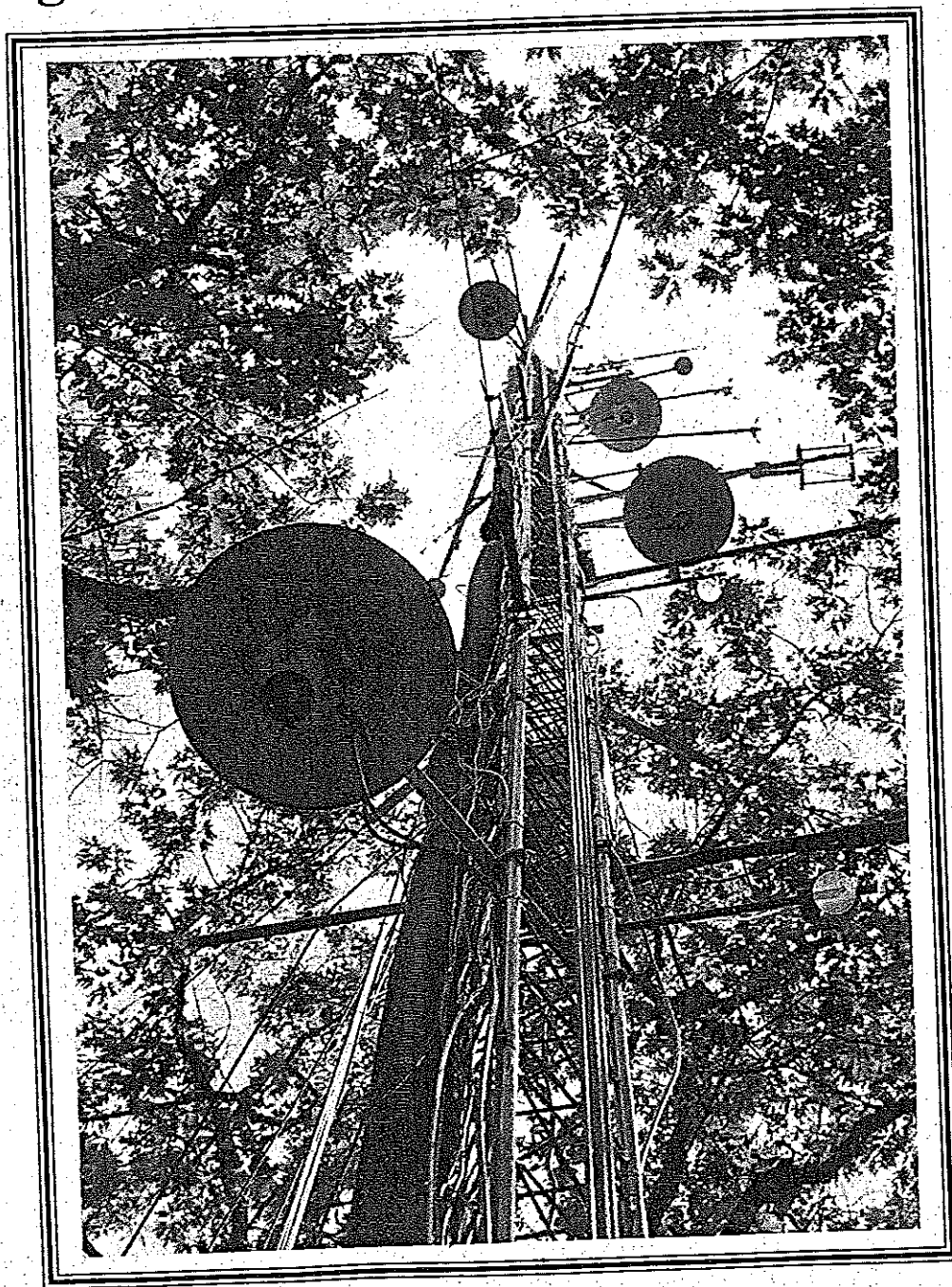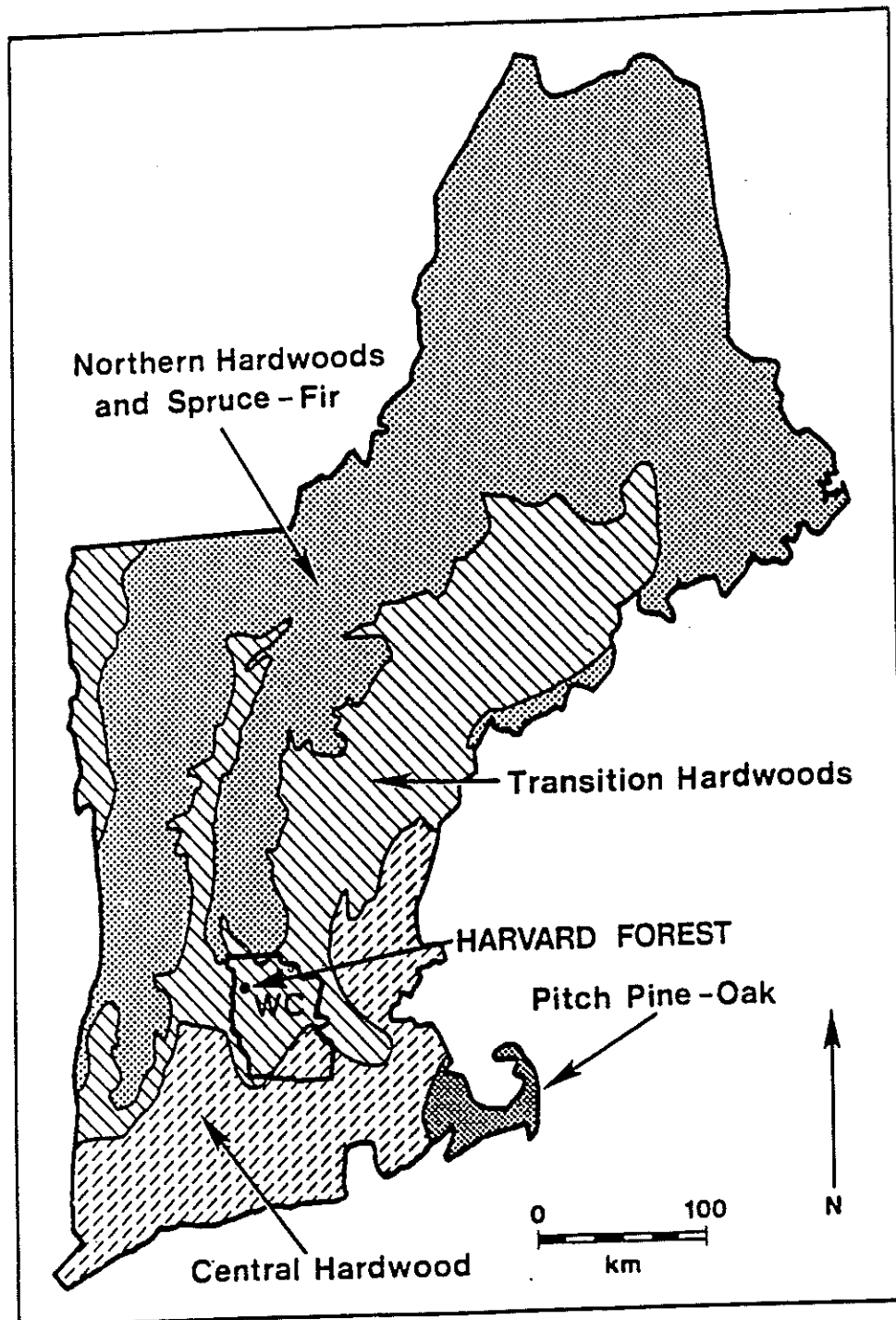# Harvard Forest
Long Term Ecological Research Program

Abstracts from the 11th Annual
Harvard Forest Ecology Symposium

3 April 2000

The Environmental Measurement Site at Harvard Forest
Photograph by Jim Gipe

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

3 April 2000

Julie S. Pallant and Dottie Recos-Smith, Editors

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). At century scales ecosystems have been impacted by broad-scale disturbance and long-term meteorological trends (Boose et al. 1994). On very short time scales interannual, seasonal, and diurnal variation has occured 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). 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). An important question facing ecologists, natural resource managers, and policy makers is: are temperate forests as resilient (and/or resistant) to these novel physical, chemical and climatic stresses as they are to natural disturbance and environmental change?

