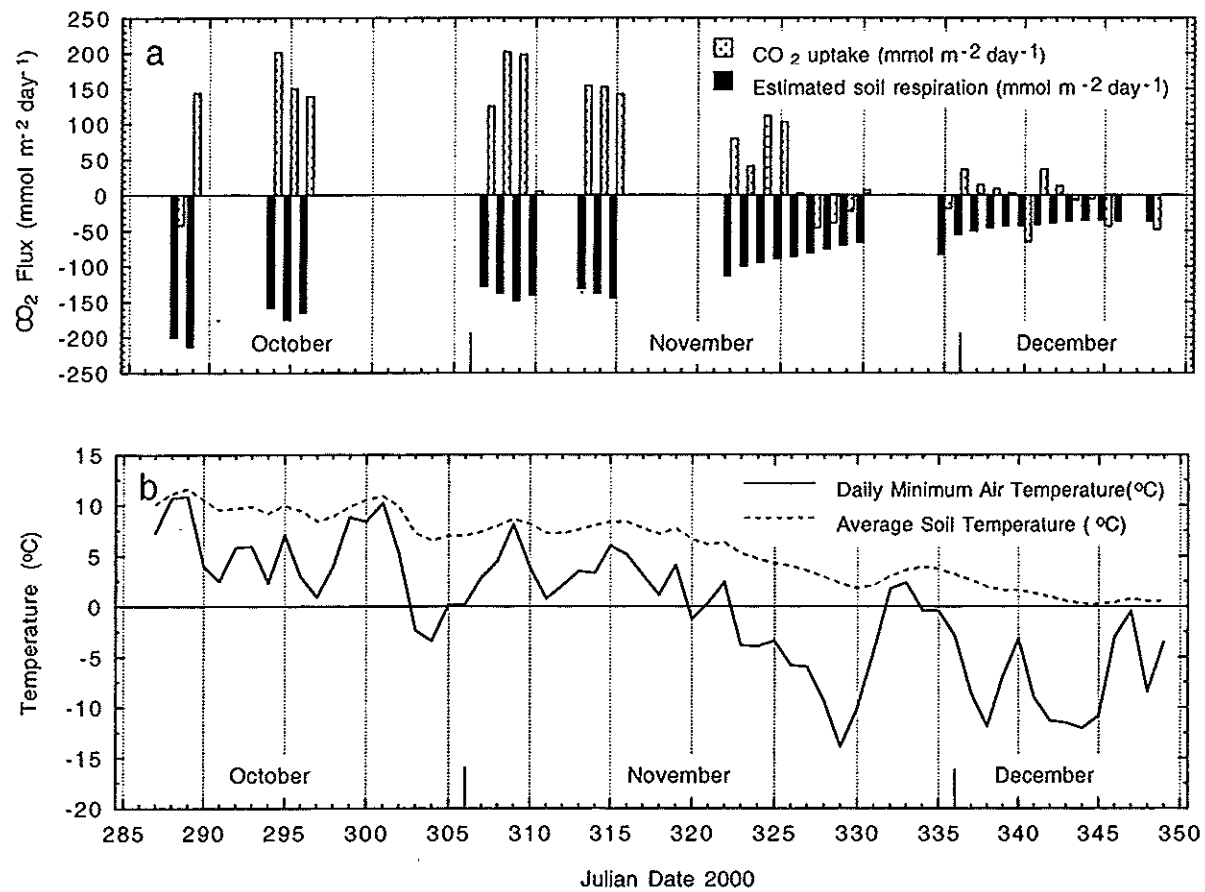
Figure 1. (a) Daily net carbon uptake as measured by eddy covariance and estimated soil respiration in fall 2000. Missing data are due to instrument failures or power interruptions. (b) Daily minimum air temperature measured at 22 m above ground in the upper part of the hemlock canopy, and daily average soil temperature at 10 cm depth (average of five locations).

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species-specific deposition of NO_y directly effects tropospheric O_3 production efficiency. A detailed understanding of the chemistry and removal mechanisms of NO_y and its constituents is thus crucial for accurate modeling of tropospheric chemistry and development of effective pollution control strategies.

For details on the measurement technique and installation of the dual Tunable Diode Laser Absorption Spectrometer (TDLAS) for unattended measurement of NO_2 and HNO_3, see Horii et al. (1999). Throughout the 15-month study period, data coverage for both species consistently improved so that by late summer 2000, the instrument experienced fewer significant data dropouts. The site was also connected to the Internet after installation of a fiber optic cable, making remote monitoring and control possible. At the beginning of December 2000, the fundamental instrument components were removed from the field site and installed in the laboratory for final calibration and validation experiments, including spectroscopic tests and inlet characterization.

Initial results for two periods during the fall of 2000 are shown in Figures 1 and 2. NO_2 and HNO_3 were measured by the TDLAS, NO by a chemiluminescence detector, and NO_y by reduction to NO on a hot gold catalyst and subsequent chemiluminescent detection. The two time series in figure 1 illustrate the highly variable conditions at the site, which make it ideal for investigating a range of photochemical regimes. Period A, Sept. 29 through Oct. 2, includes three large NO_y deposition events and elevated concentrations of all measured constituents, transported from the southwest. The correlation between HNO_3 and NO_y deposition is apparent, as is the shortfall between NO_x+HNO_3 and NO_y, where $NO_x = NO + NO_2$. Mean $(NO_x+HNO_3)/NO_y$ during period A was 0.51. Cleaner flows from the north during period B, Oct. 5-9, show much lower concentrations and a nearly closed NO_y budget with mean $(NO_x+HNO_3)/NO_y$ of 0.82. Although PAN was not measured during these particular periods, ongoing measurements at the site will provide the opportunity to validate a 1-D chemical model and simulate PAN for such times.

In Figure 2, HNO_3 deposition velocities are estimated by the slope of NO_y flux vs HNO_3

density. This estimate is only valid when NO_y deposition is dominated by HNO_3, which earlier studies predict under most conditions at Harvard Forest (Munger et al., 1996). The range of deposition velocities generally falls within those inferred from past measurements (Lefer et al., 2000; Janson and Granat, 1999). Analysis continues to determine whether points falling outside of this range are due to periodic degradations in the HNO_3 detection limit under non-ideal instrumental conditions, or whether other species such as NO_2 may be depositing.

Horii, C. V., M. S. Zahniser, D. D. Nelson, J. B. McManus, S. C. Wofsy. 1999. Nitric Acid and Nitrogen Dioxide Flux Measurements: a New Application of Tunable Diode Laser Absorption Spectroscopy. SPIE 3758: 152-1651.

Janson, R. and Granat, L. 1999. A foliar rinse study of the dry deposition of nitric acid to a coniferous forest. Agricultural and Forest Meteorology 98-99: 683-696.

Lefer, B. L., R. W. Talbot, and J. W. Munger. 2001. Dry deposition flux of nitric acid to a forested ecosystem at a rural northeastern U.S. site. J. Geophys. Res. (In Prep.).

Munger, J. W., S. C. Wofsy, P. S. Bakwin, S.-M. Fan, M. L. Goulden, B. C. Daube, ad A. H. Goldstein, 1996. Atmospheric deposition of reactive nitrogen oxides and ozone in a temperate deciduous forest and a subarctic woodland. J. Geophys. Res. 101: 12,639-12,657.

Munger, J. W., J. L. Field, J. W. Budney and S. C. Wofsy. 2001. Peroxyacetylnitrate concentrations at Harvard Forest. Harvard Forest Long Term Ecological Research Symposium (this issue).
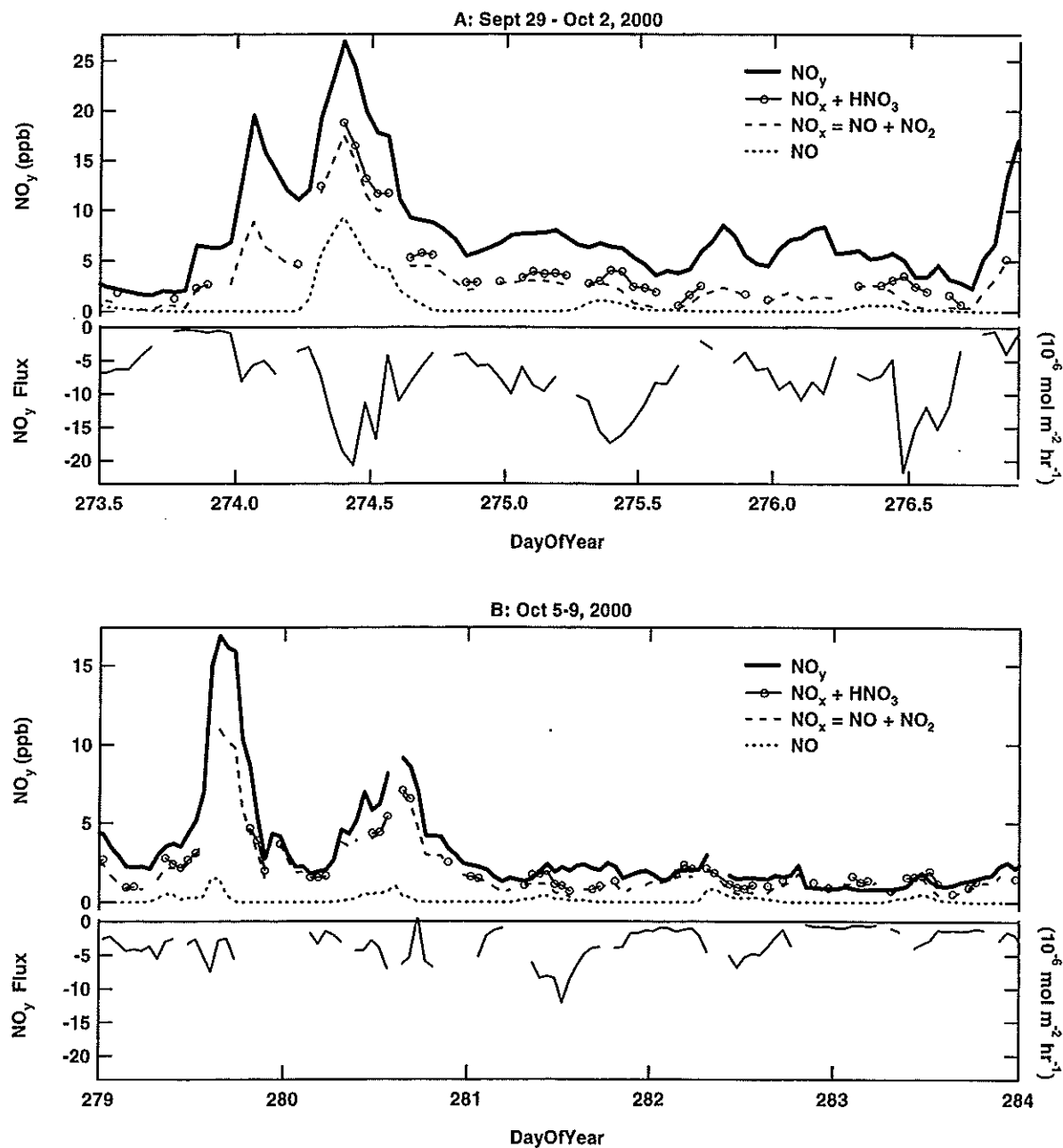
Figure 1. A: Sept 9 - Oct 2, 2000; B: Oct 5-9, 2000. NO_y and constituent concentrations (upper panels); NO_y flux (lower panels). NO_y flux events correspond to increased HNO_3, and NO_y is generally greater than $NO_x + HNO_3$ during period A. NO_y fluxes are smaller during period B, as are all of the concentrations, and the NO_y budget is at times completely attributable to NO_x and HNO_3. Although PAN was not being measured concurrently, concentrations up to several ppb were observed during the fall of 1999 (see Munger et al., this issue). Winds during period A were between 0.5 and 3.3 ms^{-1}, from the southwest until day 176, then variable. During period B, winds were from the northeast and northwest, 0.5 to 3.5 ms^{-1}.
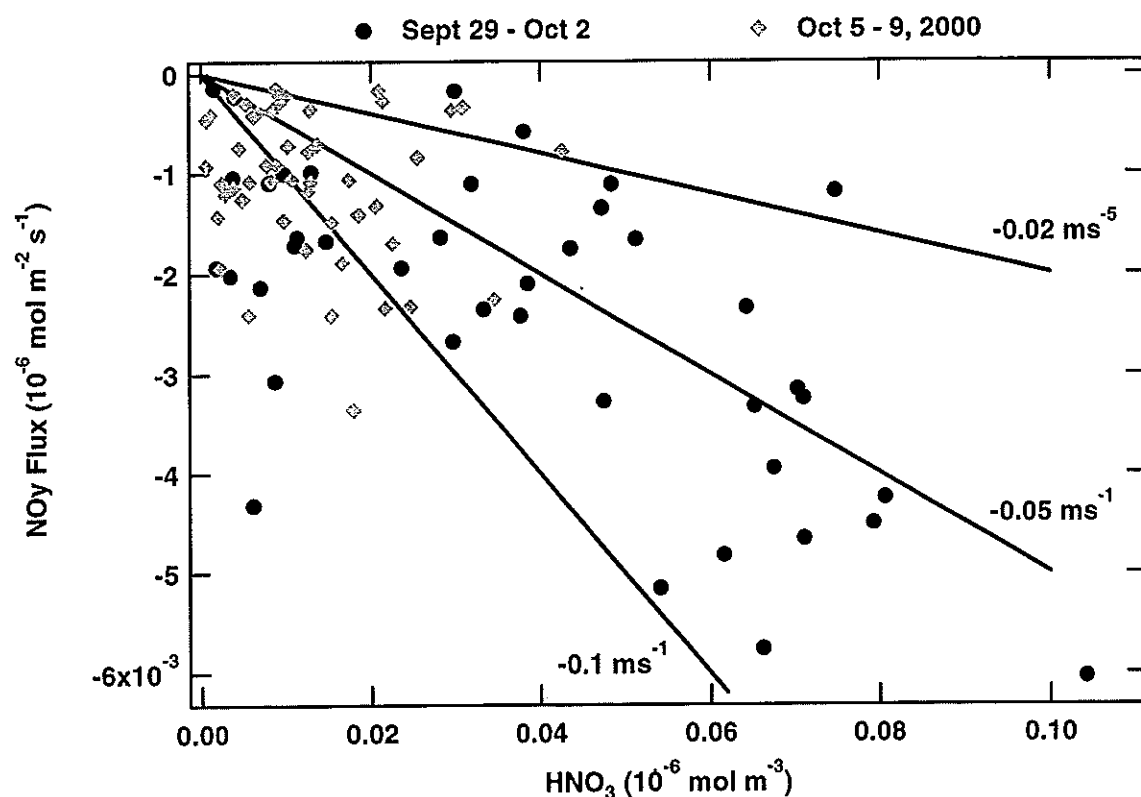
Volpe Horii et al.

Figure 2. NO$_y$ flux vs. HNO$_3$ density for periods A and B from figure 1. Under conditions where NO$_y$ deposits primarily as HNO$_3$, the slope of the line approximates the deposition velocity of HNO$_3$. The range agrees well with earlier studies where inferred HNO$_3$ deposition velocities were between -1 and -10 cm s^{-1} (Lefer et al., 2000; Janson and Granat, 1999). Some points with low HNO$_3$ and significant NO$_y$ flux (left side of plot) are close to the instantaneous TDLAS detection limit for HNO$_3$ (the detection limit varied with optical conditions in the instrument). These points may also represent NO$_y$ deposition by species other than HNO$_3$. As the eddy covariance fluxes for NO$_2$ are analyzed, we should be able to determine whether NO$_2$ deposition occurs.

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The Effect of Nitrogen Deposition on *Alliaria petiolata* and Indigenous Species Population Dynamics

S. Kaufman and F. Bazzaz

Alliaria petiolata is an herbaceous plant introduced from Europe that is invading forest understories across much of the United States. The rapid spread of *Alliaria petiolata* may be linked to increased levels of nitrogen deposition in northeastern forest ecosystems. If *A. petiolata* has a greater ability to utilize nitrogen or other resources, it may outcompete native plants in these ecosystems. This project experimentally investigates responses of indigenous plants and *A. petiolata* to increased and decreased nitrogen levels. Twelve 1 m^2 plots are established in uninvaded forest understory and 12 plots are established in adjacent forest understory invaded by garlic mustard at Harvard Forest. Similar experiments are established at a preserve in Belmont, MA and at Bartholomew's Cobble in Sheffield, MA. The two treatments and controls of no amendments and no amendments + *Alliaria* removal will be randomly assigned among the plots. Ammonium nitrate will be added to increase nitrogen levels. The decreased nitrogen levels will be achieved by adding sucrose to the plots, which increases decomposer biomass. Species diversity and percent cover of each plant species were determined in summer 2000 for each plot prior to the addition of treatments, and will be measured each year following the treatments. The plots will be treated in spring 2001 and data collected for 2 growing seasons. Photosynthetic rates and nitrogen use efficiency will be calculated for *A. petiolata* and the more common indigenous species and reproduction of *A. petiolata* and natives will be monitored. The information from this experiment, and from a complimentary common garden experiment at the Concord Field Station, will help to determine whether nitrogen deposition is changing competitive interactions between *A. petiolata* and indigenous plant species.

North Quabbin Region's Chapter 61 Spatial Database

D. Kittredge and A. Finley

Chapter 61 is a property tax incentive program, overseen by the Massachusetts Department of Environmental Management (DEM). The program offers a substantial property tax break to those private forestland owners who agree to keep their forestland under productive timber management. Enrollment in the forest management program requires preparation of a 10-year forest management plan that identifies landowner forestland objectives (e.g., improving: wildlife habitat, property esthetics, or timber resource) and active management for those forestland objectives. An explicit requirement of Chapter 61 is that the enrolled forestland be management to produce timber.