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

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

Table 1. Design of the Harvard Forest LTER Program

Research Approaches

1. **Reconstruction** of ecosystem dynamics using paleoecology, historical ecology, and modeling to evaluate long-term trends, to study infrequent processes, and to understand the development of modern conditions.

2. **Measurement** of modern ecosystem structure, composition, processes, and dynamics on permanent

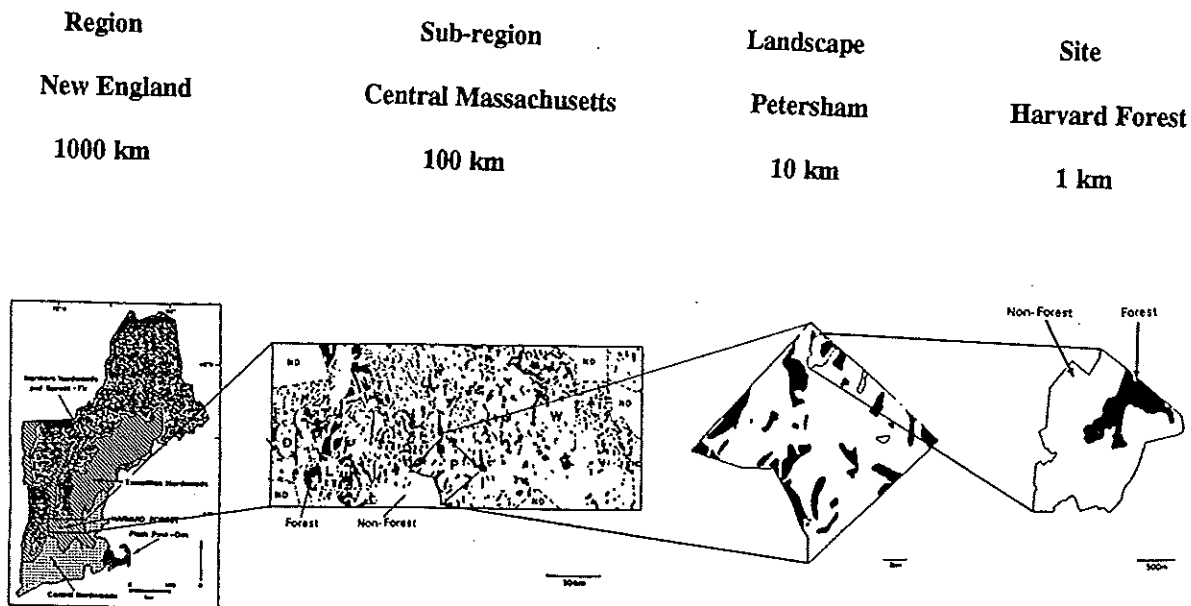| Region	Sub-region	Landscape	Site
New England	Central Massachusetts	Petersham	Harvard Forest
1000 km	100 km	10 km	1 km

Figure 1. Spatial scales of investigation in the Harvard Forest LTER program. Each map depicts the distribution of forest area in the mid 19th C, at the height of agricutural activity and deforestation
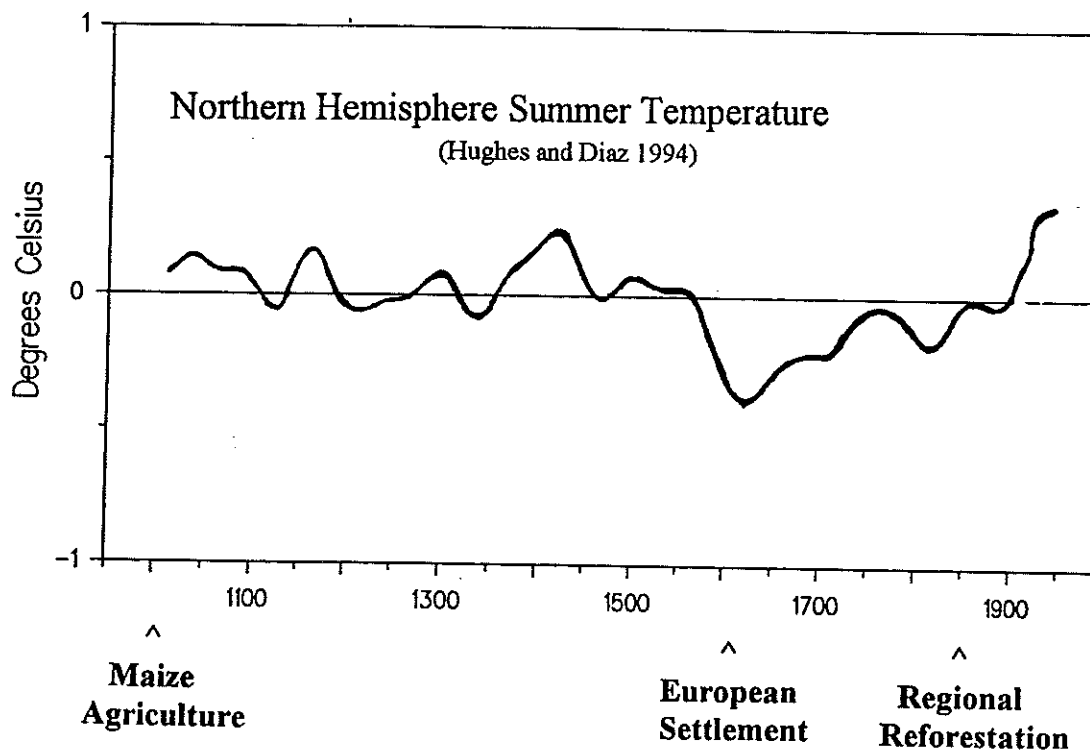

Figure 2. Northern hemisphere summer temperature.

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				
Paleoecology	*	*	*	*
Archaeology		*		
History	*	*	*	*
Dendrochronology			*	*
Hurricane Modeling	*	*	*	*
Ecosystem Modeling	*	*		
MEASUREMENT				
Vegetation Surveys		*	*	*
Soil Surveys				*
Fauna/Flora			*	*
AVIRIS/LANDSAT			*	*
Atmosphere Exchange		*		*
EXPERIMENTAL MANIPULATION				
Hurricane Pulldown				*
Nitrogen Saturation				*
Soil Warming				*
Organic Matter				*
Controlled Environment				*
APPLICATION				
Atmospheric Deposition	*	*	*	*
Water Management	*	*	*	*
Forest Management		*	*	*
Land Protection		*	*	*
Land Use Planning		*	*	*
Education	*	*	*	*

plots, through remote sensing, and through eddy 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, monthly 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 (20-25 students/yr)
2. **Informal Education Program** through the Fisher Museum (> 3,000 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).