A spatially explicit data layer of the Chapter 61 database provides a tool for projecting forest management patterns onto the state's forest landscape. During the summer of 2000, the Chapter 61 data layer for the North Quabbin Region (NQR) of north central Massachusetts was built. The 416,000 acre NQR typifies much of Massachusetts's landscape. Forest blankets over 80 percent of the NQR and private forestland owners comprise the largest category of forest ownership. All 623 Chapter 61 plans were retrieved from the region's two DEM offices and the locations of the properties and the accompanying attribute information were used to build a geographic information system spatial data layer. All together, 51,209 acres of the NQR's forest is enrolled in Chapter 61. The average size of the Chapter 61 properties is 80 acres. Chapter 61 lands represent 15 percent of all forest in the NQR and 23 percent of private forestlands. When combined with the areas of public ownership in the NQR that actively manage their lands for timber (i.e., DEM state forest lands, 31,679 acres; Metropolitan District Commission, 63,323 acres; Massachusetts wildlife, 17,813 acres), it can be seen that 164,024 acres (49 percent of all forestland) are managed in a way to produce timber products at some level of intensity and with a management plan indicative of a long-term commitment or intention. Additional analysis of

forest harvest data (Kittredge, Finley, and Foster *in prep.*) indicate that approximately 24 percent of the NQR forest has undergone some level of harvest between 1984 and 2000.

In addition to providing an indication of the extent to which this landscape is producing timber products, these Chapter 61 data have implications for land protection policy throughout the region. Towns are afforded the right-of-first refusal to purchase Chapter 61 lands that are on the market. This enables communities to make strategic choices about land protection. The Chapter 61 and other related data layers are the key tool that the public, policy makers, and conservation organizations can use to make land and resource planning possible at a landscape scale.

Pattern and Intensity of Timber Harvest in a Complex Forest Landscape of Private and Public Ownership

D. Kittredge, A Finley and D. Foster

We used regulatory data to quantify the extent to which the North Quabbin (NQ) landscape undergoes disturbance caused by timber harvest. Our objectives are to document the spatial pattern, extent, and intensity of this disturbance regime, as well as any variations in temporal patterns and ownership based on physical or biological features.

The North Quabbin region has been the focus of numerous landscape-level studies conducted at the Harvard Forest. Its topography and soils are typical of central New England. The total land area is over 168,000 ha, with 81% of the land covered in forest. Small private ownerships (61%) dominate the area, though several large public ownerships, such as the MDC Quabbin Reservation, Massachusetts Department of Environmental Management lands, and others collectively occupy 39% of the land base.

A significant portion of the North Quabbin region has undergone some level of harvest between 1984 and 2000. During this period, 26.1 percent of all NQ forest has been harvested at least once. The average area of harvest activity is 16.5 ha (sd=18.8). There were between 1984 and 2000 an average of 126.9 harvest events annually, distributed throughout the region. Based on this frequency and extent of harvest, it is estimated that 2,095.6 ha will undergo some level of harvest disturbance annually, representing 1.5 percent of the region's total forest area.

There was no discernable trend or variation in the number of harvest events or harvest area from year to year between 1984 and 2000. The majority of harvest activity occurs on non-industrial private forestland. Harvest intensity, estimated by the number of cubic meters harvested per hectare, does vary with ownership- the most intensive harvesting occurring on MDC lands. The overall average harvest intensity per event was 40.5 cubic meters/ha.

There was no apparent trend or pattern of harvest disturbance based on slope, aspect, surficial geology, or elevation. Likewise, there was no apparent pattern based on coarse covertype (i.e., hardwood, softwood, or mixed, estimated by Landsat Thematic Mapper imagery). Harvest occurrences were spatially compared with the extent of 1830 forest, and no pattern emerged. We compared harvest disturbance distribution to the presence of roads, and similarly found no pattern. Lastly, we conducted a nearest-neighbor analysis of the harvest disturbance polygons themselves, to generate an estimate of whether the occurrences were distributed randomly, evenly, or in a clustered manner. The polygons appear to be randomly distributed with respect to one another throughout the landscape.

Though we do not have similar data for areas outside the NQ, we believe given similar forest cover, ownership pattern, and population density, it is reasonable to assume that the type of harvest disturbance that we document happens elsewhere throughout much of southern New England. We believe this form of disturbance is unique compared to other natural influences such as those caused by wind or ice. Given the rate, at which harvest disturbance is occurring, we believe much of the forestland in the NQ will be harvested at least once in the next 50 years. Given the relatively light intensity compared to the total volume per hectare, we believe harvest-based disturbance will result in a homogenization of

forest overstory conditions, masking differences that occurred more naturally before human-induced disturbance.

Ecosystem and Vegetation Response to Hemlock Logging

M. Kizlinski, D. Foster, D. Orwig, M. Kelty and R. Cobb

Eastern hemlock (*Tsuga canadensis*) forests in the Northeastern U.S. are being severely impacted by an invasive forest pest, the Hemlock Woolly Adelgid (*Adelges tsugae*, HWA). Eastern hemlock has no known resistance to HWA and complete removal of hemlock from forests is possible after several years of HWA attack. All size and age classes are being affected simultaneously, which may permanently alter the appearance, structure, and function of these ecosystems.

As the range of infestation expands, more landowners and land managers are faced with the decision of how to best cope with this situation. Two major options are to let the stand succumb to HWA and allow regeneration to occur naturally, or harvest the hemlocks while still living. Hemlock salvage operations have increased as a direct result of, or in anticipation of HWA infestation. Significant work has been done in the northeast on the effects of hardwood logging on various stand and ecosystem parameters; however, there has not been any impetus for wide scale hemlock logging or research on its significance, until now.

Vegetation and ecosystem dynamics were examined in ten hemlock stands in Connecticut and Massachusetts along a 13-year post harvest chronosequence. Data was collected from two replicate stands of five harvest ages (1,2,3, 7, and 13 years old). Identical measurements were taken at each site in adjacent, unlogged portions for comparison. The additional comparison of HWA effects are possible with this design as the unlogged stands include a range from healthy to heavily damaged forests.

Prior to cutting, logged stands ranged from 50.5 to 74.7 m^2 ha^{-1} basal area with hemlock comprising 66 to 99 percent of the total. Hardwoods in these stands are mostly red maple (*Acer rubrum*), oak (*Quercus* spp.), and black birch (*Betula lenta*), which were commonly harvested with the hemlock. Total basal area harvested ranged from 67 to 100%. Health of the remaining hemlock is largely dictated by the presence of HWA in the area. Six of the intact stands are damaged by HWA and have lost an average of 36% hemlock basal area. The four uninfested stands show little natural mortality with intact, healthy canopies. Compared to undamaged stands, HWA infested stands and cut forests show major differences in understory vegetation, ecosystem parameters, and microenvironmental.

Within three years after logging, seedling and shrub densities are quite high (Fig. 1). Black birch with a smaller amount of red maple dominate the seedling layer. Several species of *Rubus*, mostly *R. allegheniensis*, compose the shrub layer. Light demanding herbaceous species such as *Erechtites hieracifolia* and *Phytolacca americana* were also common in recently cut areas. The presence of these species decreased with age as the dense birch seedling layer formed a low, dense, canopy shading the forest floor. Attaining sapling size (>1.5 cm d.b.h.) by 7 years after harvest, the black birch cohort became quite uniform in species composition, height, and density. After 13 years, new seedling establishment, still dominated by black birch, decreased considerably indicating that birch will not be replaced by another species, and continue be the most common species at these sites for some time.

HWA and logging also impact ecosystem properties in the forest floor and in the underlying mineral soil. Logged and heavily infested stands have higher N concentrations in the forest floor (Fig. 2). A decrease in forest floor mass accompanying disturbance coupled with increased N concentrations combine to form similar total pools when compared on an area basis. Nitrogen mineralization rates were lower in disturbed stands (Fig. 3) indicating retention and accumulation in the forest floor and mineral soil. Despite similar N pools, resin bags in newer cuts intercepted much more N than those in older cuts implicating lack of vegetative uptake. This contradiction is possibly due to the complete conversion of a hemlock litter based forest floor to
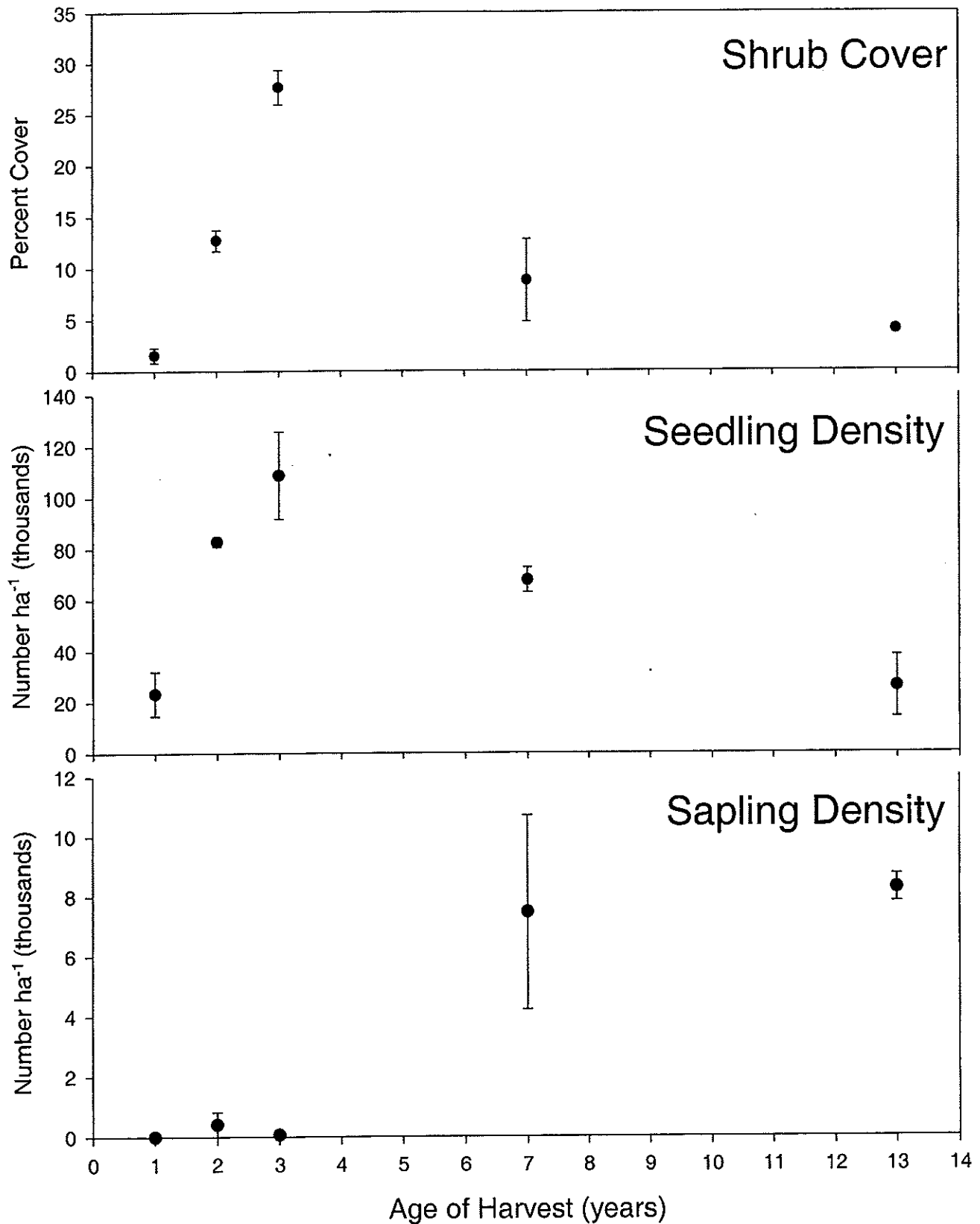
Figure 1. Vegetation compostion following hemlock harvesting. N=2 for each age, bars are SE. Seedlings are <1.5 cm d.b.h. and saplings are 1.5 to 9.9 cm d.b.h.. Shrub species are dominated by *Rubus* and both seedling and saplings are dominated by black birch.
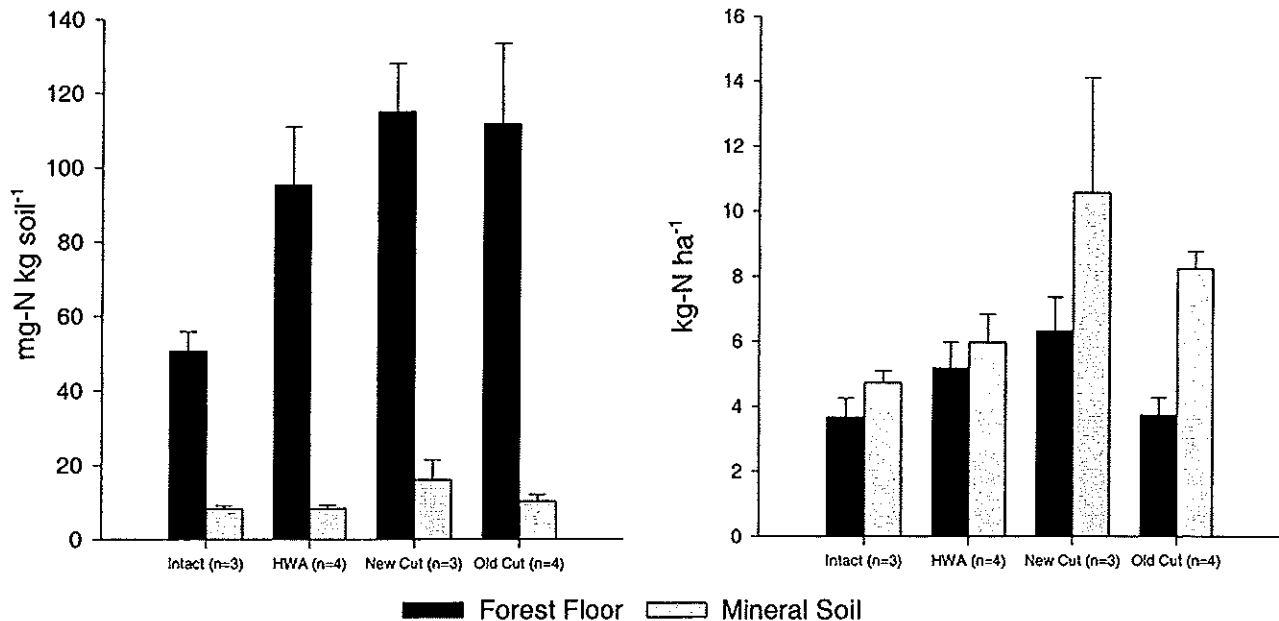
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Figure 2. Average inorganic N pools (NH_4+ NO_3) in healthy (Intact), HWA damaged, and harvested hemlock stands. Means and SE from number of stands in that treatment. Changes to forest floor environment and composition following disturbance yield dramatic increases in concentration of N in the forest floor.

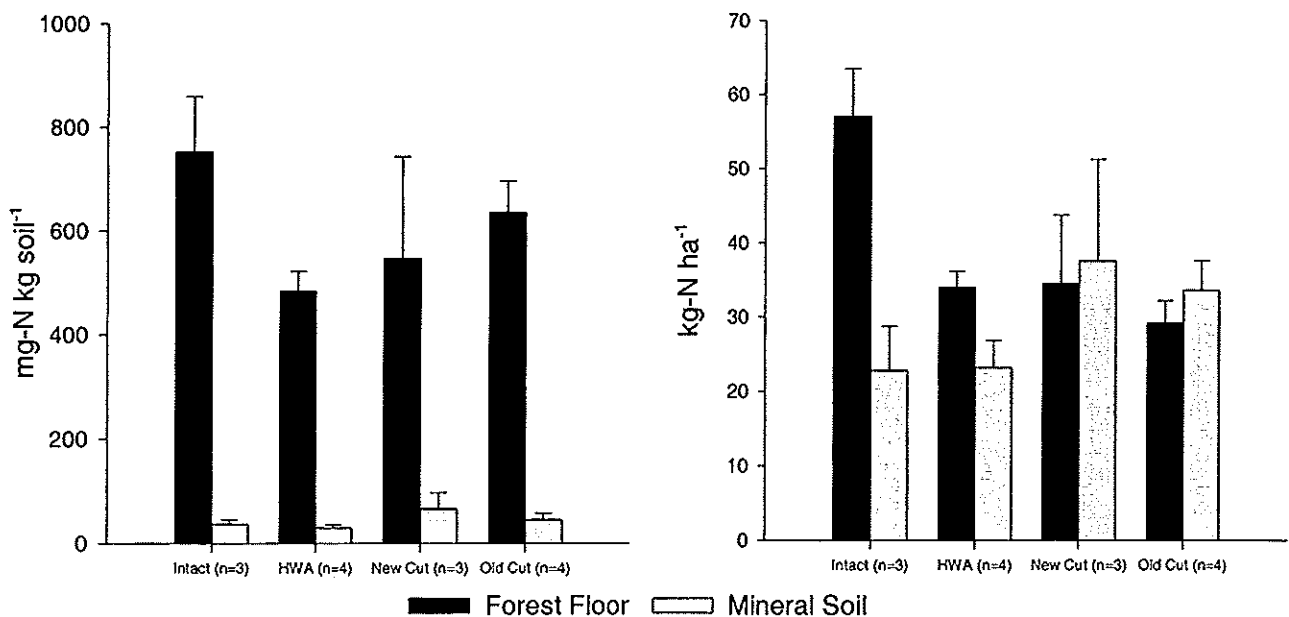**Figure 3.** Nitrogen mineralization (NH_4+ NO_3) in healthy (Intact), HWA damaged, and harvested hemlock stands. Means and SE from number of stands in that treatment. Despite lower production rates in the disturbed stands, N pools are higher in those stands (Figure 2) indicating interactions between plant uptake and changes to type and quantity of litter inputs.