Reconstructions 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). 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
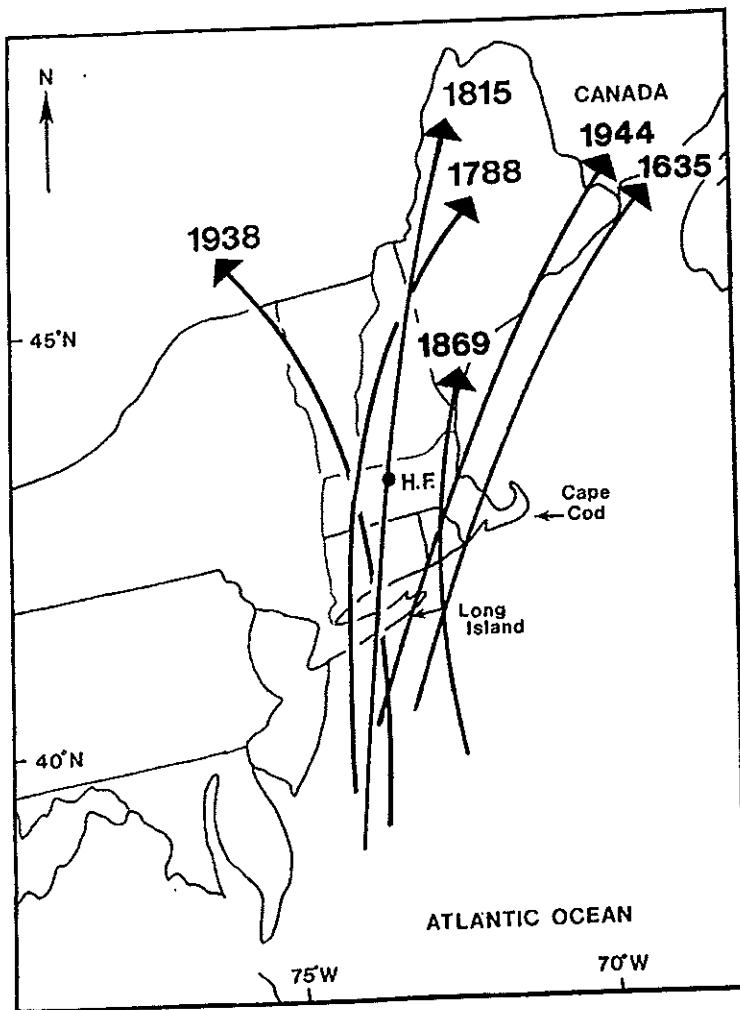
Figure 3. Paths of major hurricanes that have impacted New England and the Harvard Forest during the historical period.
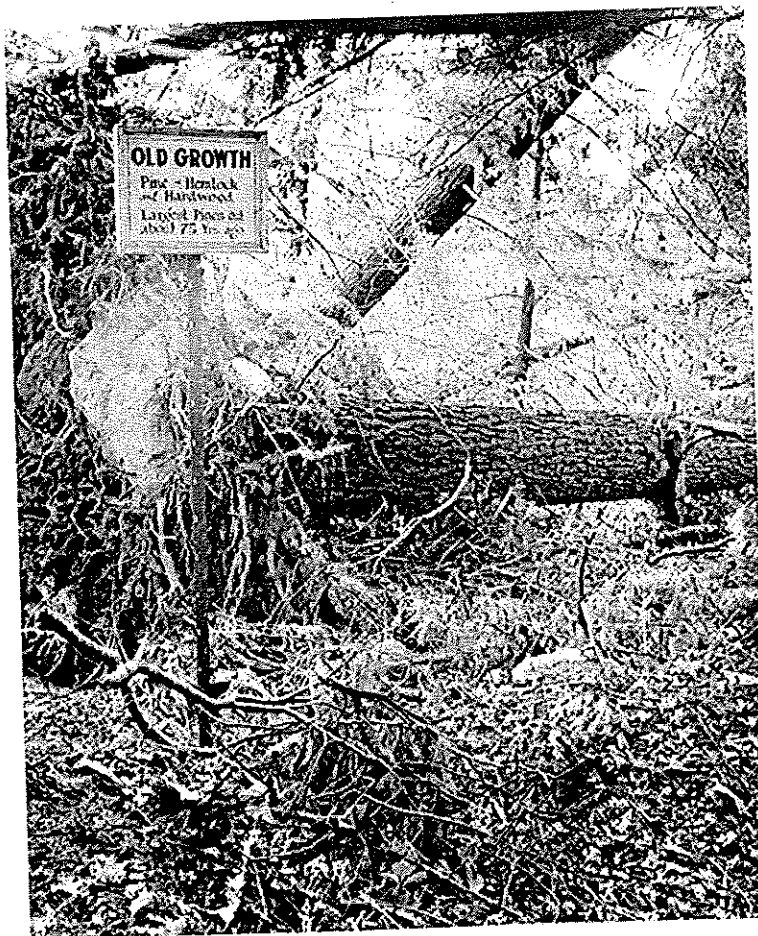

Figure 4. Damage from the 1938 Hurricane was particularly severe for old conifer-dominated forests located on sites exposed to wind such as the old-growth Pisgah Forest in southwestern New Hampshire. Photograph from the Harvard Forest Archives.

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). 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, consequences on plant performance and ecosystem processes (Bazzaz and Miao 1993; Bazzaz *et al.* 1996). The interaction and comparative impact of

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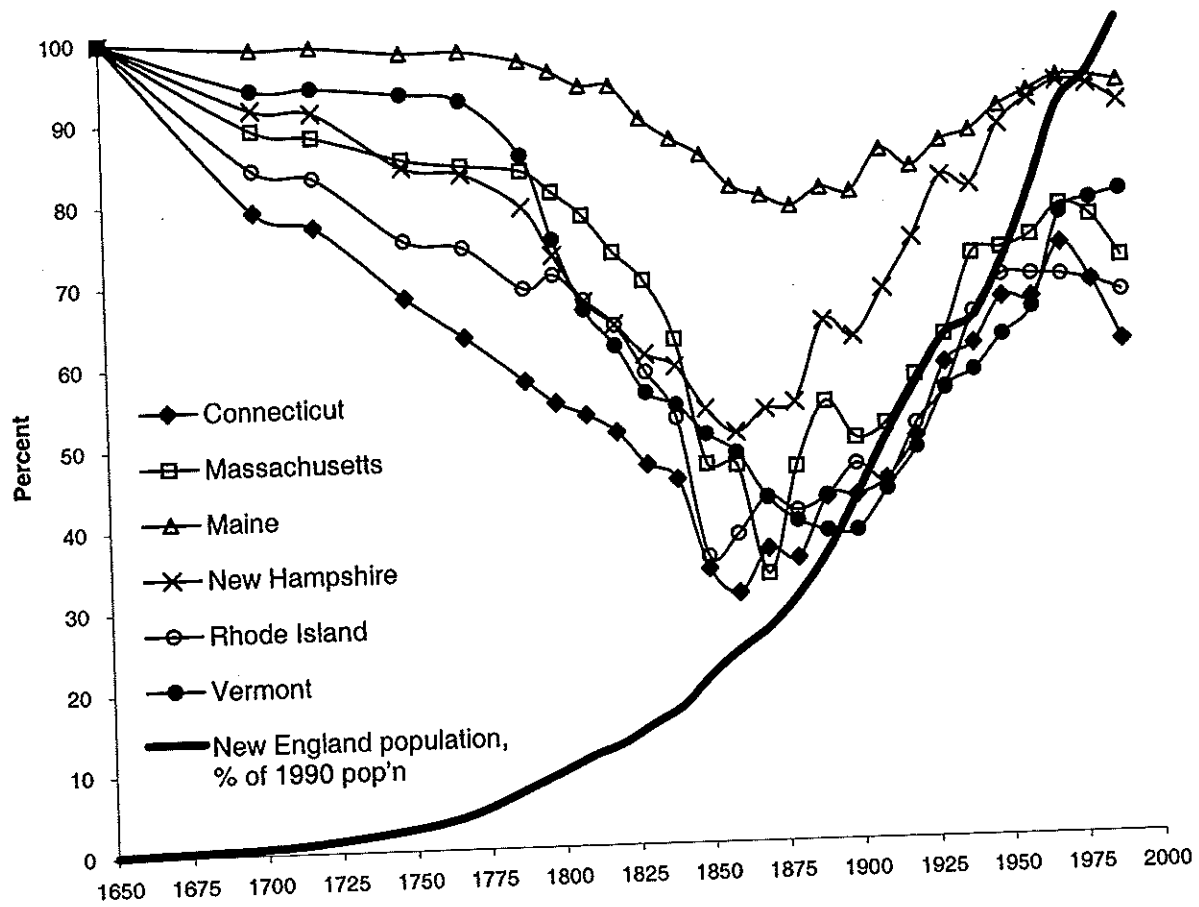
Figure 5. Forest cover and population trends for the New England states.

Massachusetts Landscape of Henry Thoreau (ca. 1830)

North

Forest

Open Land

N.D.

Km
0   10
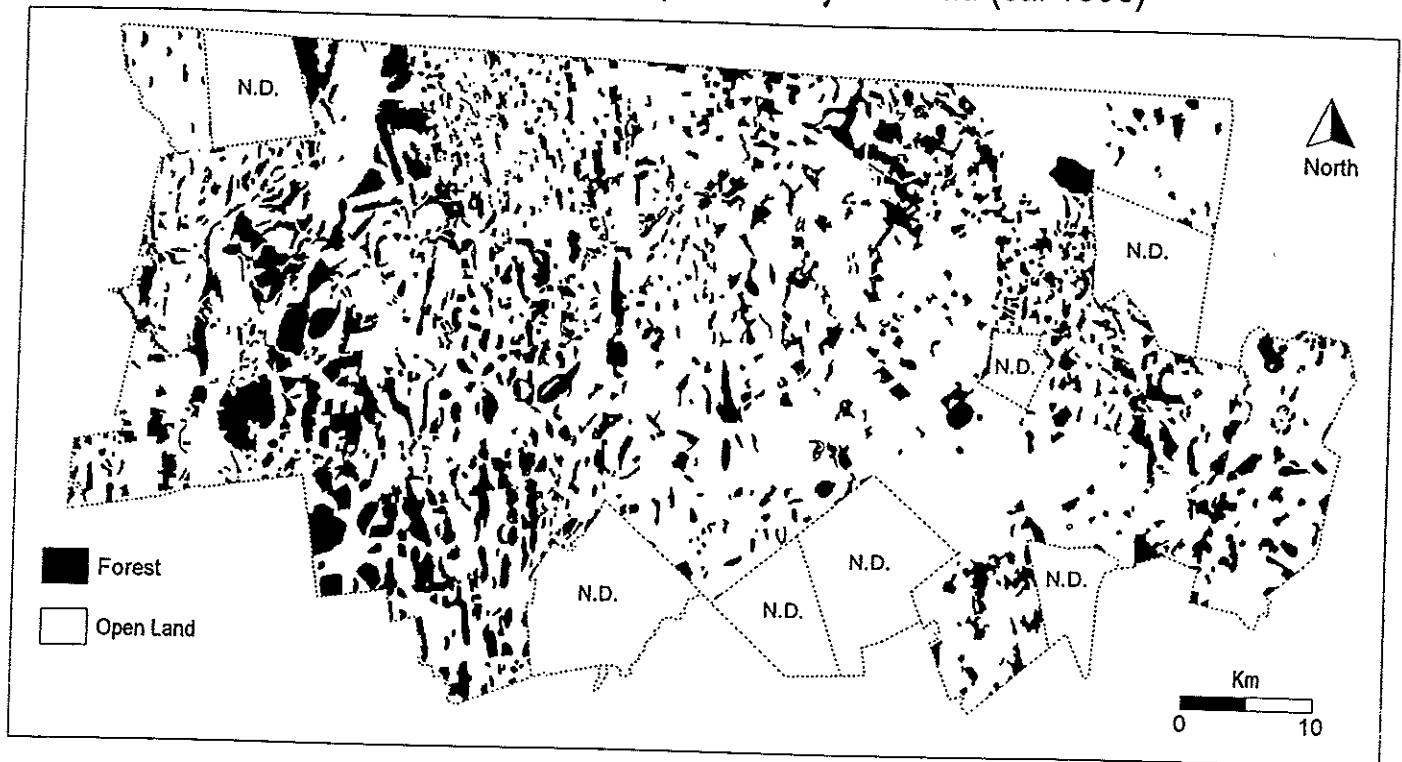
The Modern Massachusetts Landscape (ca. 1985)

Forest

Open Land

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.

Hemlock Woolly Adelgid Distribution - 1996

Figure 7. Hemlock woolly adelgid infestation and the range distribution of hemlock across the eastern U.S.

(Produced by: USDA Forest Service, North-Eastern Area – Forest Health Protecton GIS Group)

Native Range of Eastern Hemlock

Hemlock Woolly Adelgid reported

TOTAL N DEPOSITION
Kg/ha · yr

3.31 - 4.09
4.09 - 4.87
4.87 - 5.65
5.65 - 6.43
6.43 - 7.21
7.21 - 7.99
7.99 - 8.77
8.77 - 9.55
9.55 - 10.33
10.33 - 11.11
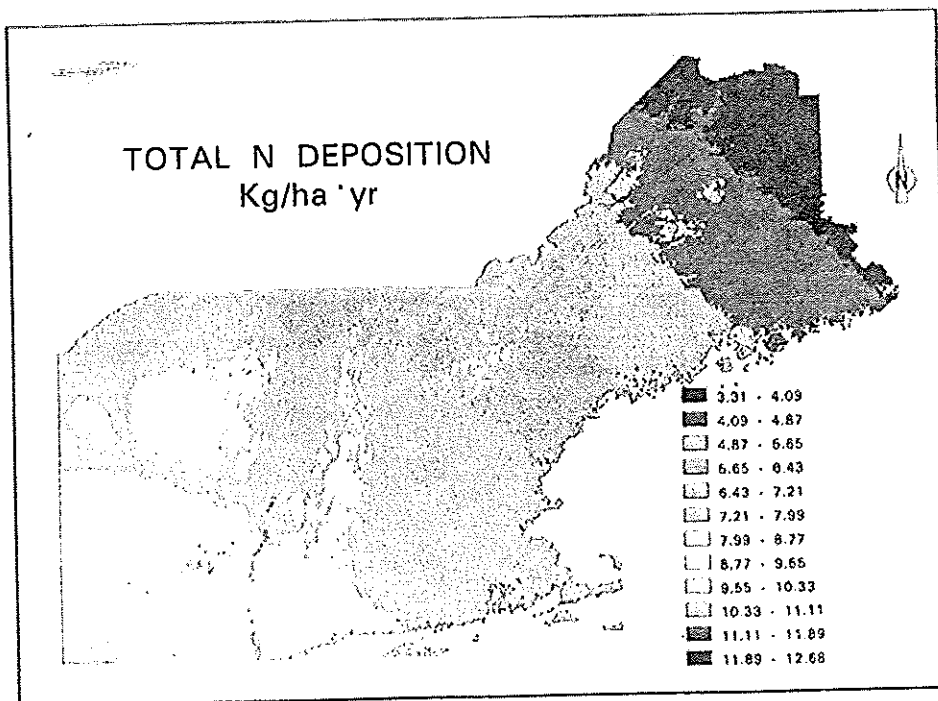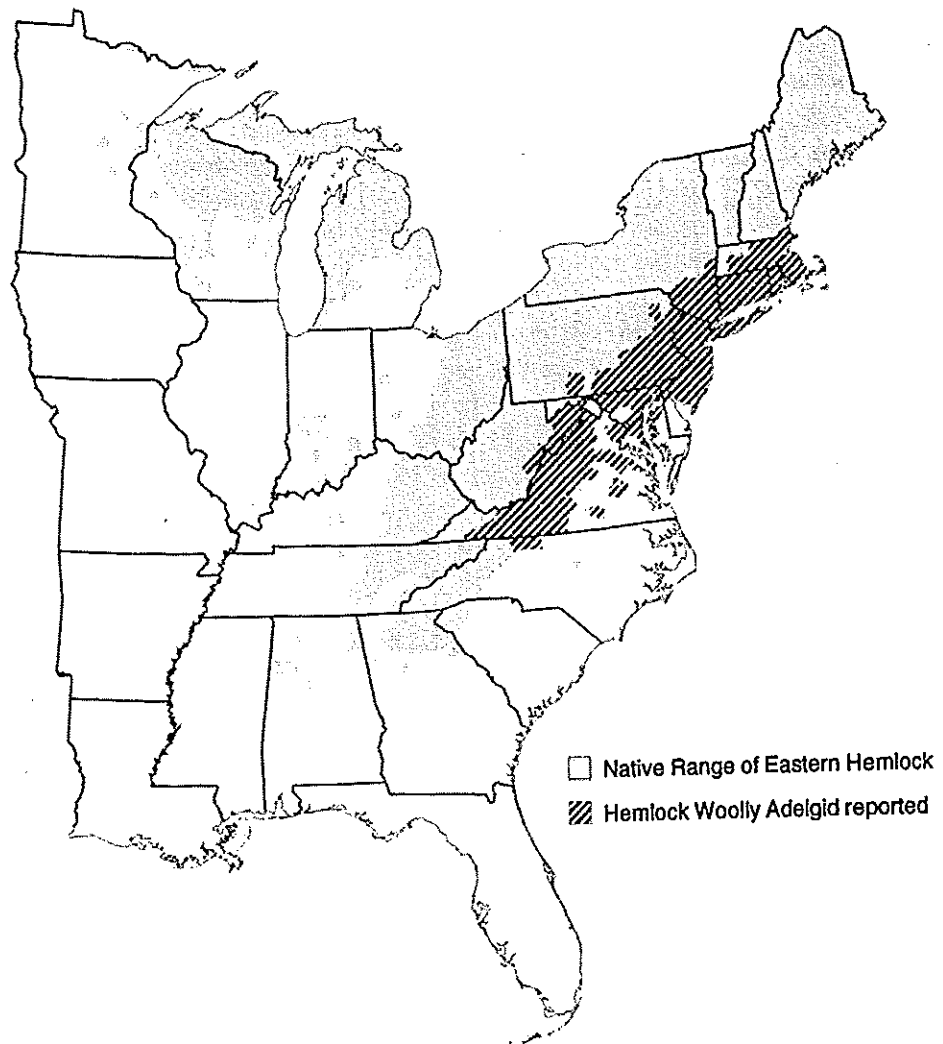11.11 - 11.89
11.89 - 12.68