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one developing under the regenerating hardwoods. Other factors studied include soil moisture levels, decomposition rates, and light environment.

Hemlock logging, unlike HWA damage, creates more predictable regeneration patterns. Soil processes and characteristics also show different impacts for years following disturbance. Results suggest that HWA is having a profound influence on forest structure and function directly through reduced vigor and increased mortality, and indirectly though the increase of hemlock logging.

Paleoecological and Ecological Studies on Diatoms in Four New England Lakes

D. Köster and R. Pienitz

Human disturbance in the context of environmental change: re-evaluating the long-term dynamics of New England forests

Results from prior studies indicate that the vegetation of northeastern North America underwent pronounced changes for 300-500 years before European arrival. Many of the forest dynamics ascribed to human land-use were actually continuations or modifications of trends initiated centuries earlier by climate change coincident with the Little Ice Age. Using biological (diatoms, chironomids), geochemical, and stable isotope proxies from New England lake sediment cores in conjunction with historical and dendrochronological databases, we will interpret the timing, magnitude, and nature of climate change for this region over the past 1500 years. Diatom analysis will be carried out on cores from four lakes to reconstruct past changes in nutrients, pH and other limnological parameters.

Two lakes have been anlysed to date: Levi Pond in Northern Vermont and Walden Pond in Massachussetts. In the diatom stratigraphy of the 80 cm long core from Levi Pond, two major shifts in the assemblages were observed. The greatest change occurred at a depth of 19cm (~1820 yr AD, ^{210}Pb-dated), coincident with widespread logging in the area. The second change occurred recently (depth = 6cm, ~1910 yr AD, ^{210}Pb-dated),

probably reflecting the reforestation of the catchment. This latter change is indicated by the replacement of benthic (pennate) diatoms (e.g. *Navicula* spp., *Pinnularia* spp.) with planktonic (centric) diatoms (e.g. *Melosira, Aulacoseira* spp), possibly indicating increasing water turbulence and/or higher water levels. Furthermore, a long-term trend of slight acidification was indicated by a decline of circumneutral taxa and an increase of acidophilous species, most likely due to progressive cation (e.g. Mg, Ca) leaching in the watershed resulting in a decreased buffering capacity of the system.

The analysis of the Walden Pond sediments revealed one dramatic change between about 1920 and 1970 AD (^{210}Pb-dated). The species *Cyclotella stelligera*, which prefers oligotrophic waters of low conductivity, drops from an abundance of 75 % down to less than 5% and is replaced by two species indicative of higher nutrient concentrations and increased conductivity (*Asterionella formosa* and *Fragilaria nanana*). This reflects the well-documented eutrophication of Walden Pond caused by the rising recreational use in the last century.

Future work will apply the model of Dixit *et al.* (1999) for inferring quantitative changes in limnological parameters, such as pH, total phosphorus, and chloride. Statistical analyses will test the appropriateness of this model for our sites and the reliability of the reconstructed trends. Analysis of two more lake sediment cores will allow us to interpret our results on local and regional scales. A sediment trap study in one of the lakes will identify the seasonal succession of diatoms and give insight into the sediment formation, thus aiding interpretations of our reconstructions. The synthesis of our data with data contributed by the other indicators will facilitate the separation of climatic and anthropogenic effects on ecosystems in New England, as well as giving a detailed picture of the Little Ice Age episode in this region.

Responses of Invasive Species to Release from Herbivory: Evolutionary and Phenotypic Changes in Chemical Defenses and Reproductive Vigor in Three Plant Species in the Brassicaceae

K. Lewis and F. Bazzaz

We will investigate the evolutionary and phenotypic changes that occur in invasive species in their new ranges in response to escape from herbivory. We have selected three species: *Alliaria petiolata*, *Hesperis matronalis*, and *Cardamine impatiens*, all ⁻ from the family Brassicaceae and all introduced from Europe and invasive in Massachusetts. Plants in this family produce defense compounds in the form of glucosinolates, which are high in nitrogen and sulfur, two often limiting elements in plant communities.
Specifically, we will determine if invasive populations differ significantly from original populations in defense chemistry, defense allocation (inducible or constitutive defenses), and reproductive capacity. We will determine the role of resource availability (nitrogen and sulfur) in geographic patterns of chemical defense statement. Finally, we will determine the proportional contribution of genetics, abiotic environmental factors, history of herbivory, and intergenerational (maternal) effects on defenses in these plants.

Warming, Carbon Storage, and the Question of Feedbacks to Vegetation

H. Lux, J. Melillo, T.Ahrens, P. Steudler and F. Bowles

Ten years of elevated soil temperatures at the Harvard Forest soil warming experiment suggest that there are limits to a positive feedback to the global warming cycle. In years nine and ten of treatment we have observed no significant differences in releases of CO_2 between the heated and control plots (Fig. 1). These results are in contrast to theories of Woodwell and others (Kirschbaum 1995, Woodwell 1995), proposing that the acceleration of global warming due to carbon cycle feedbacks may be an important component of future climate change.

Results from modeling experiments conducted by Cox *et al.* (2000) suggest that carbon-cycle feedbacks could significantly accelerate climate change over the twenty-first century but allow that the magnitude of these feedbacks is still highly uncertain. Gaps in the basic understanding of terrestrial ecosystem processes prevent the formation of a clearer picture. For example, the potential switch of the terrestrial biosphere from its current role as a carbon sink (Schimel *et al.* 1995) to a carbon source is critically dependent upon the long-term sensitivity of the respiration of soil microbes to global warming, which is still a subject of debate (Giardina and Ryan 2000).

Field results from the soil warming experiment indicate that only a small fraction of the soil carbon in this mid-latitude forest ecosystem will be lost to the atmosphere in response to warming. We find that a 5°C warming of the soil for a decade results in a loss of about 11% of the carbon stored in the top 60 cm of soil, with most of this loss occurring in the first four to five years. By the end of the decade, warming no longer stimulates soil carbon loss. In addition, we find that warming accelerates the soil nitrogen cycle, particularly in the early years of warming (Fig. 2). This acceleration has the potential to stimulate plant carbon storage.

Calculations based on nitrogen uptake in vegetation at the Chronic N Experiment (Magill *et al.* 2000) allow us to estimate how much additional carbon might be stored in plants as a result increased N availability at soil warming. Our calculations show that the potential increase in carbon stored is large enough to more than compensate for the soil carbon loss, so that warming may actually stimulate carbon storage at the ecosystem level in this mid-latitude forest.

An experiment in Flakaliden, Sweden provides the most convincing field evidence to date of enhanced carbon storage in vegetation as a result of warming. In 10x10m heated plots Linder and colleagues found increased concentrations of foliar N and a more than 50% increase in stem-wood growth after 5 years (Bergh and Linder 1999, Jarvis and Linder 2000). We propose that
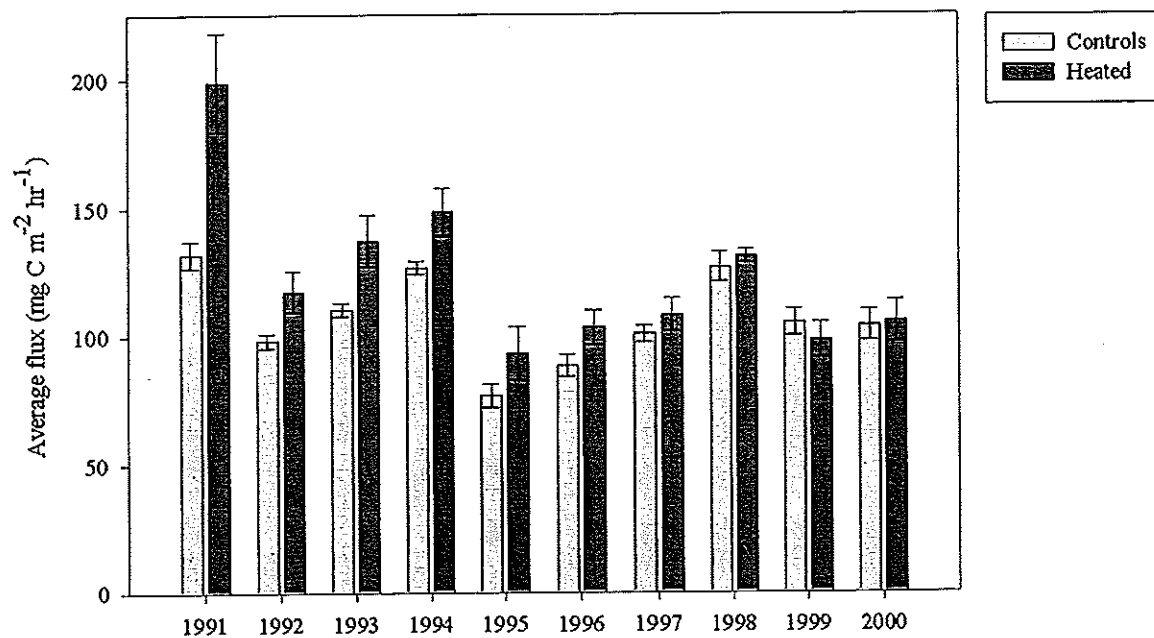
Figure 1. Average yearly fluxes at the Harvard Forest soil warming experiment.
Measurements are made April - November. No significant differences were found
between the Control and Disturbance Control Plot: both sets were used in Control data.
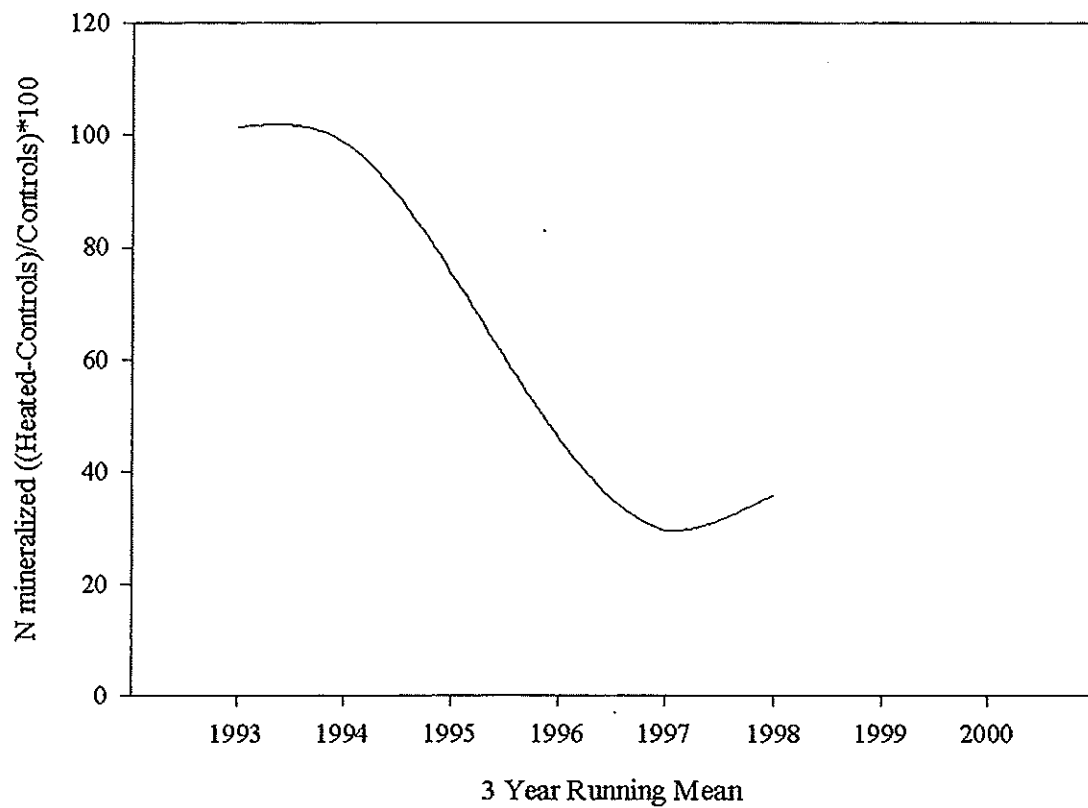
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Figure 2. Nitrogen mineralization at the Harvard Forest soilwarming experiment.
NMIN in Heated plots, percent increase from Control plots.

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this increase in C storage is the result of increased N availability due to warming.

We are currently expanding our research from the original soil warming experiment to investigate this important feedback at the Harvard Forest. The existing 6x6m plots on the Prospect Hill tract are not large enough to allow for the study of treatment effects on trees, so we are installing a larger warming experiment. The new experiment will have two 30x30m plots, a heated and a control plot, on the Tom Swamp Tract of the Harvard Forest. Many aspects of this experiment will be the same as the original. Using resistance heating cables and thermisters, we will maintain a 5°C differential between the heated and control plots, year-round. In addition to the trace gas, nitrogen mineralization and soil water parameters measured to date, we will also be measuring woody increment and other vegetation metrics to allow us to investigate the plant response to perturbations in the carbon and nitrogen cycles.

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Chronic Nitrogen Additions to Two Forest Stands

A. Magill and J. Aber

The nitrogen saturation potential of temperate forests in the Northeastern United States and in Europe is of mounting concern as nitrogen deposition from anthropogenic sources continues to increase. In order to determine the long-term impact of N inputs, key indicators of nitrogen saturation, such as forest productivity, foliar chemistry, soil net mineralization rates and soil solution chemistry, have been measured on plots receiving NH$_4$NO$_3$ additions at the rate of 0, 5 and 15 g N m^{-2} yr^{-1} since 1988. A nitrogen plus sulfur treatment was also included through 1998 with NH$_4$NO$_3$ additions at the same rate as the low N plots plus 7.4 g N m^{-2} yr^{-1} of sodium sulfate. Beginning in 1999, the N+S plots received only the NH$_4$NO$_3$ additions. Plots were established in two forest stands, a red pine plantation and a mixed hardwood stand, located in the Prospect Hill tract of Harvard Forest.

Root biomass cores were collected in 1999 to a depth of 20 cm. Data from these reveals that the largest percentage of fine roots (kg roots ha^{-1} soil) were found in the 10 – 20 cm depth (Fig. 1). However there were no significant differences in root mass between treatments. Soil water nitrate

Chronic Nitrogen Amendment Plots
Total root biomass by soil horizon

Live and dead root mass from soil cores collected July 5, 1999. Cores were separated by horizon, sorted, washed dried and weighed. Values are means of 10 samples taken in each plot. Table below lists percent of total root biomass by horizon.
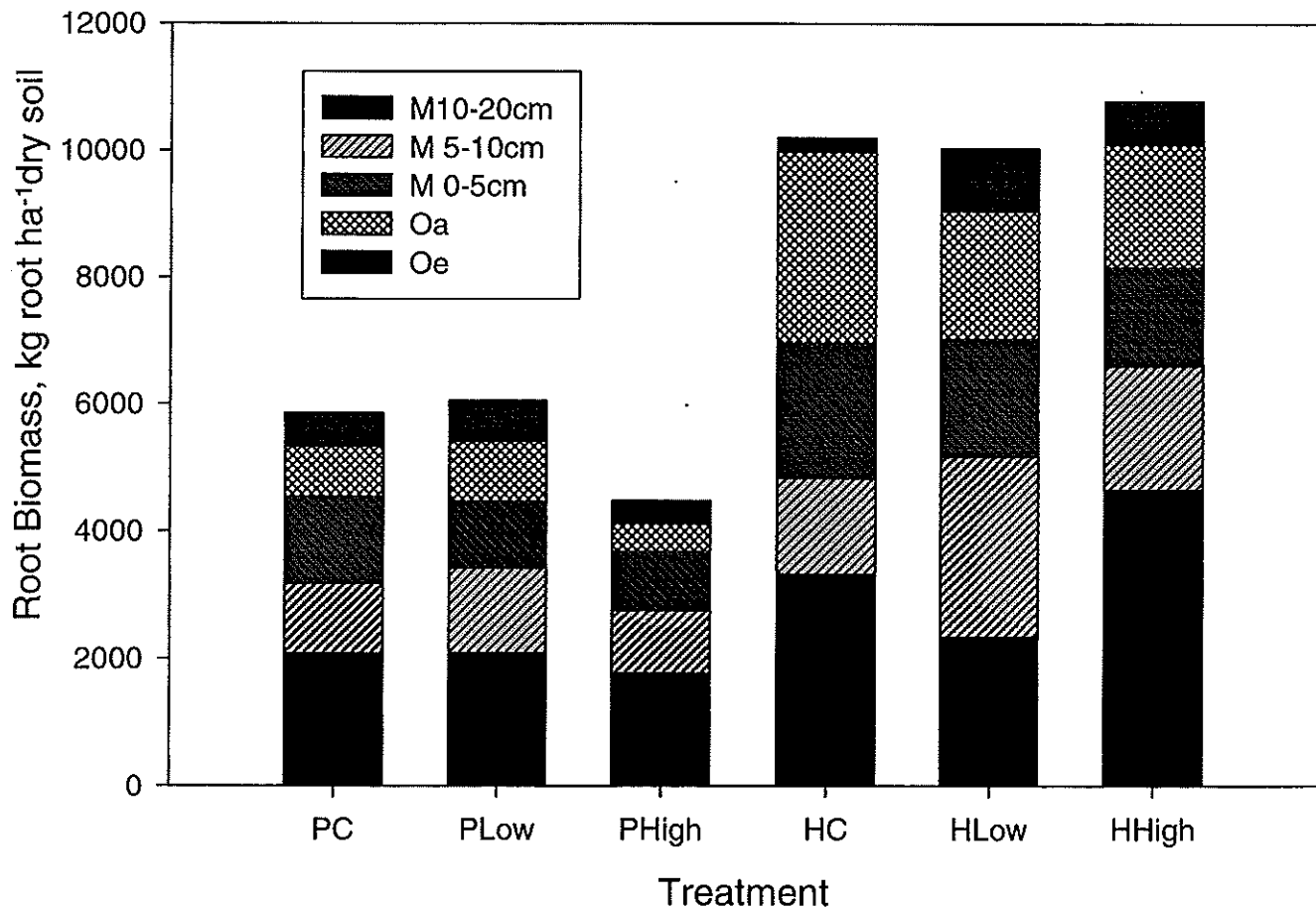
Horizon	PC	PLow	PHigh	HC	HLow	HHigh
Oe	8.8	10.4	8.0	2.1	9.8	6.2
Oa	13.4	15.5	9.4	29.5	20.0	18.0
M0-5	23.4	17.4	21.0	20.9	18.5	14.5
M5-10	18.6	21.9	21.8	14.6	28.3	18.0
M10-20	35.7	34.8	39.9	32.8	23.4	43.3

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concentrations remain elevated in the high N treatment plots of both stands, as does green foliar nitrogen content. Data currently under analysis include root nitrogen and carbon content, soil bulk density, fungal and microbial biomass, and zero tension lysimeter cation concentrations.