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)

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 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. Recon-structive 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), 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 eco-system 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 conse-quently 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 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,

HARVARD FOREST
Long-Term Study Sites

Prospect Hill
Tract

PHILLIPSTON

ATHOL
PETERSHAM

▲ Prospect Hill

NITROGEN
SATURATION

HEMLOCK
HOLLOW

ENVIRONMENTAL
MONITORING
STATION

HURRICANE
PULLDOWN

BLACK GUM
SWAMP

Riceville
Pond

SOIL
WARMING

Shaler
Hall

LYFORD
PLOTS

⋈ = CANOPY TOWER

Tom Swamp
Tract

Route 32

Tom Swamp Rd.

Harvard
Pond

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
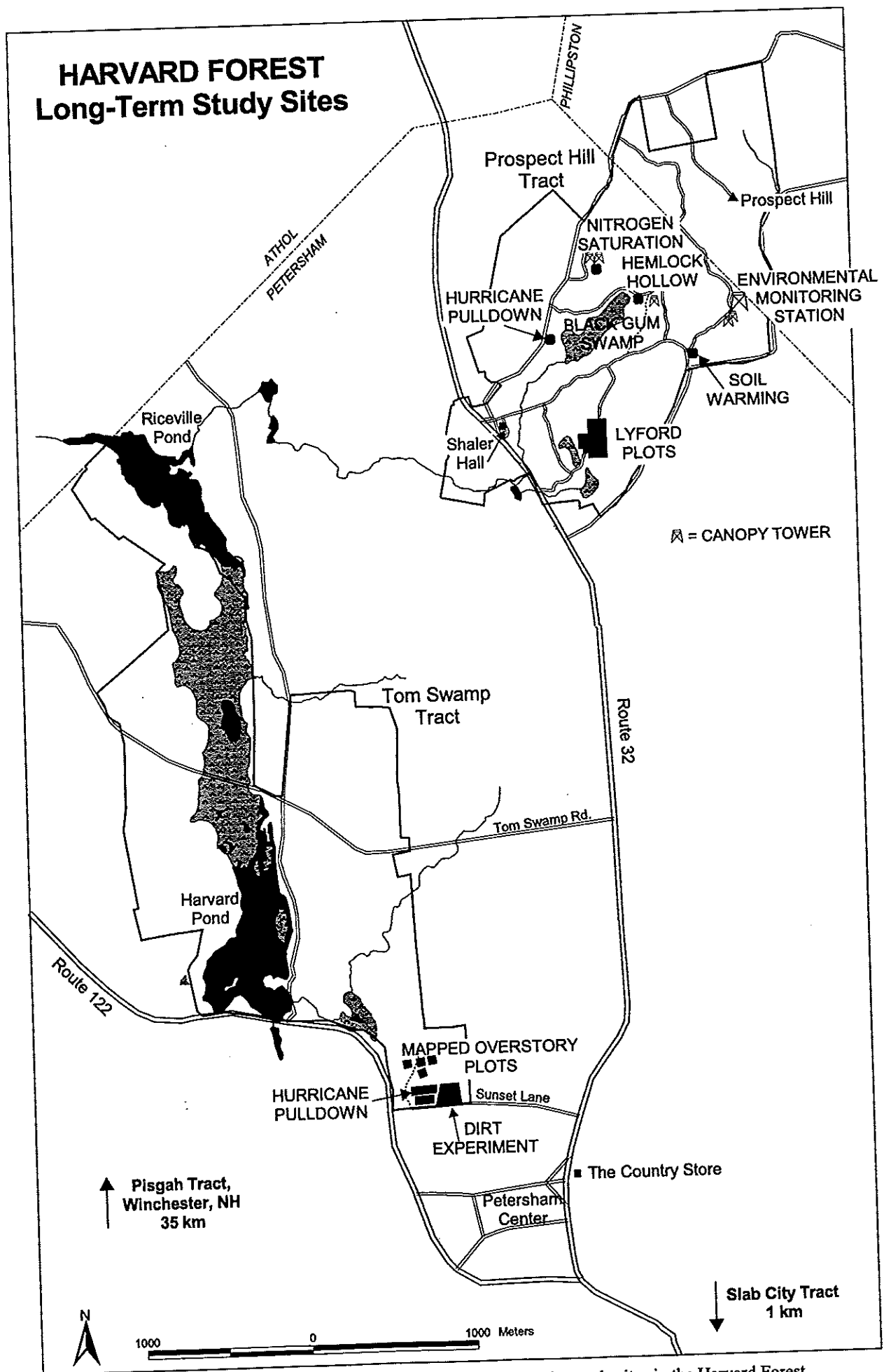1 km

1000   0   1000   Meters

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

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 (approximately 3560 km^2) extends 100 km east of the Connecticut River Valley through the central upland region into the eastern lowlands west of Boston, and south from the New Hampshire border approximately half-way (50 km) to the Connecticut border (Fig. 1). Petersham and the Harvard Forest lie approximately in the center of the area. The region 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).

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 20-25 undergraduates and recent graduates to the Forest to work on all 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. 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

Ongoing studies at the Forest by researchers from the Harvard Forest (Barker Plotkin, Boose, Clayden, Foster, Hadley, Motzkin, O'Keefe, Orwig, Parshall and Perez-Salicrup), Department of Organismic and Evolutionary Biology (Bazzaz), the Ecosystem Center at Woods Hole (Melillo, Newkirk, Nadelhoffer, Steudler), the University of New Hampshire (Aber, Martin), Mount Union College (McClaugherty), Rutgers University (Russell) and University of Massachusetts (Mulholland) provide a background and framework for the proposed research. This group is particularly strong in organismic, community and ecosystem studies and in cartographic analysis and modeling. A significant

complement to this established research effort is brought by investigators from the Department of Earth and Planetary Sciences at Harvard University (Wofsy, Munger) in atmospheric sciences and trace-gas analysis. This group provides experience in long-term studies and a strong interdisciplinary background.

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 moderate 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 borealis*), 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 lutea*), 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 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 physical plant of the Harvard Forest is unusually complete as a base for experimental research in forest ecology, ecosystem sciences and forest microbiology. The brick headquarters complex consists of Shaler Hall, the J. G. Torrey Labs, the Harvard Forest Archive complex and the Fisher Museum.

Shaler Hall, nearly 15,000 square feet of space, contains offices, research laboratories, a seminar room, the Harvard Forest Archives and a library of 22,000 volumes. In addition Shaler Hall provides dormitory accommodations, dining room and kitchen facilities. Common research space includes a photographic suite and darkroom, a graphics and mapping room, a projection and film analysis room for video microscopy, and 40 microcomputers with Internet access through Harvard University. Three laboratories in Shaler Hall are used primarily for dendrochronological, morphological and GIS studies. One laboratory has recently been renovated for research in paleoecology; another has been renovated for research in forest microbiology. A computer room equipped with a digitizing board and related equipment is used extensively for research in spatial analysis and GIS and is being renovated with state-of-the-art computers. An adjacent garage complex has been converted into an archive facility for historical data, plant and soil samples, and materials in cold storage and for air photo interpretation. The Torrey Lab provides space for nutrient analyses, glasshouse studies, and trace gas analysis. Nine

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additional houses provide accommodation for staff, visiting researchers, and students.

The woods crew of four men 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.

University-owned houses and apartments include the Raup house and four residences currently occupied by research staff, or post-doctoral fellows and their families. Two houses provide eight additional rental apartments for staff, graduate students and visiting scientists. The Fisher House, recently donated to the Forest, was renovated in 1998 for accommodation of 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 fifty 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. Offices and a complete herbarium of the local flora also occupy the second floor. Thus, the Fisher Museum Building provides some 10,000 sq ft of space devoted primarily to public education and partly to scientific research.

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 20 years studies have focussed on organism-, community- and ecosystem-level research. Particular strengths have been in tree physiology (Zimmermann 1978, 1983), plant development and architecture (Tomlinson 1983, 1987), forest microbiology (Torrey 1978, Tjepkema *et al.* 1981) and vegetation dynamics (Foster 1988a, 1988b). Research by investigators from Woods Hole (Melillo *et al.* 1983, Melillo and Aber 1984, Nadelhoffer *et al.* 1986, Steudler *et al.* 1986), University of New Hampshire (Aber *et al.* 1983, Aber *et al.* 1985), Clarkson University (Linkins *et al.* 1984), and Mount Union College (McClaugherty *et al.* 1982, 1984) 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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Interannual Variability in Soil Respiration in an Aggrading Mixed Hardwood Stand at the Harvard Forest

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

We have observed significant year-to-year variability in soil respiration on control plots at the soil warming experiment. Soil temperature can explain much of the variability in soil respiration over the 9 years of the study, but soil moisture appears to limit respiration in dry summers. Relative contributions from the root and microbial respiration to the total soil respiration have remained relatively constant across years irrespective of summer moisture conditions.

Over the 9-year study, annual soil carbon efflux has varied by as much as 30% in consecutive years (Fig. 1). Although soil temperature is generally a good predictor of monthly CO_2 release (Fig. 2a and b), the two years with the lowest CO_2 efflux coincided with years with low summer soil moisture (1995 and 1999) rather than years with low mean annual temperature. Soil temperature measured at 4 cm was able to account for 66% of the variability in monthly CO_2 efflux from the control plots in the soil warming experiment, and 69% of the soil respiration when the years with the two driest summers are excluded (Fig. 2a and b). Soil temperature could only account for 20% of the variability in monthly CO_2 efflux during summers when average soil moisture dropped below 0.15 g H_2O/cm^3 soil (1995 and 1999).

The Q_{10} index, a coefficient describing the exponential relationship between CO_2 efflux and soil temperature, has been variable over the 9 years of the soil warming experiment. The annual Q_{10} ranged from 1.97 to 3.68 in the control plots. Our measurements suggest that the Q_{10} index varies predictably with changes in summer precipitation. The cumulative precipitation for the period June through August was linearly correlated with the annual Q_{10} estimated for the control plots in the soil warming experiment over the last 9 years (Fig. 3).

Although there has been a large amount of variability in annual carbon efflux from the soil, relative contributions of respiration from microbial communities and the root and root-associated rhizosphere have remained relatively constant. A trenching experiment was established in 1994 to quantify the relative contributions of root and microbial respiration to the total carbon efflux from the forest floor. Microbial respiration has accounted for an average of 81% of the total measured soil respiration, and has ranged from 79% in 1998 to 85% in 1996. The dry conditions in 1999 decreased total soil respiration by 20% compared to 1998, but the relative contribution from microbial respiration remained constant (79% in both years).

We are now using these results to improve biogeochemistry models we have developed such as the Terrestrial Ecosystem Model (TEM). We use TEM to study the effects of various kinds of natural and human perturbations of the carbon cycle at regional and global scales.

The Effect of Chronic Carbon and Nitrogen Manipulation on the Relationships Between Soil C:N, Soil Respiration and Soil Solution DOC in Temperate Forests

J. Aitkenhead, G. Berntson and W. McDowell

Losses of carbon in forest ecosystems are likely to be affected by climate and global change. Soil respiration and dissolved organic carbon export are two major pathways for carbon cycling in temperate forests. The effects of chronic carbon and nitrogen manipulation on relationships between dissolved organic carbon export, soil respiration and soil C:N were quantified in the DIRT plot hardwood and Chronic – N hardwood and coniferous stands. Soil solution DOC concentrations were significantly higher in the double above-ground litter input and significantly lower than the zero above-ground litter input (p < 0.01 n = 102). Soil respiration, while significantly lower with zero litter input (p < 0.001 n = 49) was not significantly different from the control plots when double litter was added (p > 0.05 n = 50). With nitrogen additions of 150 kg ha^{-1} yr^{-1}, DOC concentrations in soil solution were significantly higher in both the hardwood and coniferous stands compared to their controls (p < 0.05 n = 204). Soil respiration was significantly affected by high N

† indicates years with average summer
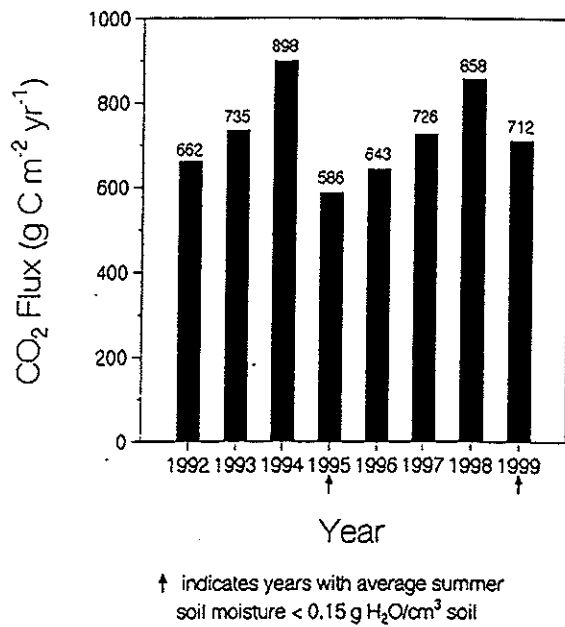soil moisture < 0.15 g H_2O/cm^3 soil