Forest Soil Respiration and Organic Matter Dynamics after Ten Years of Manipulated Above- and Belowground Litter Inputs

P. Micks and K. Nadelhoffer

In 2000 we completed the first ten years of treatments and data collection at the Harvard Forest DIRT experiment (Detritus Input and Removal Treatments), a long-term study of linkages between forest soil organic matter (SOM) and above- and belowground plant litter inputs across decadal time scales. We are integrating the results of process-level studies to characterize how plant litter inputs feed back to influence SOM dynamics and nutrient cycling in this forest ecosystem. Results from this study and two similar experiments Pennsylvania and Wisconsin forests provide valuable insights into the ways in which microbial processes and labile C and N pools in forest soils are linked to amounts and sources of plant inputs.

Treatments established at the Harvard Forest in 1990 include: doubling aboveground litter (double litter), exclusion of aboveground litter (no litter), exclusion of root inputs by trenching (no-roots), and exclusion of aboveground litter and root inputs (no inputs), on replicated 3m x 3m plots (n=3). An additional treatment (O/A-less) was implemented in 1991 to track the recovery of impoverished soil by replacing O and A horizon soil with B horizon material and allowing normal litter inputs to occur thereafter.

Aboveground litter inputs affected soil C and N masses more than did root inputs throughout 10 years of manipulations. Soil C and N masses (Oea+0-10 cm depth mineral soil) after year 1 were similar among the six litter manipulation treatments, but by year 10, C and N stocks increased and decreased, respectively, in response to doubling and excluding aboveground litter inputs to root-intact soil. However, aboveground inputs did not have the same effect when root inputs were also excluded; C and N stocks declined only slightly in no-inputs soils relative to no-roots after ten years. O/A-less soil C stocks remained at 20% of control C stocks. Soil C/N ratio increased in double-litter, no-roots, and no-inputs treatments, and declined in O/A-less soil.

In contrast, soil respiration was influenced more by root inputs than aboveground litter (Figs. 1 and 2). Respiration rates in root-excluded soils were consistently below root-intact soils from year 1 on. Doubling or excluding aboveground litter respectively increased or decreased respiration, in proportion to input amounts, from root-intact soils during the first four years. However, double-litter soil respiration fell below control rates by year 8. Root-excluded soil respiration declined markedly relative to controls between years 8 and 10, largely attributable to plot retrenching in year 9. Respiration in the impoverished O/A-less soil slowly increased to 45% of control respiration in 10 years.

Changes in soil respiration relative to total soil C mass indicate changing SOM quality across treatments and time (Fig. 3). Root inputs remain the stronger influence on the proportion of labile C, which declined to 40% of control levels by year 10 in the root-free soils. Lack of aboveground litter continued to decrease labile C relative to total soil C in root-intact soil after 10 years but not in root-free soil. These results suggest that aboveground inputs more strongly influence SOM mass, but root inputs have a stronger effect on SOM quality. 10 years of doubling litter inputs increased total soil C but the labile proportion ultimately declined below the control, demonstrating a long-term negative effect on decomposition. Although total C in the impoverished soil did not increase markedly, the large labile proportion dropped by half as the young organic matter became more stabilized after 10 years of decomposition.

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Mean Daily CO2 Efflux from Harvard Forest DIRT Plots
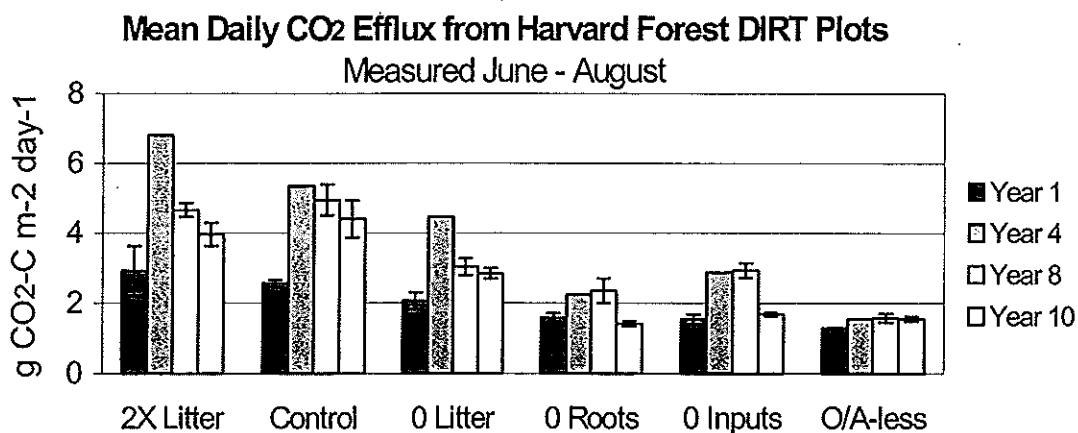### Measured June - August

Figure 1. Soil respiration rates measured at the Harvard Forest DIRT plots. Flux data were collected approximately from June-August. Year 1 data were collected with the soda lime technique which may underestimate fluxes. Data for other years were collected with and IRGA (infrared gas analyzer). Climatic factors contribute to interannual variation.

Treatment Soil Respiration Relative to Control
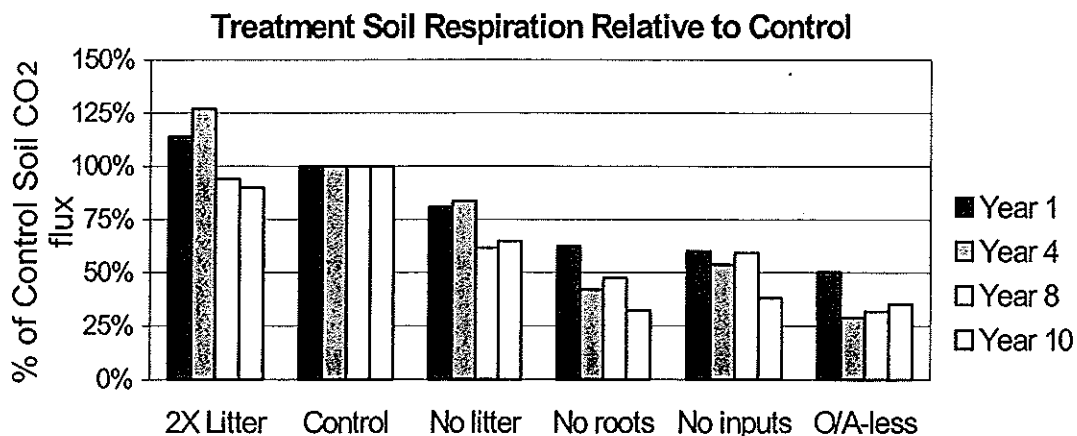

Figure 2. Data from Figure 1 with treatment respiration shown relative to control respiration for each year.
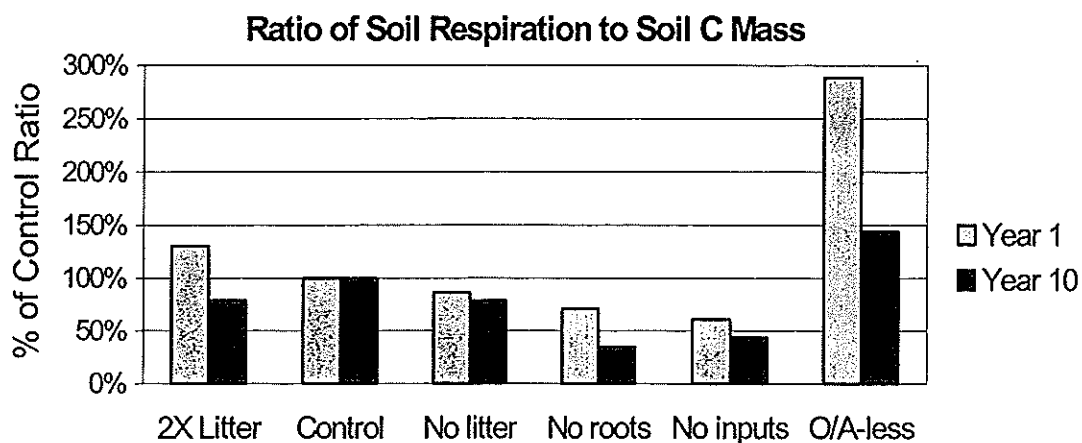
Ratio of Soil Respiration to Soil C Mass

Figure 3. Ratios of June-August CO2-C fluxes to soil C mass (Oea + 0-10 cm mineral soil) by treatment, after one and ten years of litter manipulations. Ratios for treatments are shown relative to controls.

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

Q. Min and K. Moore

Regional and interannual variability in solar radiation, cloudiness, and aerosol concentrations are important to studies of regional carbon balance. Such variation influences the light environment of forest and other plant canopies, and has an impact on carbon uptake. Our project approaches these issues through the use of a network of multifilter rotating shadowband radiometers (MFRSR), the use of GOES satellite data to retrieve surface solar radiation and models of the solar spectrum to infer changes in the spectral composition of radiation under varying cloud and aerosol influence. Testing of the influence of light on canopy uptake is being done with radiation use efficiency models, and with PnET (see abstract by Moore, this issue).

Figure (1) is a ten-year time series of aerosol optical depth at 415 nm and Angstrom exponent coefficient from MFRSR at several sites in the Northeastern US. The Angstrom coefficient is related to the aerosol particle size distribution: the smaller Angstrom coefficient, the bigger aerosol particle size. These data show the clearing of the stratosphere following the 1991 eruption of Mt. Pinatubo, the excursion of the Pinatubo event above the apparent local annual cycle and recovery of the stratosphere to "background" levels in magnitude as well as in particle size distribution. Good agreement among the several stations is evident overall, suggesting the dominance of large-scale factors in the aerosol climatology; differences among them, for instance the generally lower AOD and Angstrom coefficients at the Maine site (Figure 2), may point to the importance of local circulations, such as the sea breeze. Sea salt aerosols, generally, have relatively larger particle size, resulting smaller Angstrom coefficient. Urban environment at Albany has higher aerosol concentration, exhibiting larger AOD.

Statistics of aerosols and clouds over Albany and Harvard Forest sites are shown in Figure 3. Probability density distributions of aerosols and clouds show the similar characteristics at both sites even for different periods. The probability density distributions behave like gamma distributions for overcast cloud conditions. However, for overcast cloud cases, the mean cloud optical depth in 1995 (a drought year) was smaller than that of 1996 at Albany. Further, most occurrences of cloud optical depth at Harvard Forest were larger than that at Albany, consistent with the regional climatology of solar radiation, i.e. there is more sunshine in river valleys due to the presence of local circulations.

The spectral quality of diffuse light reaching the surface is influenced by clouds and aerosol. In Figure 4, solar spectra derived from a rotating shadowband spectrometer (RSS) operated at the Southern Great Plains ARM site are shown for several cloud optical depths (Tau). The figure clearly illustrates the enhancement of diffuse PAR irradiance under very cloudy conditions (Tau 2.72 and 9.27), and the change in spectral composition of the diffuse light under those conditions. We have also developed a model to predict of radiation flux at various wavelengths. Figure 5 shows results of direct, diffuse, and total irradiances at varying optical depths at two wavelengths corresponding to two MFRSR channels. The model ultimately will predict forest canopy diffuse light environment, so that photosynthesis can be modeled under various aerosol and cloud conditions.

A rapid inversion algorithm for constructing synthetic solar spectra from measurements made by instruments with multiple narrowband detectors (e.g., MFRSR) has been developed based on Min and Harrison [1998]. We construct a weighted measure of PAR, in which the visible portion of the spectrum is convolved with an action spectrum $(A(\lambda))$ for photosynthesis:

$$PAR = \int_{\lambda 2}^{\lambda 1} A(\lambda)F(\lambda)d\lambda = \int_{\lambda 2}^{\lambda 1} A(\lambda)\sum_{i=1}^{s} BiFid\lambda = \sum_{i=1}^{s} CiFi$$

This measure of PAR is being used in a light use efficiency model to study canopy net photosynthesis under varying cloud and aerosol regimes. The total effective PAR, as the summation of direct PAR and effective diffuse PAR, interacts with the canopy, resulting in carbon uptake. The diffuse use efficient coefficient is determined by maximum correlation

Aerosol Optical Depths (415 nm)
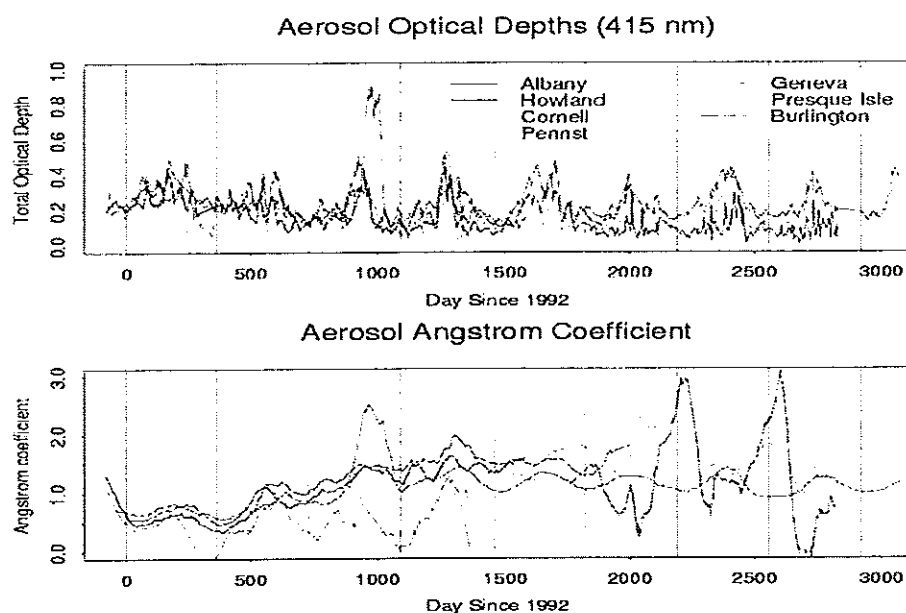

Aerosol Angstrom Coefficient

Figure 1. Time series of aerosol optical depth and angstrom coefficient for seven sites in Northeastern US.
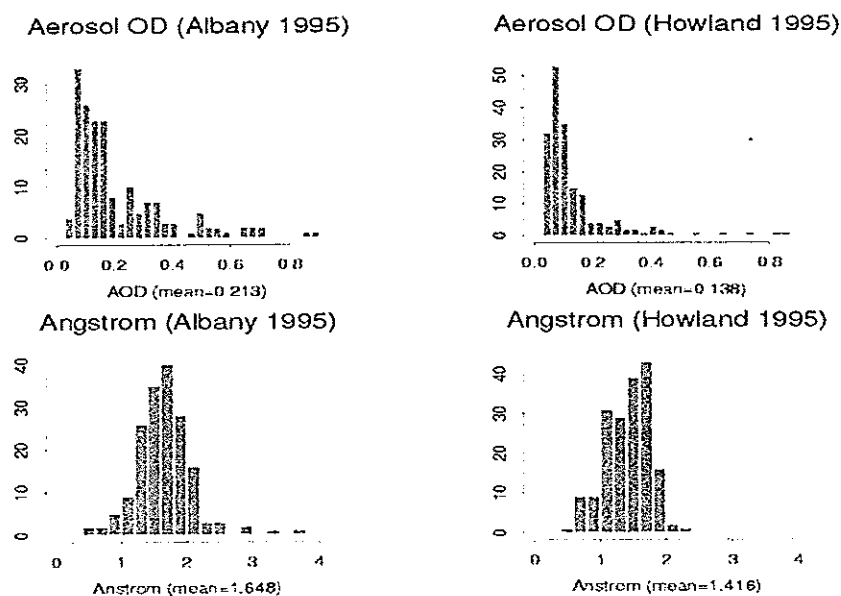
Figure 2. Aerosol optical depth and Angstrom coefficients for two sites in the network, Albany, NY and Howland, ME.
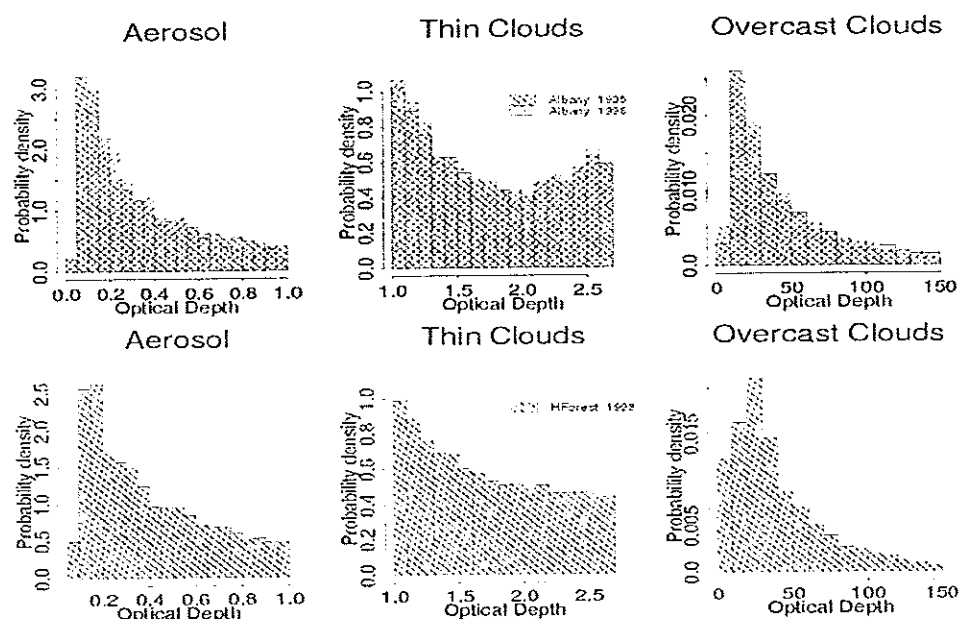
Figure 3. Statistics of aerosol and cloud optical depths at Albany site for 1995 and 1996, and at Harvard Forest for 1998.
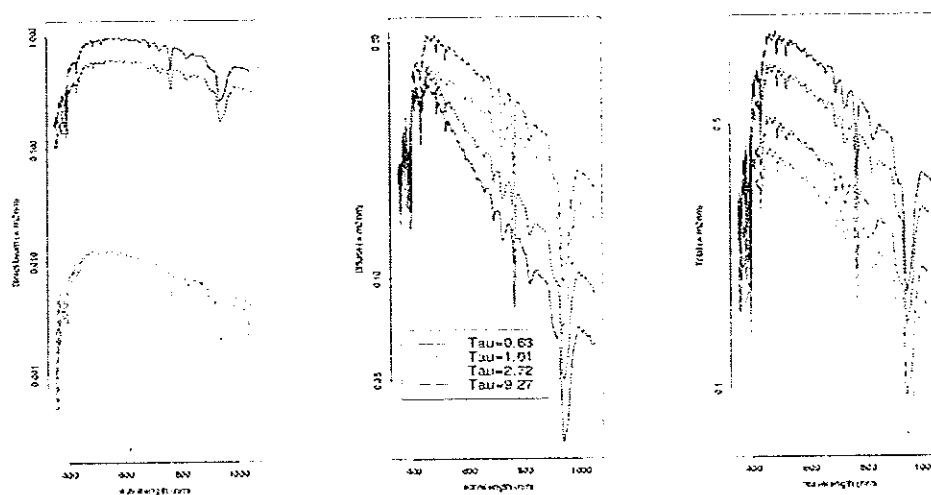
Figure 4. Solar spectra observed from the Rotating Shadowband spectrometer (RSS) at the ARM SGP site, on day 321 in 1997, under a range of cloud and aerosol optical depths (Tau). Direct beam (left), diffuse (center), and total (right) irradances are shown.