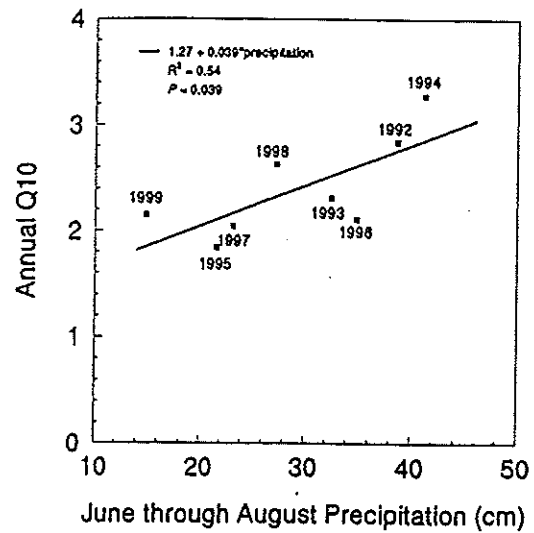Figure 1: Annual carbon flux from control plots

Figure 3: Summer precipitation shows a strong relationship to the annual Q_{10}, a coefficient describing the exponential relationship between soil respiration and soil temperature.
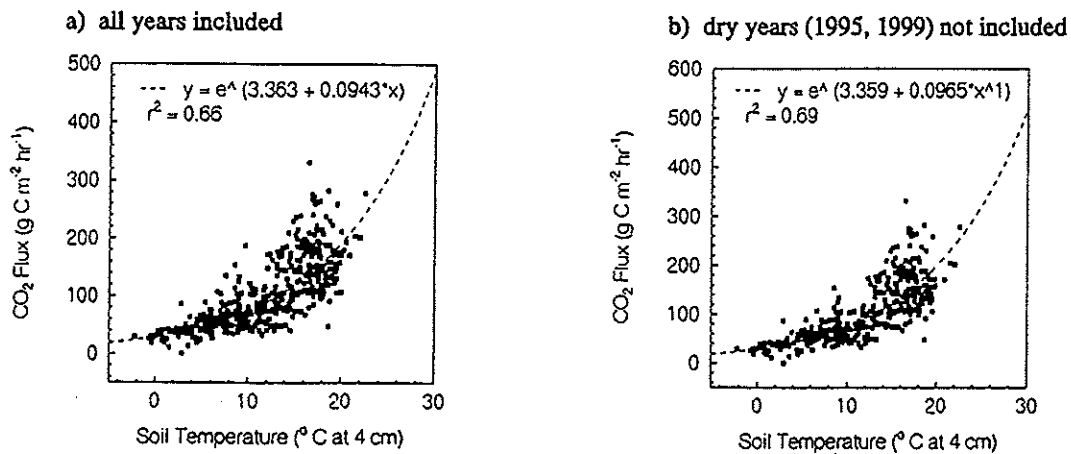
a) all years included

$y = e^{\wedge} (3.363 + 0.0943 \cdot x)$
$r^2 = 0.66$

b) dry years (1995, 1999) not included

$y = e^{\wedge} (3.359 + 0.0965 \cdot x^{\wedge}1)$
$r^2 = 0.69$

Figure 2: Soil respiration as a function of soil temperature in (a) all 9 years of the experiment and in (b) only mesic to wet years

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inputs in the coniferous stand only (p < 0.05 n = 69).

DOC concentration was significantly related to soil respiration in both hardwood and coniferous stands ($R^2 = 0.61$ p < 0.0001; $R^2 = 0.92$ p < 0.05). Neither manipulation of above-ground carbon inputs nor chronic-N input had an effect upon the relationship between DOC and CO_2 in hardwood forests. When the coniferous stand was fertilized with nitrogen, the relationship between the two variables was lost. Soil C:N ratio was able to explain 75% of the variance in soil solution DOC when hardwood and coniferous stands and treatments were combined (p = 0.01). No relationship was found between soil respiration and soil C:N.

The findings of this study show that manipulation of above ground carbon and chronic nitrogen applications to hardwood forests are unlikely to affect the fundamental mechanisms of DOC production in the short-term. However, there appears to be a de-coupling of the carbon and nitrogen cycles with chronic-N application to coniferous forests. Fertilization of coniferous forests will inevitably lead to reduced surface water quality in terms of increased carbon and nitrogen concentrations.

The Development and Lateral Expansion of Peatlands in Central New England

R. Anderson, D. Foster and G. Motzkin

On a global scale, peatlands are fundamentally important because they contain approximately one third of the earth's carbon pool and play a critical role in global carbon dynamics. In order to understand how peatlands might respond to impending climate change, it is imperative to study how peatland development was influenced by past climatic fluctuations.

With adequate moisture, peatlands form through the mechanisms of terrestrialization and paludification. Terrestrialization, also known as lakefill, occurs when a body of water is slowly filled-in by peat, turning open water into a vegetated community. In contrast, paludification converts upland communities to peatland through lateral extension of the peat mass.

The relative importance of these two mechanisms of peatland development 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, such as silt or lake mud. The progress of paludification can be conclusively demonstrated by dating basal peat deposits. When a site has paludified, the basal peat deposits are younger towards the edge where expansion has occurred than at the site of initiation.

Both climate and topography function as fundamental controls on the development of peatlands and the dynamics of paludification. It is possible to determine the relative influence of each factor by comparing the ages of basal peat deposits from multiple sites or different areas of the same site. When climate is a driving force across a region, multiple sites may be expected to have similar dates of peat initiation or lateral spread. In contrast, when topography is the dominant influence, the limits of expansion should mirror the basin topography and periods of paludification are asynchronous at different sites.

Worldwide, most peatlands have formed through paludification, rather than lakefill. Yet, based on very general models of wetland formation for temperate regions and due to the high summer temperatures that limit peat accumulation in central New England, terrestrialization has been viewed as the main process of peatland development in the area. The result is that the dynamics of paludification have yet to be examined in temperate areas, despite evidence suggesting that paludification may be fairly widespread and important.

We propose to investigate the developmental history of peatlands in central New England by examining two questions. 1. Has paludification been an important process in the formation of peatlands in central New England? 2. If so, what influence have climate and topography had on the pattern of development and the rates of expansion?

To address these questions, we will study three forested peatlands. At each site, a detailed basin map and descriptions of the sediments will be prepared. Then, a series of basal peat samples

will be collected and radiocarbon-dated in order to determine rates of lateral spread.

Net Ecosystem Exchange of CO_2 and Carbon Cycling by the Harvard Forest

C. Barford, E. Pyle, L. Hutyra, D. Patterson, J. Munger and S. Wofsy

Micrometeorology-based measurements of forest-atmosphere CO_2 exchange indicate that secondary forest growth in the eastern U.S. currently sequesters about one-third (0.7 Gton yr^{-1}) of the of atmospheric CO_2 -carbon fixed by forests globally (2 Gton yr^{-1}). However, this estimate is more than double the forest inventory-based estimate for the same region. The goals of our carbon cycling study are: (1) to interpret the continuous record of net ecosystem exchange of CO_2 (NEE) at Harvard Forest with respect to ground-based measurements of C allocation and efflux; (2) to place our results in the context of past land use, disturbance, and current tree species demography; and (3) to investigate the effects of selective harvest on C cycling in an adjacent forest. Meeting these objectives over several years can assist in predicting forest response to climate variation and in relating NEE to forest history and composition on a regional scale.

Annual NEE in 1998 and 1999 were -1.1 and -2.0 tons C ha^{-1}, respectively. The timing of ecosystem C uptake and efflux differed greatly, depending on weather features such as early budbreak and late summer drought in '98, and severe summer drought followed by September rain in '99. Above-ground wood increment in early successional species constituted a slightly higher proportion of the NEE in '99 than in '98 (12% vs. 7%, respectively), possibly due to their predominance in more mesic microsites. However, in both years the above-ground wood increment in all live trees > 10 cm DBH was 60-70% of the whole ecosystem sequestration (0.7 and 1.2 tons C ha^{-1}, respectively). Oaks (*Quercus rubra* and *Q. velutina*) gained well over half the total wood increment in both years.