415 nm (SZA=45. Alb=0.1)

665 nm (SZA=45, Alb=0.1)
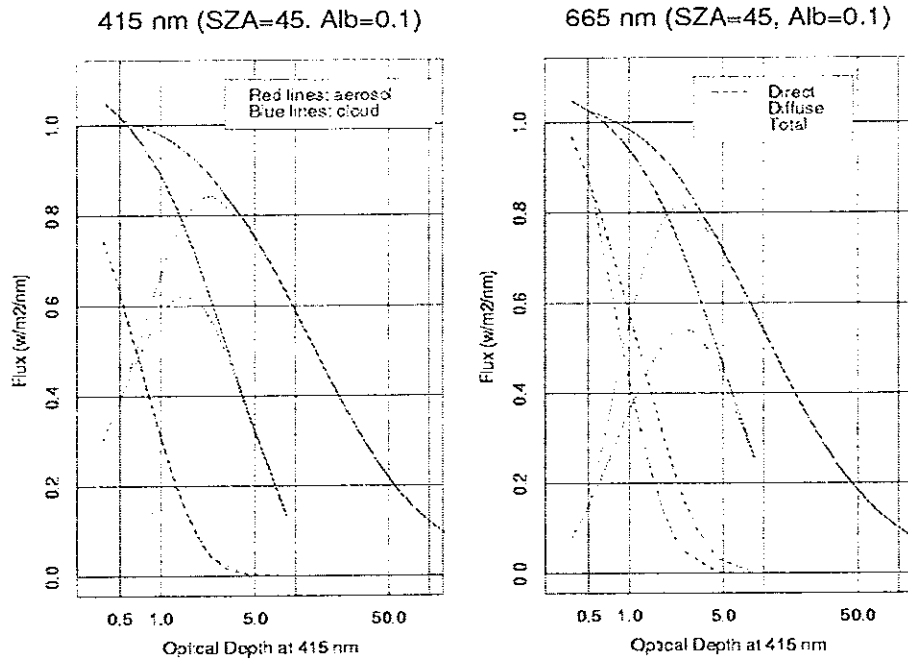
Figure 5. Results of a model predicting direct and diffuse irradiances at varying optical depths.
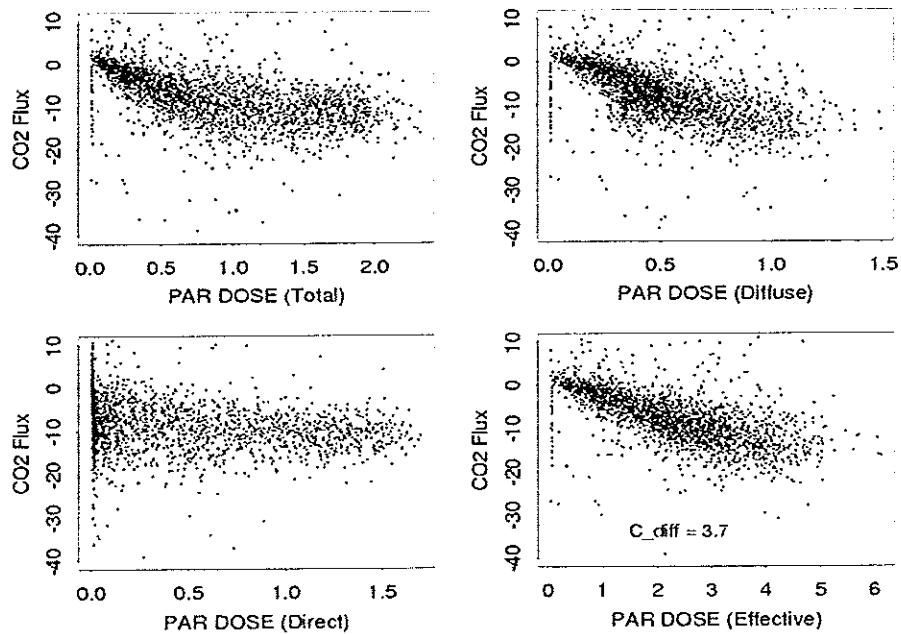
Figure 6. The scattergram of PAR (DOSE) vs. CO_2 flux at Harvard Forest over the growing season of 1998.

between the total effective PAR and CO2 flux, shown in Figure 6.

Modeling the Effect of Diffuse Light on Canopy CO$_2$ Uptake

K. Moore, D. Fitzjarrald and Q. Min

At Harvard Forest we have found that light use efficiency (LUE) for net CO$_2$ flux is directly related to the fraction of the total solar irradiance that is diffuse light, accounting for the greater C uptake on partly cloudy days (Freedman *et al.*, 2001). In this study a simple light use efficiency model, and the PnET models (Aber and Federer, 1992) have been used to test the effects of regional and interannual variation in cloud cover on canopy photosynthesis. Canopy photosynthetic and soil moisture characteristics for Harvard Forest were used in all model runs. For the LUE model, carbon uptake was calculated as the product of LUE and GOES satellite-based solar radiation (Ineichen and Perez, 1999). For PnET input, temperature and precipitation were varied according to the climatology represented in the "Climcalc" program (Olllinger *et al.*, 1995). PnET was run in two ways: 1) for a grid representing the Northeastern US, using solar radiation derived from GOES satellites (Ineichen and Perez, 2000) and 2) PnET Day was exercised using a 9-year record of solar radiation data from Harvard Forest, in which the daily average diffuse fraction was estimated from hourly atmospheric transmittances. Under the assumption that better light use efficiency under diffuse light conditions results from enhanced penetration of light into the canopy, the extinction parameter for light, *k*, in the PnET model was varied linearly according to the diffuse fraction (Parker and Beaty, in press).

The model results include: the light use efficiency model would suggest a tradeoff between inhibition of carbon uptake by clouds (through reduced light) and cloud enhancement (due to greater diffuse light). For example, in June of 1998, among regions varying by more than 20% in solar radiation, the difference in carbon uptake would have been only 12% (Fig. 1).

Incorporating a diffuse light dependence for the canopy light transmittance caused PnET-predicted enhancements of 5-20% in gross carbon exchange, as well as more variability in the resultant light curves (Fig 2).

Bringing satellite estimates of the solar radiation into PnET improves the coherence of precipitation regional pattern and cloudiness. Orographic effects, the sea breeze, and local circulations are all reflected in the regional distribution of clouds.

PnET predicted as much as a 50% decrease in net ecosystem productivity across the region for the cloudy summer of 1998, and a 10% increase for the relatively sunny summer of 1999, compared to a "base case" where solar radiation varied only by latitude.

Further experiments with satellite-derived solar radiation datasets as input to canopy photosynthesis models, as well as synthetic solar spectra are ongoing (see abstract by Min and Moore, this volume).

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Ineichen, P. and R. Perez, 1999. Derivation of cloud index from geostationary satellites and application to the production of solar irradiance and daylight illuminance data. Theo. and Appl. Clim. 64: 119-130.

Ollinger, S. V., J. D. Aber, C. A. Federer, G. M. Lovett, J. M. Ellis, 1995. Modeling physical and chemical climate of the Northeastern United States for a geographic information system. USDA General Technical Report NE-191, 30 pp.

Parker, G. G., and R. M. Beaty. An empirical evaluation of the Beer-Lambert law relating canopy foliage profile and light transmittance in five forests of contrasting structures. Ecological Applications (In Press).

CO2 flux = Global*LUE
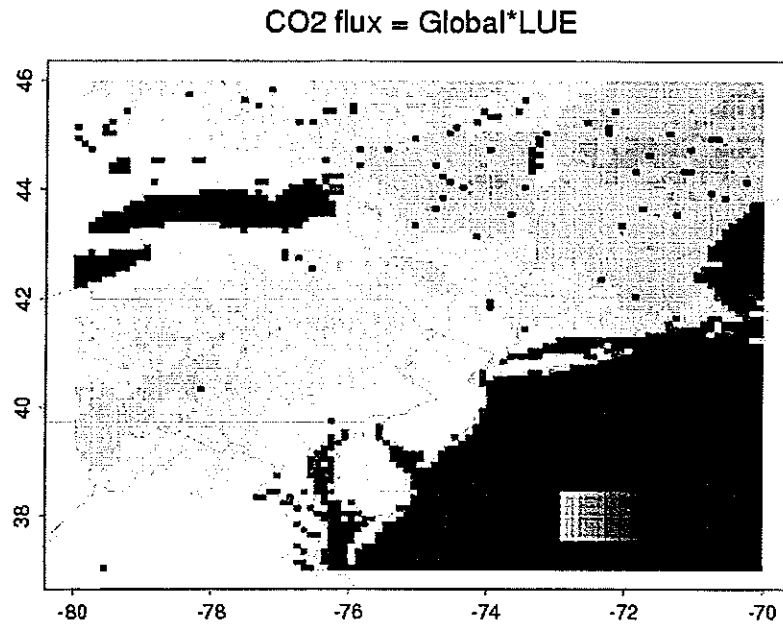
Figure 1. Results of a simple light use efficiency model for the month of June, 1998, showing carbon dioxide flux as a product of the solar irradiance (estimated from GOES satellites) and the light use efficiency (derived from Harvard Forest, using diffuse fraction as input).

gross C exchange by year
g C/m2/yr, days 185-225

pndavcomp Tue Mar 20 13:51 29 EST 2001
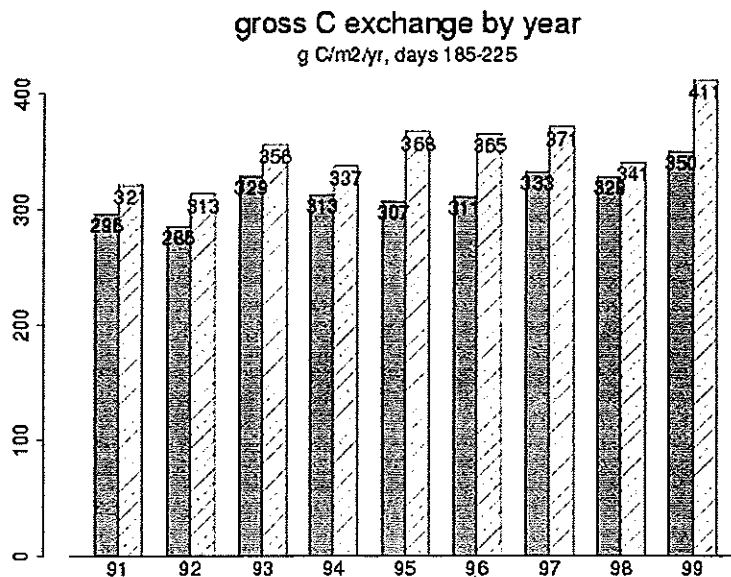
Figure 2. Gross C exchange predicted by the PnET-day model run with the Harvard Forest in situ solar radiation as input; striped bars included the effect of diffuse light on canopy light penetration, solid bars did not.

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Peroxyacetylnitrate Concentrations at Harvard Forest

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

Peroxyacetylnitrate (PAN) is an important reservoir species of reactive nitrogen oxides in the atmosphere. Peroxyacetyl radicals that are formed during photochemical oxidation of hydrocarbons react with NO_2 to form PAN. A wide variety of hydrocarbon precursors are present in urban air; isoprene, which is emitted by vegetation, is an important precursor in forested rural areas. As part of a more detailed investigation of nitrogen oxide speciation at Harvard Forest (see also Horii *et al.* 2001) we have measured PAN concentrations at the Harvard Forest EMS using GC separation and electron-capture detection. Measurements were made for a period in spring and early summer of 2000 and January 2001 until the present. An instrument malfunction interrupted the measurements during the summer and fall of 2000. During the spring and summer months PAN dynamics were dominated by a diel cycle with high concentrations during daylight hours and depletion at night. (Fig. 1) This pattern implies rapid formation when photochemical activity provides an excess of peroxyacetyl radical and thermal decomposition at night when the source of radicals is turned off. Rapid turnover makes PAN less effective as a NO_x reservoir. The winter data shows only a weak diel cycle and is instead dominated by large variations on synoptic time scales. The highest concentrations are associated with the southerly air flow that comes from urban areas (see Fig. 2). The lowest concentrations, which are associated with clean air from the north have been fairly constant over the period January-March. The high concentrations in polluted air have increased as more sunlight becomes available to promote PAN formation, yet the temperatures have remained cold enough to give PAN a long lifetime. Under these conditions PAN is an efficient reservoir species that will transport NO_x to remote areas. Without PAN formation NO_x would react with O_3 to form N_2O_5 and be rapidly removed.

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Tree seedling canopy responses to conflicting photosensory cues

C. Muth and F. Bazzaz

Decreased red/far red ratios can serve as signals of neighbor presence and trigger developmental responses before shading ever occurs. There is some evidence of herbaceous annual canopies growing towards increased red/far red ratios even when this means growing towards lower light quantities. It is unclear to what extent light quantity versus light quality leads to canopy foraging responses among forest trees. Our objective in this study was to determine which photosensory cues lead to tree canopy foraging responses. We hypothesized that trees forage towards high red/far red ratios and towards light quantities close to their light saturation points.

Seedlings of *Betula papyrifera* Marshall (paper birch) were grown in an experimental garden at the Harvard Forest Long Term Ecological Research (LTER) site. Each seedling was germinated and grown in its own shading structure and exposed to two spatially separated light environments, in a factorial design of light quantity and quality. Plant canopy foraging was evaluated at the end of one growing season in terms of canopy displacement, canopy area, direction of stem lean, and leaf number, position, and orientation with respect to experimental light treatments. Leaf number and canopy area were greater on the sides of plants with high light quantity, irrespective of the light quality treatment. Seedling canopies were displaced from their stem bases. The direction of canopy displacement corresponded with the high light quantity sides of plants, but this trend was not significant across all treatments. The direction of leaf position was random and showed no significant directedness towards any of the light

PAN at Harvard Forest,
June-July 2000
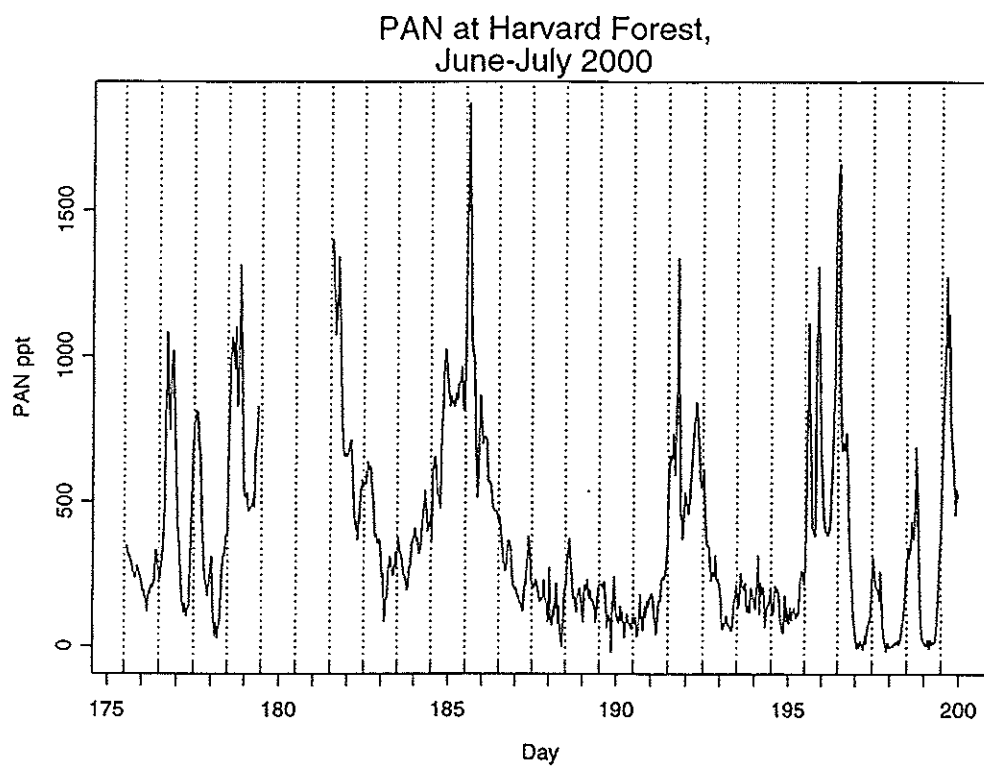
Figure 1 Time series of PAN for a three week period in early summer of 2000. Dashed lines indicate noon (EST). Note that the maximum concentrations occur in the afternoon and that on some nights the concentrations of PAN drop rapidly to near zero.

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PAN at Harvard Forest
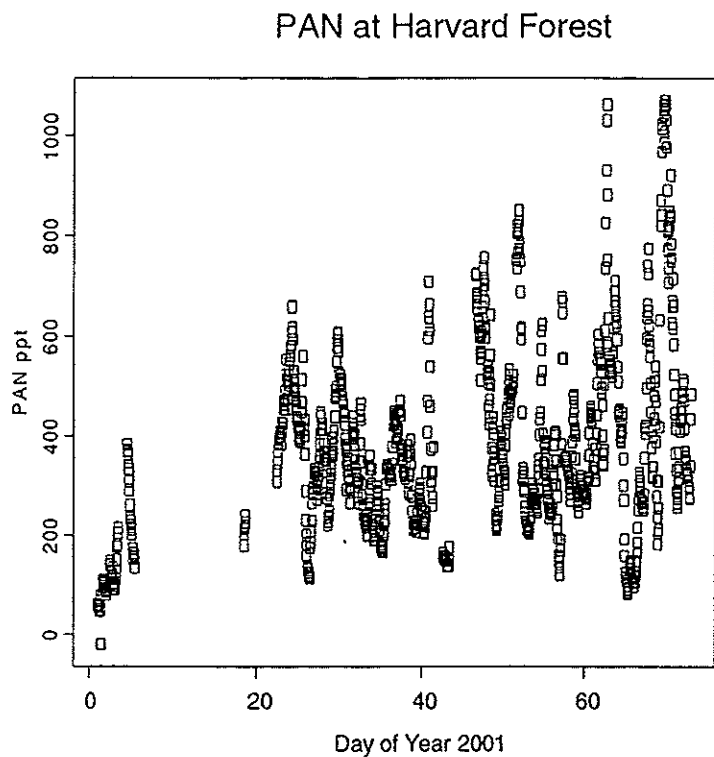
Figure 2. Time series of PAN concentration at Harvard Forest during January, February, and March 2001. PAN concentrations at Harvard Forest during the peak episodes show a general increase from January to March. Peak episodes are associated with advancing storm systems with relatively warm air advection from the south. Minimum values associated with clean background conditions and cold air from the north have not changed noticeably.

treatments. Leaf orientation (Fig. 1) and the direction of stem lean (Fig. 2) were distributed towards the direction of high light quantity, irrespective of the light quality treatment. Overall, first year *B. papyrifera* seedlings used light quantity rather than R/FR ratio as a photosensory cue for canopy light foraging. In order to determine how generally these results apply to trees, longer term and multi-species studies are needed.

Influence of Branch Demographic Processes on Tree Canopy Displacement

C. Muth, K. Capecelatro and F. Bazzaz

Tree canopy displacement refers to the condition where a tree's canopy is not positioned directly over its stem base. Tree canopies are often displaced towards areas of greater light availability and reduced competition. Morphologically, tree canopy displacement occurs due to either leaning of the main stem or differential branching. In the mixed deciduous forests of central New England, differential branching is the primary means by which tree canopies are displaced. A variety of branch demographic processes could lead to tree canopy displacement. Trees may produce additional branches towards areas of greater light availability. They may also have increased growth or increased survival of branches facing high light areas. We conducted a branch demography study to determine the relative importance of branch production, growth, and survival for the canopy displacement responses of trees along forest gap edges.

For trees along the edges of six experimental gaps, all live and dead branches were counted on both the gap-facing and the forest-facing side of each tree. For a subset of gap edge trees, lower branches were harvested and aged to determine branch age structure on the gap-facing versus forest-facing sides of trees. For a subset of gap edge trees, one major gap-facing branch and one major forest-facing branch were harvested. Tree rings are currently being counted at regular intervals along these branches in order

to calculate annual lateral branch growth before and after gap formation.

Trees along gap edges had more total branches and a greater percentage of live branches on their gap-facing sides than on their forest-facing sides. Branch age structure did not differ substantially between the gap-facing and forest-facing sides of trees. This suggests that the greater number of branches on the gap-facing sides of trees is due to both increased survival of older branches and increased production of new branches since gap formation. We are currently counting annual rings in order to investigate variation in branch growth rates between the pre- and post-gap time periods and between the gap-facing and forest-facing sides of trees. Investigating the production, survival, and growth of branches provides a mechanistic understanding of how displaced canopies develop in response to asymmetrical light environments.

Regeneration Following Clearcutting of Red Pine Overstory - Year 11

J. O'Keefe

Measurements of regeneration following removal in 1990 of a 64-year old red pine plantation on the Prospect Hill tract were continued for the eleventh year in 2000. Species, height, origin and evidence of browsing were recorded for all woody stems on 50 milacre (1.13 m radius) plots established on a five meter grid within the clearcut. A fenced exclosure was initially erected around half of the plots. The exclosure fence has not been maintained since year 5 because no evidence of significant differences in regeneration between the exclosure and the open area was found. Extensive mixed hardwood regeneration (generally less than 7 m tall) was cut back to the ground during harvest, ensuring at least initial dominance by sprouts.

Browsing in 2000 remained at very low levels (<2% of stems). White ash and red maple were the major tree species browsed. As mean tree height continues to increase both the amount of browsing and the impact of browsing on future stand characteristics should remain low. Overall, our observations show that browsing has had little
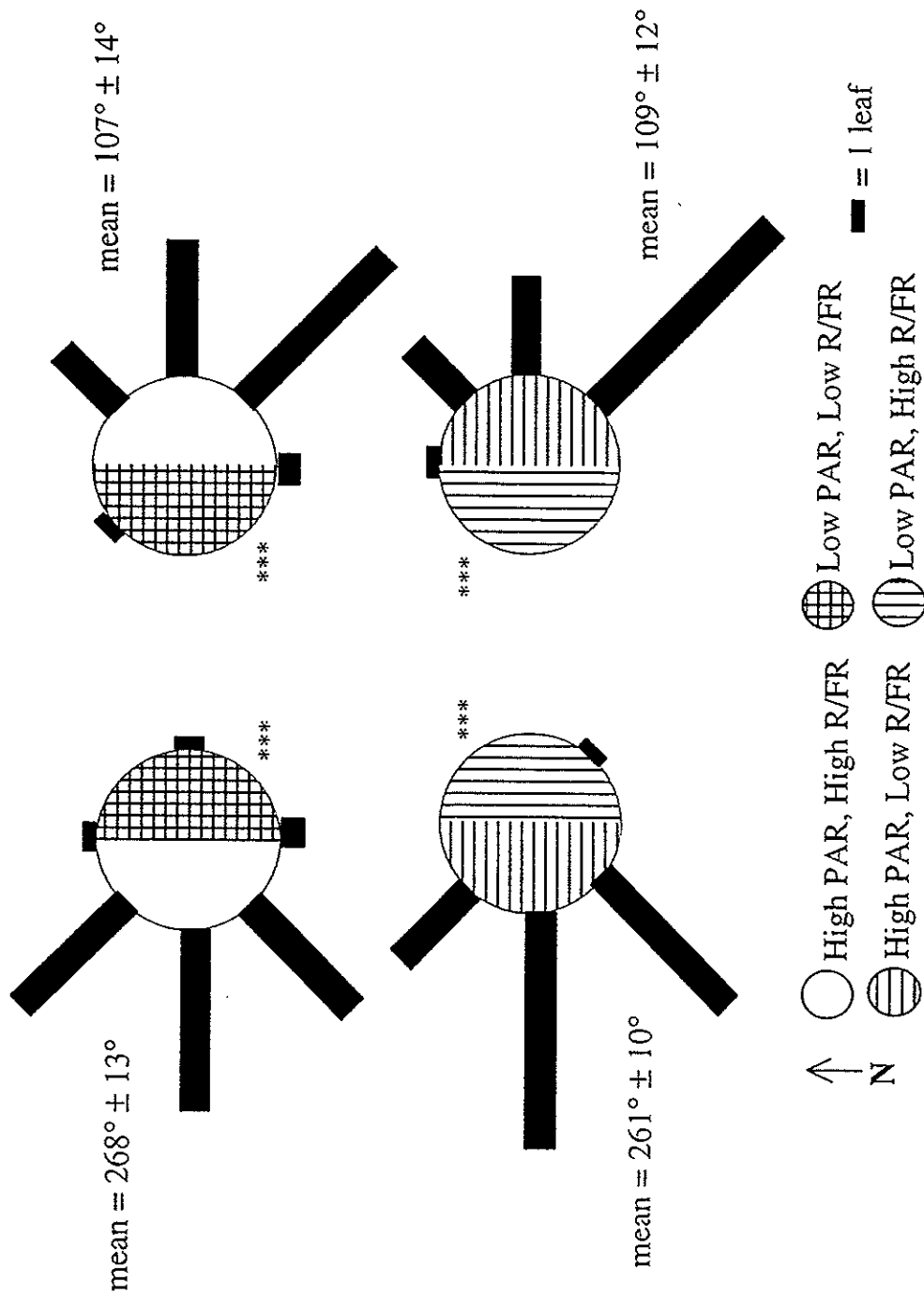
Figure 1. Direction of leaf orientation for *Betula papyrifera* seedlings grown in four light environments. Each seedling was exposed to two contrasting light treatments that differed in light quantity and quality. Hatch marks repsesent light treatments, as shown in legend. Bar lengths represent the number of leaves oriented in a given direction. Within each treatment, the direction of leaf orientation was not random, but showed directedness towards high PAR (***p<0.001, Rayleigh test). A chi squared test revealed that treatments with high PAR to the east differed from treatments with high PAR to the west (p<0.001).
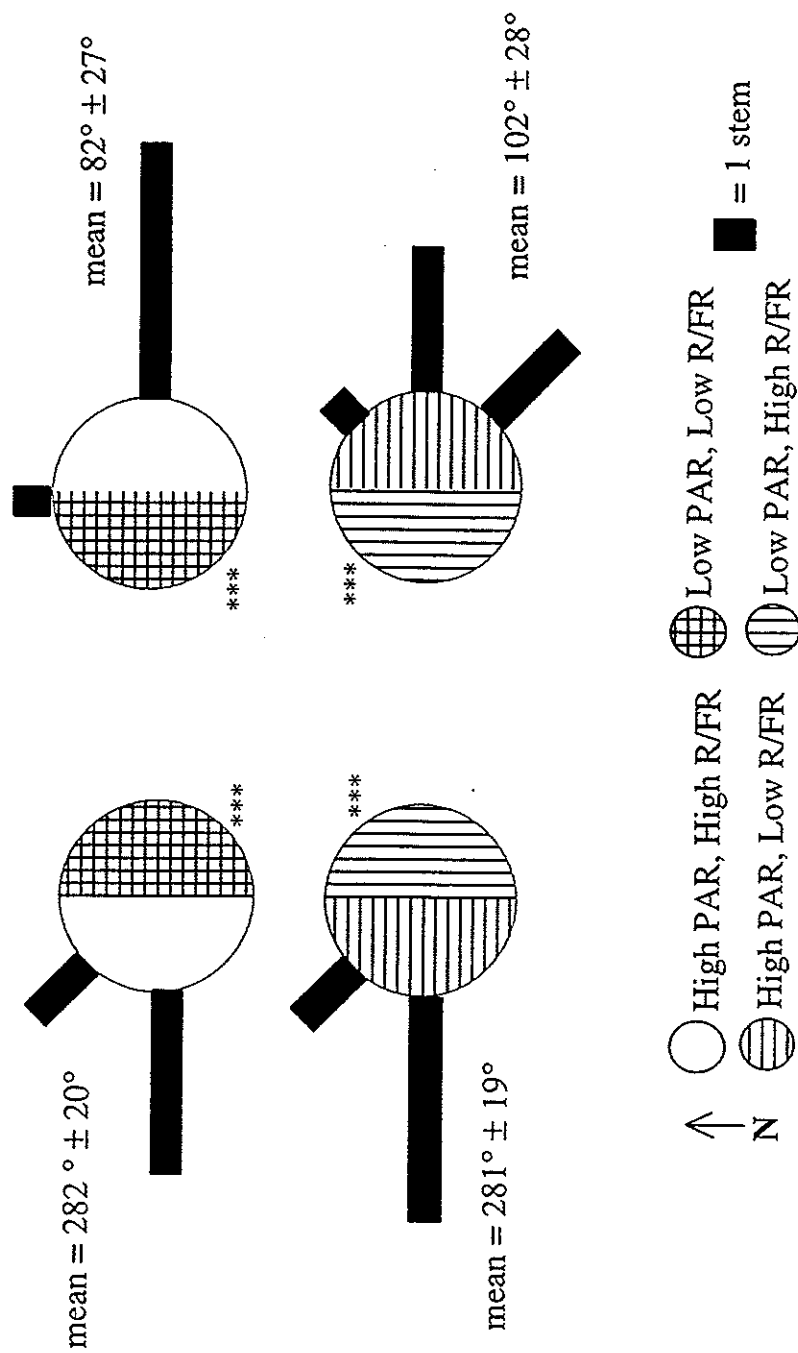
Figure 2. Direction of stem lean for *Betula papyrifera* seedlings grown in four light environments. Each seedling was exposed to two contrasting light environments that differed in light quantity and quality. Hatch marks repsesent light treatments, as shown in legend. Bar lengths represent the number of stems leaning in a given direction. Within each treatment, the direction of stem lean was not random, but showed directedness towards high PAR (***p<0.001, Rayleigh test).

impact during the regeneration of this stand. Stem density of tree species has been quite stable over the past five years. In 2000, overall stem density of tree species was 19,464 stems/ha, compared with 19414 stems/ha in 1999, 19,958 stems/ha in 1998, 19,414 stems/ha in 1997, and 20,696 stems/ha in 1996. The relative importance of major species has also remained the same over the past five years (Fig. 1). In 2000, white ash (38.6%) remained the most numerous tree species, followed by red maple (26.4%), sugar maple (13.5%) and black cherry (8.4%). These percentages changed little from 1999. After decreasing for the first time last year, red oak increased slightly to 7.1% of tree stems, the majority of which were small seedlings. Overall, the percentage of stems that originated as seedlings rather than sprouts decreased slightly to 23.1%, down from 23.4% in 1999, 25.4% in 1998, and 23.7% in 1997. The majority of these seedlings (56.0%) were white ash, most less than .5 m tall.

Mean stem height was to 3.20 m, compared to 3.24 m in 1999, 3.01 m in 1998, 2.92 m in 1997, 2.87 m in 1996 and 2.67 m in 1995. The stabilization in mean height over the past year probably reflects ingrowth of seedlings and new sprouts less than .5 m tall along with the death of some intermediate height sprouts. The tallest stems were 15 white ash, 12 red maples, 11 sugar maples, 5 pin cherries and 5 black cherries and 3 paper birches over 7 m tall, all sprouts. Diameter at breast height (dbh) is now being recorded for all stems taller than seven meters. Of the five most common species, sugar maple had the tallest mean height (4.41 m), followed by red maple (3.79 m), black cherry (3.66m), and white ash (2.60 m). Because of the preponderance of small seedlings, red oak mean height was only 0.79 m. It remains to be seen how many seedlings will survive to play a role in the developing stand.

Woody Species Phenology, Prospect Hill Tract, Harvard Forest - 2000

J. O'Keefe and S. Johnson

2000 was the eleventh year in our ongoing investigation of the timing of woody vegetation development during the growing season. 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. Weekly observations 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 1999-2000 was much milder than normal with slightly below average precipitation and well below average snowfall. During spring temperatures cooled to about normal and they were considerably below normal through summer and fall. Spring and early summer were quite wet, but precipitation in late summer and fall was below normal.

For most species initial leafout in 2000 was rather late (Table 1), but not as late as the latest years (1992, 1997). Leaf development then progressed quite slowly so that for many species 75% leaf development occurred close to the dates observed in the late years (1992, 1997). The shift from somewhat late to quite late again highlights the difficulty in absolutely categorizing a year as the early or late. The complex factors controlling these processes vary over the development period and each plant and species presumably integrates these factors somewhat differently as it develops.

After the latest fall in our 9 years of observation in 1999, fall coloration and leaf fall in 2000 returned to their more typical pattern, with color peaking about one week into October. Leaf senescence has generally shown much less variability than leaf development (Fig. 1). For most species only a week to ten days has separated the earliest and latest falls during nine years of observations.

% STEMS BY SPECIES 1990-2000

% stems

Year

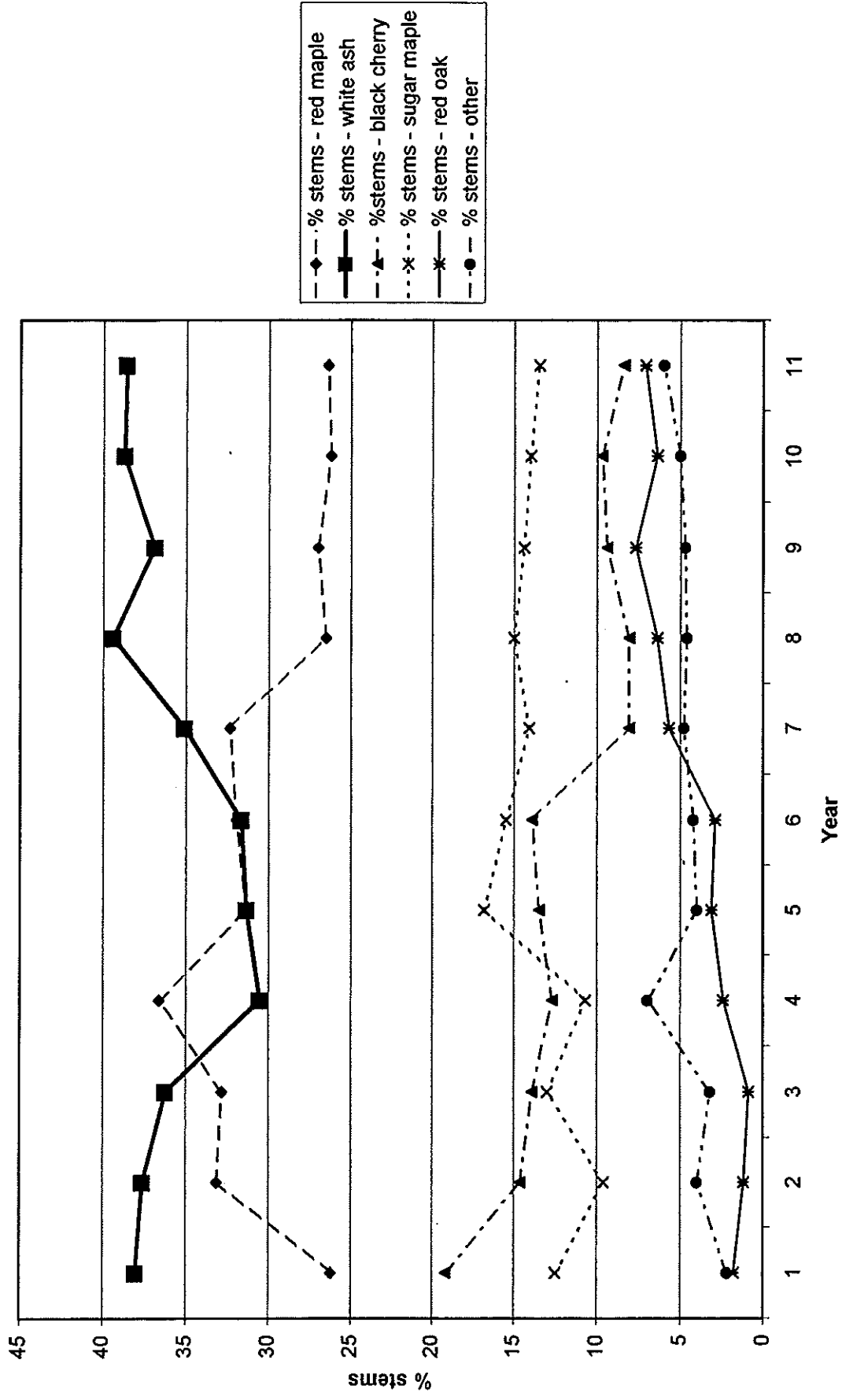| Legend |
| --- |
| ◆ — % stems - red maple |
| ■ — % stems - white ash |
| ▲ — %stems - black cherry |
| ✳ — % stems - sugar maple |
| ✴ — % stems - red oak |
| ● — % stems - other |

O'Keefe

Table 1. Estimated mean leaf development dates (month-day) for individuals of six representative species over nine years (IBB = initial bud break, 75% = 75% leaf development).

	Quercus rubra (n=4)		*Acer rubrum* (n=5)		*Betual allegheniensis* (n=3)	
	IBB	75%	IBB	75%	IBB	75%
1990	127 (5/7)	166 (6/15)	121 (5/1)	164 (6/13)	122 (5/12)	155 (6/4)
1991	128 (5/8)	143 (5/23)	123 (5/3)	142 (5/22)	117 (4/27)	141 (5/21)
1992	134 (5/14)	162 (6/11)	132 (5/12)	169 (6/18)	131 (5/11)	163 (6/12)
1993	122 (5/2)	153 (6/2)	118 (4/28)	154 (6/3)	113 (4/23)	136 (5/16)
1994	129 (5/9)	154 (6/3)	124 (5/4)	151 (5/31)	122 (5/2)	147 (5/27)
1995	132 (5/12)	150 (5/30)	129 (5/9)	148 (5/28)	126 (5/6)	144 (5/24)
1996	132 (5/12)	150 (5/30)	120 (4/30)	149 (5/29)	117 (4/27)	144 (5/24)
1997	136 (5/16)	158 (6/7)	133 (5/13)	154 (6/3)	134 (5/14)	153 (6/2)
1998	123 (5/3)	142 (5/22)	120 (4/30)	140 (5/20)	121 (5/1)	138 (5/18)
1999	126 (5/6)	148 (5/28)	126 (5/6)	146 (5/26)	127 (5/7)	141 (5/21)
2000	129 (5/8)	161 (6/9)	129 (5/8)	156 (6/4)	129 (5/8)	149 (5/28)

	Quercus alba (n=3)		*Hammamelis virginiana* (n=3)		*Acer pensylvanicum* (n=4)	
	IBB	75%	IBB	75%	IBB	75%
1990	132 (5/12)	163 (6/12)	124 (5/4)	163 (6/3)	119 (4/29)	155 (6/4)
1991	127 (5/7)	150 (5/30)	116 (4/26)	144 (5/24)	118 (4/28)	141 (5/21)
1992	137 (5/17)	157 (6/6)	131 (5/11)	167 (6/16)	124 (5/4)	158 (6/7)
1993	124 (5/4)	150 (5/30)	121 (5/1)	149 (5/29)	121 (5/1)	144 (5/24)
1994	134 (5/14)	160 (6/9)	126 (5/6)	148 (5/28)	128 (5/8)	151 (5/13)
1995	135 (5/15)	157 (6/6)	127 (5/7)	148 (5/28)	127 (5/7)	148 (5/28)
1996	138 (5/18)	158 (6/7)	122 (5/2)	149 (5/29)	129 (5/9)	150 (5/30)
1997	146 (5/26)	164 (6/13)	130 (5/10)	154 (6/3)	133 (5/13)	153 (6/2)
1998	126 (5/6)	145 (5/25)	113 (4/23)	139 (5/19)	118 (4/29)	142 (5/22)
1999	132 (5/12)	155 (6/3)	122 (5/2)	142 (5/22)	125 (5/5)	146 (5/26)
2000	132 (5/11)	162 (6/10)	126 (5/5)	151 (5/30)	127 (5/6)	155 (6/3)

O'Keefe and Johnson

50% BUD BREAK(bottom), 75% LEAF SIZE(middle), 50% LEAF FALL(top)
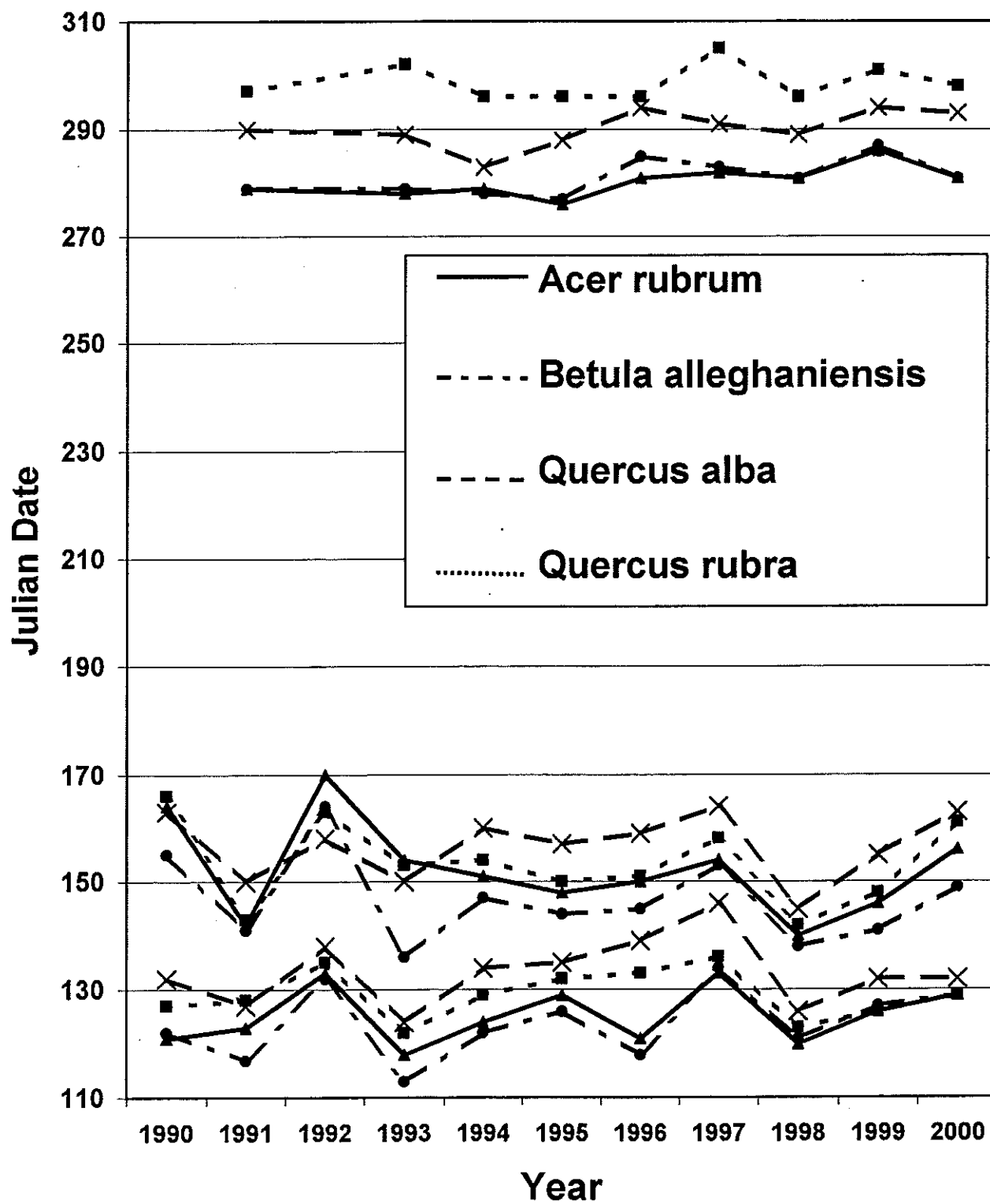
Landscape Patterns of Hemlock Decline in Southern New England: Infestation and Impact of the Introduced Hemlock Woolly Adelgid

D. Orwig, D. Foster and D. Mausel

Recent arrival of the hemlock woolly adelgid (*Adelges tsugae*; HWA) to eastern North America threatens to eliminate eastern hemlock (*Tsuga canadensis*), a long-lived shade tolerant species across its range. To interpret the stand, landscape, and historical factors controlling the spread of HWA in southern New England, we used aerial photographs and extensive field checking to map and develop GIS overlays of 1000 hemlock stands in a 5900 km^2 study transect. To document patterns of hemlock infestation, vigor, and mortality in relation to stand and site characteristics, we intensively sampled a random selection of 114 hemlock stands across the study region. The majority of stands were located along ridge tops, steep hillsides, and narrow valleys. Overstory hemlock importance values ranged from 22 to 96% and total stand densities varied from 300 to 1450 stems ha^{-1}. Adelgid presence and adelgid-induced hemlock mortality was found in 88% and 74% of the sampled forests, respectively. Approximately 25% of stands were logged recently. A geographical trend in reduced mortality and enhanced crown vigor of both overstory and understory hemlock occurs from south to north, coincident with the temporal migration pattern of HWA. Mantel analyses indicated that latitude was the strongest landscape correlate with hemlock mortality and crown vigor. Mortality was also related to aspect and stand size. Average mortality was highest on western aspects but exceeded 20% on most slopes (Table 1.). Remaining trees averaged over 50% foliar loss, with no significant difference among aspects. Results suggest that as HWA becomes abundant, stands on xeric aspects succumb more rapidly, but that stand and landscape variables such as overstory composition and structure, slope, and elevation, exert little impact on the susceptibility or eventual mortality. Ultimately, duration of infestation controls morality and decline, and it appears that no location is immune from hemlock decimation once HWA is well established.

Ecosystem Analyses of Hemlock Woolly Adelgid Outbreaks in Southern New England

D. Orwig, R. Cobb, M. Kizlinski 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 should reverse this trend, due to dramatic increases in light levels and soil temperature. Within 8 study sites varying in HWA infestation level, we measured nitrogen (N) mineralization rates using close-topped soil cores to capture the magnitude and duration of N dynamics associated with HWA infestations during the last three years. In addition, ion-exchange resin bags were used to estimate the spatial availability of N within sites and the extent to which NO_3 is being lost. Measurements of gravimetric moisture content and soil temperature were used with hemispherical photographs to assess microenvironmental changes. Preliminary analyses suggest that thinning canopies from heavy HWA damage resulted in increased light and decreased forest floor moisture content. Heavily infested sites tended to have higher net N mineralization rates, larger extractable $NH_4 - N$ pools, and had net nitrification rates 25 times greater than healthy hemlock forests. In addition, resin bags captured more ammonium and nitrate in infested versus uninfested stands (Table 1). Higby Mountain, the most heavily damaged stand, exhibited increasing amounts of nitrogen capture over time at levels 5 to 40 times greater than control stands. Low and undamaged stands typically showed net immobilization of nitrate. 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. 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.

Table 1. Hemlock stand distribution and mean overstory hemlock mortality and crown vigor among slope aspect classes in hemlock stands sampled in southern New England (n = 114).

Slope Aspect	Frequency of occurrence (%)	Mean overstory Mortality (± S.E.)	Mean overstory crown vigor (± S.E.)
N (337.5 - 22.5°)	14.0	26.6 ± 6.8ab	3.9 ± 0.4a
NE (22.5 - 67.5°)	16.7	18.0 ± 5.3ab	3.3 ± 0.4a
E (67.5 - 112.5°)	11.4	5.0 ± 2.0a	3.2 ± 0.4a
SE (112.5 - 157.5°)	7.0	31.1 ± 13.6ab	3.8 ± 0.7a
S (157.5 - 202.5°)	0.1	0	2.45a
SW (202.5 - 247.5°)	3.5	39.0 ± 19.9ab	4.7 ± 0.6a
W (247.5 - 292.5°)	20.2	45.0 ± 7.7b	4.6 ± 0.3a
NW (292.5 - 337.5°)	26.3	25.7 ± 5.4ab	3.6 ± 0.3a

Aspect values in a column with the same letter are not significantly different at $P < 0.01$.

Orwig et al.

Table 1. Ammonium and nitrate capture on ion-exchange resin within eight central Connecticut *Tsuga canadensis* study sites with various levels of HWA infestation.

	Salmon River*	Crooked Road*	Ash Brook	Lievre Brook	Devil's Hopyard	Willington Hill	Higby Mountain	Sunrise Resort
NH$_4$ – N (mg/g ± SE)								
1998	0.11 ± 0.06	0.37 ± 0.09	2.05 ± 0.60	2.16 ± 0.51	0.41 ± 0.34	0.49 ± 0.16	2.11 ± 0.51	0.36 ± 0.17
1999	0.53 ± 0.12	0.41 ± 0.20	1.00 ± 0.44	1.81 ± 0.55	3.41 ± 1.07	0.38 ± 0.16	4.90 ± 1.51	0.82 ± 0.26
2000	0.22 ± 0.15	0.33 ± 0.24	1.44 ± 0.91	3.29 ± 0.78	0.69 ± 0.30	0.52 ± 0.19	2.78 ± 0.69	0.56 ± 0.19
NO$_3$ – N (mg/g ± SE)								
1998	0.39 ± 0.13	2.38 ± 0.89	2.63 ± 0.92	3.09 ± 0.87	0.93 ± 0.47	1.01 ± 0.29	5.78 ± 1.35	2.42 ± 0.95
1999	0.56 ± 0.11	0.80 ± 0.21	2.06 ± 0.64	2.51 ± 0.73	4.76 ± 1.95	0.85 ± 0.25	28.90 ± 9.10	2.18 ± 0.56
2000	0.70 ± 0.19	0.50 ± 0.13	2.17 ± 0.75	1.84 ± 0.48	1.24 ± 0.55	1.19 ± 0.66	40.40 ± 15.48	2.51 ± 1.33

*Uninfested control stands.

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

D. Orwig, G. Motzkin and D. Foster

As part of a broader investigation of ridgetop communities in the Northeast, we initiated a study examining the long-term history, development, and vegetation dynamics of Mt. Everett and nearby summits in the southern Taconic region of southwest Massachusetts. We propose to use a combination of dendroecological, historical, and field studies to address several questions: 1) What is the historical fire and disturbance history of the region and how has this influenced vegetation composition and structure? 2) What is the history of land-use and how has this influenced vegetation composition and structure? 3) What is the age structure of the current stand and how is this related to disturbance history? 4) How do the composition, structure, and dynamics of Mt. Everett compare with other sites in the southern Taconics and elsewhere in central New England? The methods we will employ to address these questions include historical reconstructions, age structure and dendroecological analyses, aerial photo and GIS analyses, and vegetation and soils characterization.

We have visited several sites and intensively sampled the dwarf pitch pine community on Mt. Everett. This rare forest type, occurring in only a few locations in the northeastern U.S., is characterized by exposed bedrock, shallow soil depths of 10 to 18 cm, and abundant stunted pitch pine 0.5 to 2.0 m tall. The uneven-aged stand includes red maple, red oak, and birch species. Pitch pine exhibits continuous recruitment since the 1830s and range in age from 12 to 170 years old. Hardwood species established in most decades since 1860 and in higher densities in the 1950s and 1960s. Diameter is a poor predictor of age in this forest as trees with diameters of only 10 cm differ in age by more than 100 years. Many pines exhibit multiple stems, prostrate growth forms, and evidence of terminal branch damage. There is no historical or site-based evidence of fire or human impacts in this forest, but on this exposed summit (795m

a.s.l.), wind, snow, and ice damage are dominant disturbance factors. Pitch pine ring-width patterns displayed extremely slow growth, with many individuals averaging < 0.40 mm yr.$^{-1}$, and a few growing only 0.08 to 0.30 mm yr.$^{-1}$ for periods of up to 50 years. The unusual structure, extremely slow growth rates, and continuous recruitment in the absence of fire suggest that weather and harsh site conditions continue to maintain this unique community of disturbance–adapted species.

We will continue to examine additional ridgetop communities to place the results of this site into a broader landscape context and to make comparisons with forests that have been influenced by fire and other factors.

Landscape-scale History of Vegetation and Fire on Cape Cod, Massachusetts

T. Parshall, D. Foster, E. Faison, D. MacDonald, B. Hansen and E. Doughty

Over the past three centuries the structure and composition of forests in New England have been dramatically influenced by intensive human land use, the effects of which can be seen today even after forests have been allowed to recover. Over the same time period, human land use has altered other ecological processes such as the frequency and intensity of disturbances, which also influence vegetation composition. The landscape occurrence of fire, in particular, is an important component of many ecosystems but is much different today because humans now play a central role in its ignition and spread. The interacting effects of changing land use on both fire and vegetation are difficult to tease apart from modern observations alone, and paleoecological studies can help disentangle these interacting effects by providing the only source of information on the status of ecosystems before human impacts became large.

Long-term records of ecological change provide descriptions of the range of variation that has existed in the past, which is essential information for modern ecological, conservation, and management-oriented questions. These

Deep Pond, Falmouth
Anaysts: E. Faison & T. Parshall
2/27/2001

Figure 1 (Parshall et al.)

Presettlement

DCA Axis 2

DCA Axis 1

Group I = moraine sites (oak-hardwood)   Group II = outwash sites (pine)

Postsettlement

DCA Axis 2

DCA Axis 1
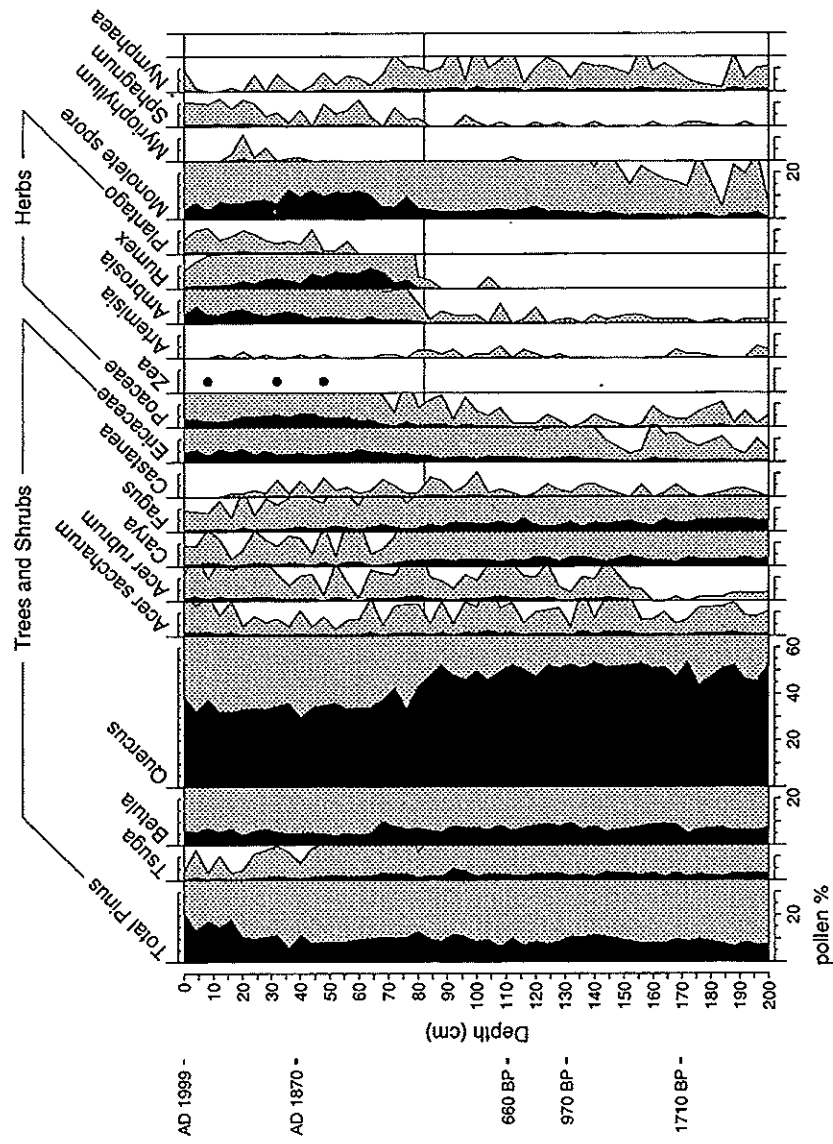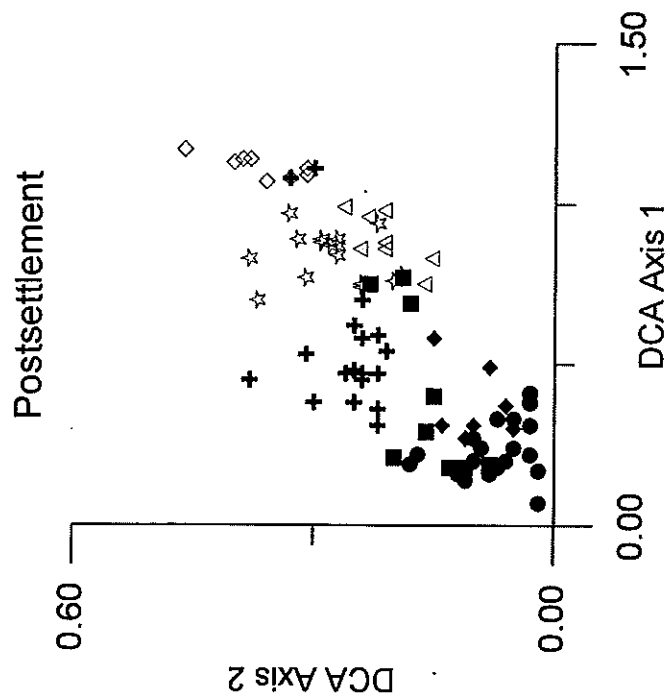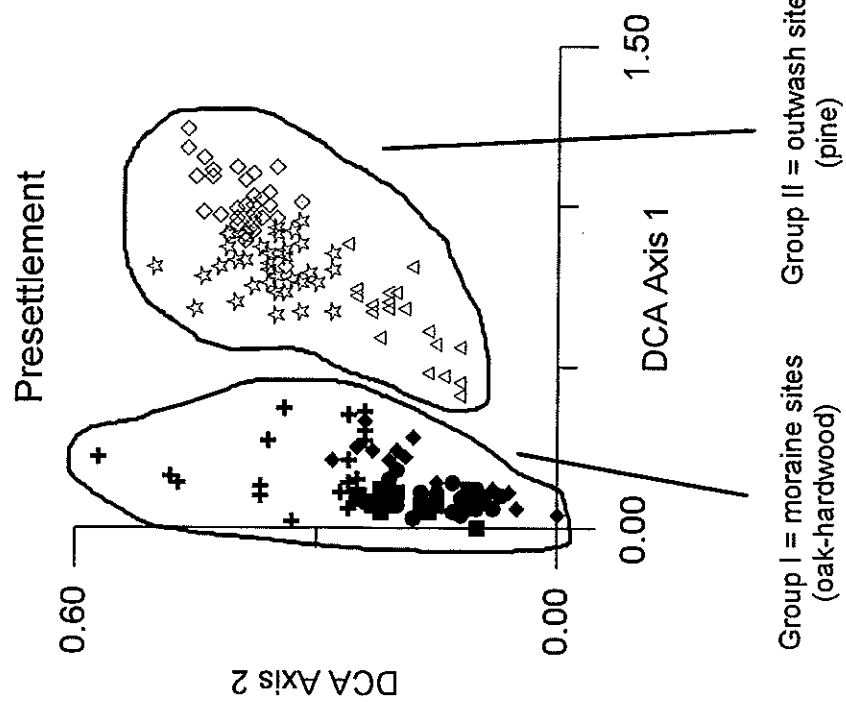
Figure 2   Detrended Correspondence Analysis of all fossil pollen samples from seven sites (indicated by different symbols) on Cape Cod. (Parshall et al.)

approaches are particularly relevant along the coast of New England where 1) human impact on the vegetation (especially sandplain communities) has been large, and the rate of human development continues to increase; 2) fire disturbances are important for vegetation distribution on this landscape and their occurrence can be understood only on the scale of hundreds to thousands of years; and 3) there are high concentrations of rare and uncommon species whose distributions are closely linked to the unusual environment and the history of fire and human activity. Our work provides a coherent picture of landscape changes in fire and vegetation over the past 2000 years along the coast of New England from changes in the abundance of fossil pollen and charcoal preserved in sediments from seven lakes. This information also serves as an independent and continuous record of ecological change that can be compared with modern and historical vegetation studies along the southern coast of New England also underway at the Harvard Forest.

The pollen and fire records show clear changes in vegetation associated with the arrival of Europeans. All sediments capture the transformation of the forested landscape to open fields. Oak, beech and hickory decline at settlement almost everywhere as herbaceous pollen, such as sorrel, ragweed and grasses increase in abundance (Fig. 1). A reduction in sediment organic content indicates an increase in the influx of inorganic sediments from upland land clearance. Charcoal influx increases dramatically at most sites, indicating that fires were more common in the settlement period. At some sites the abundance of charcoal is greater during the early settlement period indicating that fires may have been more common at that time. However, even though there is a relationship between vegetation composition and landform following settlement, the strength of this relationship is not as great as it was in the presettlement forest.

On the presettlement landscape, there are two distinct groups of sites that differed in the composition of vegetation (Fig. 2). Sites dominated by pine occur exclusively on sandy, well-drained outwash landforms from western Cape Cod to the outer Cape, while sites dominated by oak and other hardwoods occur

primarily on moraines or ice-contact features, which include a larger component of fine-textured soils. Related to this grouping, the occurrence of fire on the landscape is higher in the pine forests on outwash and lower in the oak-hardwood forests on moraines. However, fires appear to have been less common on the outer Cape than on the inner Cape, even though much of the landscape was heavily dominated by pine.

Variability in the Long-term Occurrence of Fire in New England

T. Parshall, D. Foster, S. Barry, S. Clayden, E. Faison and D. MacDonald

For most ecological systems, fire plays a central role in ecosystem dynamics because it kills living vegetation (selectively), removes dead biomass, changes soil composition, and alters nutrient cycling. Like most disturbance agents, fire is heterogeneous. Ignition and spread is influenced by site and landscape-scale characteristics, once started macro and microclimatic variables influence fire intensity and magnitude, and some species are better able to survive fire than others. Humans currently play a central role in the modern fire regime, not only as the leading source of ignition but also by controlling the spread of fire once it starts. The traditional view that fires have increased in abundance since European settlement in New England is undoubtedly true in many cases, but some studies have shown that fire has declined since settlement. Furthermore, Native American activity likely increased the frequency of fire before European settlement, but probably not to the same degree throughout New England. An understanding of the presettlement fire regime across a range of vegetation types is critical for developing a better understanding of ecosystem dynamics and for management plans that include prescribed fire.

The goal of this study is to evaluate the variation in fire occurrence across the range of vegetation types that occur in New England (from pitch pine-oak to spruce fir) and to assess how these fire regimes have changed through time as

climate and human land use have changed. We are using the Harvard Forest paleoecology database, which now includes a wide range of lakes in New England, in combination with existing studies of fossil charcoal. Our initial assessment of the available data is that fire occurrence is lowest at sites in the north, corresponding to spruce-fir and northern hardwood forests, and is highest along the southern coast of New England, where pitch pine and oak forests dominate. The variability from site to site is high in the central part of New England. For example, charcoal in lake sediments on the sandy outwash plains in the Connecticut River valley and the eastern lowlands of Massachusetts is as abundant as it is in lakes in coastal pitch pine-oak forests, whereas sites in the central uplands of Massachusetts have low charcoal values on the scale of those in northern spruce-fir forest. We are currently analyzing fossil charcoal from lakes that will allow us to determine how much of this variation can be attributed to locality and vegetation type and to address how much of an effect human activities have had on fire occurrence throughout New England.

An Assessment of Accuracy in Soil Surface Carbon Dioxide Flux Measurements Using a Chamber Technique

E. Sundquist, L. Polansky, G. Winston, L. Bergen and B. Stephens

We have conducted extensive experiments and model calculations to assess the accuracy of soil surface CO_2 efflux measurements using a chamber technique. Our experiments utilize two different methods for imposing known CO_2 fluxes through columns of sand. We compare steady-state column fluxes to chamber measurements at the column sand surface. These experiments enable us to estimate measurement artifacts due to variations in column and chamber geometry, flux magnitude, and gas transport conditions (both diffusion and advection). In comparing our experimental results to model calculations, we see no evidence for large artifacts caused by pressure anomalies within our chambers. We have extended our model calculations to estimate potential artifacts for chamber measurements on soils with depth-dependent CO_2 production, stratified transport properties, and non-steady-state surface fluxes.

Massachusetts In 1830: Woodlands and Cultural Features

M. Syfert, G. Motzkin, and B. Hall

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 a local level.

The Harvard Forest has recently received funding from The Massachusetts Natural Heritage Program to digitize the town maps for the whole state into a Geographic Information System (GIS) to facilitate analysis. Such analysis is 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.

All features on the 1830 maps are currently being digitized and geo-referenced to fit U.S. Geological Survey topographic maps and half of the state is completed. When the data layers are complete, they will be available from

the MassGIS website. Completion is expected in mid-to-late 2002.

An Ecological Comparison Between European and North American Ancient Forest Plant Species

K. Verheyen and M. Hermy

In both Europe and North America, it has been observed that some of the species in the original forest flora - the so-called 'ancient forest plant species' - are reluctant to colonize secondary forests. Therefore, the question raises if these ancient forest plant species share some traits which inhibit dispersal, establishment and/or persistence in secondary woodlands? Until now, no such comparison between traits of slow and good colonizing forest plant species has been made. Furthermore, the existence of ancient forest species in comparable communities on both sides of the Atlantic Ocean offers a unique opportunity to make an intercontinental comparison between these species.

During a two and a half month stay at the Harvard Forest last autumn, the northeastern American research comparing the vegetation in primary vs secondary forest was compiled. The study area was restricted to the area covered in Gleason and Cronquist's Flora. A total of 14 independent studies was found in which 401 different vascular plant species were cited. Unfortunately, most studies were clustered in a rather small area covering Massachusetts, New York, New Jersey and Delaware and the quality of some studies was rather low (e.g. small data-sets, improper sampling design). Back home, the northwestern European research on this topic was compiled in a similar way. This resulted in 12 independent studies in which 388 species were cited. In contrast with the American studies, the quality of all European studies was good.

For each species that was cited at least two times (respectively 170 and 240 species), a 'primary forest affinity index' was calculated taking into account the species frequency in secondary vs primary forest and the number of studies in which it was cited.

Next, the database was completed by adding plant species traits for 410 (170 + 240) species. Data about 14 different traits were included (Table 1). Most traits deal with the regenerative phase, due to its importance in the colonization process.

The data-analysis is about to start and will consist of two parts: (1) In an intracontinental analysis, an ecological comparison between slow and good colonizing species will be made, based on the species traits and (2) in an intercontinental analysis, taxonomic, phylogenetic and ecological similarities between northwestern European and northeastern American ancient forest plant species will be assessed.

Table 1. Overview of the plant species traits incorporated in the database

Trait	Description
Age of first reproduction	Timespan between germination and flowering (in years)
Diaspores per plant	Number of diaspores per plants/ramets in four classes (1: ≤ 25; 2: 25-100; 3: 100-1000; 4: > 1000)
Dispersal type	Anemochory, exozoochory, endozoochory, myrmecochory, ballistochory or unassisted
Flowering phenology	Five classes were distinguished (1: before 15/6; 2: 15/6-15/8; 3: before 15/6 - 15/8; 4: after 15/8; 5: dimorphic, 15/6 - after 15/8)
Fruit type	Fruit types defined in Gleason and Cronquist
Germ. requirements	Classes according to the New England Wildflower Society
Growth form	Distinction between lycopodiophyta, equisetophyta, ferns, graminoids, herbs, shrubs and vines and trees
Leaf phenology	Evergreen, deciduous
Life history	Annual, biennial or perennial
Max. height	Maximum height (in m) of species
Seed mass	Dry mass (in mg) of one seed without accessoires
Seed size	Seed length, width and thickness (in mm)
Seeds per fruit	Number of seeds per fruit in three classes (1: 1-3; 2: 4- +/- 20-30; 3: numerous, minute)
Vegetative spread	Absent, intermediate (little lateral spread; this includes tillering, short rhizomes and stolons, tuber-like and stocky rhizomes if no add. elongated portion, bulb, corm, layering for species that normally do not have horizontal stems) and strong lateral spread

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