Within our 40 sample plots (total 1.3 ha), 57 trees containing 4.6 tons C died between 1993 and 1999. Thirty-three of these (3.3 tons C) were

red maple (*Acer rubrum*). In 1999, 23 trees (1.3 tons C) died, including 7 red maples (0.6 tons C). For all tree species in the sample, tree growth into the > 10 cm size class between 1993 and 1999 was far less than mortality in terms of both number of stems and carbon. Our preliminary survey of coarse woody debris (CWD) in the spring of '99 indicates that the total pool of logs and snags > 7.5 cm diameter at Harvard Forest contained about 6 tons C ha^{-1}. Our mortality and CWD data together suggest that C storage in dead wood within the fetch of the EMS will increase as a proportion of NEE as the forest matures.

One year of pre-harvest measurements on private property immediately south of the Prospect Hill Tract indicate subtle differences with respect to existing study plots. Total tree biomass is slightly less than in Prospect Hill plots (81 vs. 98 tons C ha^{-1}, respectively). Biomass distribution among species is slightly different, with hemlock (*Tsuga canadensis*), birch (*Betula* spp.) and beech (*Fagus grandifolia*) comprising a greater proportion of stand biomass. Soil respiration and phenology trends are similar to Prospect Hill.

Regeneration Trends in the Experimental Hurricane, 1990-1999

A. Barker Plotkin and D. Foster

The hurricane experiment was designed to simulate the impacts of catastrophic wind 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 purpose of the experiment is to systematically study the mechanisms of tree regeneration and changes in species composition following such disturbance. Regeneration has been tracked from 1990 (pre-manipulation) - 1999 in 10m^2 plots along transects in the experimental (0.8 ha) and control (0.6 ha) sites (see Cooper-Ellis *et al.* 1999 for a complete description of experimental design and methods). We are particularly interested in the role of sprouting in a hardwood-dominated forest, which was an uncommon stand type when the last major hurricane struck this region in 1938.

From 1990 – 1993, saplings and sprouts

increased four-fold in the experimental plot (>25,000 stems/hectare), then decreased to 17,500 stems/ha in 1999 (about a three-fold increase from 1990). In the control plot, saplings and sprouts increased 70% from 1990 to 1999; much of this increase was the result of a 1992 winter storm. Red maple, birch species, white ash and black cherry dominate regeneration (Fig. 1). Red oak is less abundant (<5% relative density of saplings and sprouts in 1999) and below average in height. In comparison, the original overstory was composed mainly of red maple and red oak (52% and 19% relative density respectively, with large red oak comprising the majority of the basal area).

Sprouting was an important mechanism for maintaining canopy cover initially, which aided in muting ecosystem-level response to the manipulation (Cooper-Ellis *et al.* 1999, Foster *et al.* 1997). However, the long-term importance of sprouting in shaping forest structure and composition is less than advance regeneration and new seedlings/seedling sprouts. As the number of sprouts per tree and number of trees with sprouts have declined, tree sprouts have proportionally decreased, whereas other types of regeneration have proportionally held steady or increased (Table 1).

Ingrowth into the >5cm diameter class gives a preliminary sense of which components of regeneration will successfully establish the new stand. Most ingrowth is advance regeneration, whereas sprouting plays a minor role in forming the new cohort (Fig. 2). Black and yellow birch make up 50% of the ingrowth; red maple and white pine each comprise 10%. We plan to map and measure all new stems >5cm dbh in summer 2000 in the experimental and control plots, so we can track the dynamics of this new cohort as it undergoes self-thinning and interacts with the remaining overstory trees.

Cooper-Ellis, S., D.R. Foster, G. Carlton, and A. Lezberg. 1999. Vegetation response to catastrophic wind: results from an experimental hurricane. Ecology 80:2683-2696.

Foster, D.R., J.D. Aber, J.M. Melillo, R.D. Bowden, and F.A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. BioScience 47:437-445.

Extending Spatially Explicit Land-use of the Southern Yucatan

A. Barker Plotkin and D. Foster

The Southern Yucatan Peninsular Region contains the most extensive tropical forest in Mexico, but is facing rapid deforestation. Since the late 1960s, government resettlement programs and the construction of a paved highway bisecting the region have led to an influx of people to this region that has been sparsely populated since the collapse of the Mayan civilization 1000 years ago. Harvard Forest is collaborating with Clark University and El Colegio de la Frontera Sur (ECOSUR), Mexico, to document the natural, historical and economic factors driving land use and land cover change in the region. Spatially explicit models of land cover transitions are being developed using remotely sensed imagery from 1975 to the present by researchers at Clark University. However, the satellite imagery begins after major agricultural settlement was well underway. Through the 1900s but especially since 1950, large forestry concessions and forestry ejidos were engaged in selective logging of high-value hardwoods (e.g., mahogany) in the region. As high-value hardwoods have been depleted and agricultural activity has increased, logging has declined. The paved highway was completed in 1967, allowing more agricultural settlements to establish. To extend the history of regional land cover available from remotely sensed imagery, we are interpreting land cover patterns from aerial photographs of the region taken in 1969, capturing spatial patterns at this critical transition in the region's land-use history.

The black and white, fairly small-scale (~1:80,000) photos cover approximately the northern half of the entire study area (Fig. 1). With the aid of a stereoscope, we delineated all observable roads and apparently disturbed land. The undisturbed forest matrix was not classified into different natural forest types. Land cover was divided into two major categories: agricultural lands (parcel borders sharp and square-edged, and vegetation shorter than surrounding land) or disturbed forest (discontinuous forest cover, which could be a result of human activity or natural disturbance). Each of these major categories was subdivided into finer classifications based on
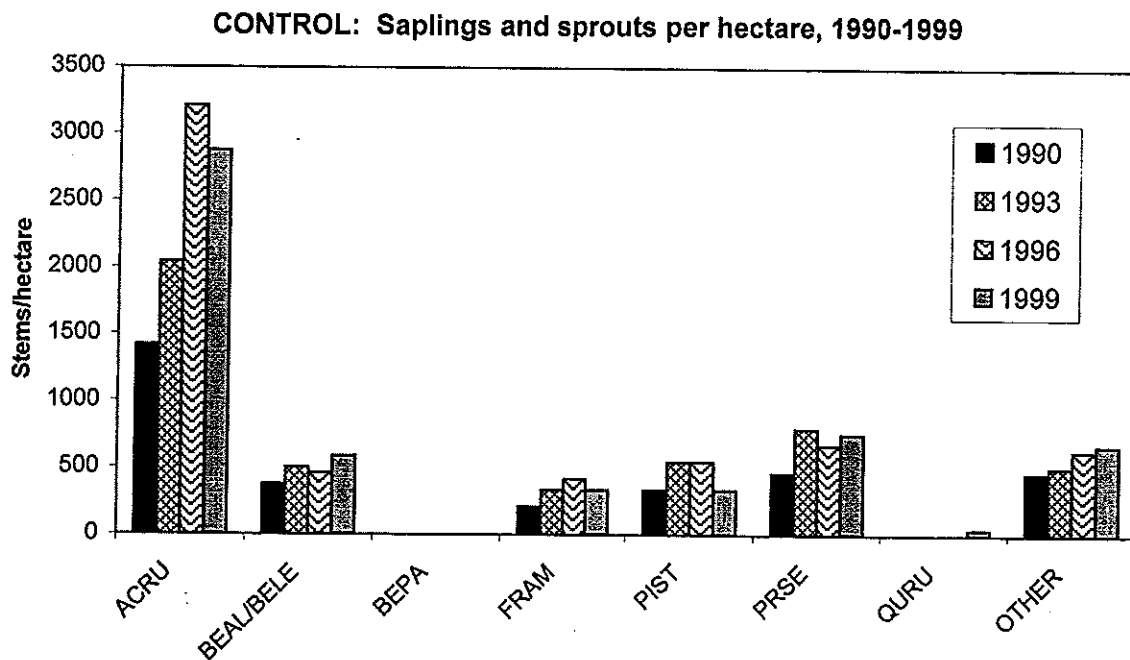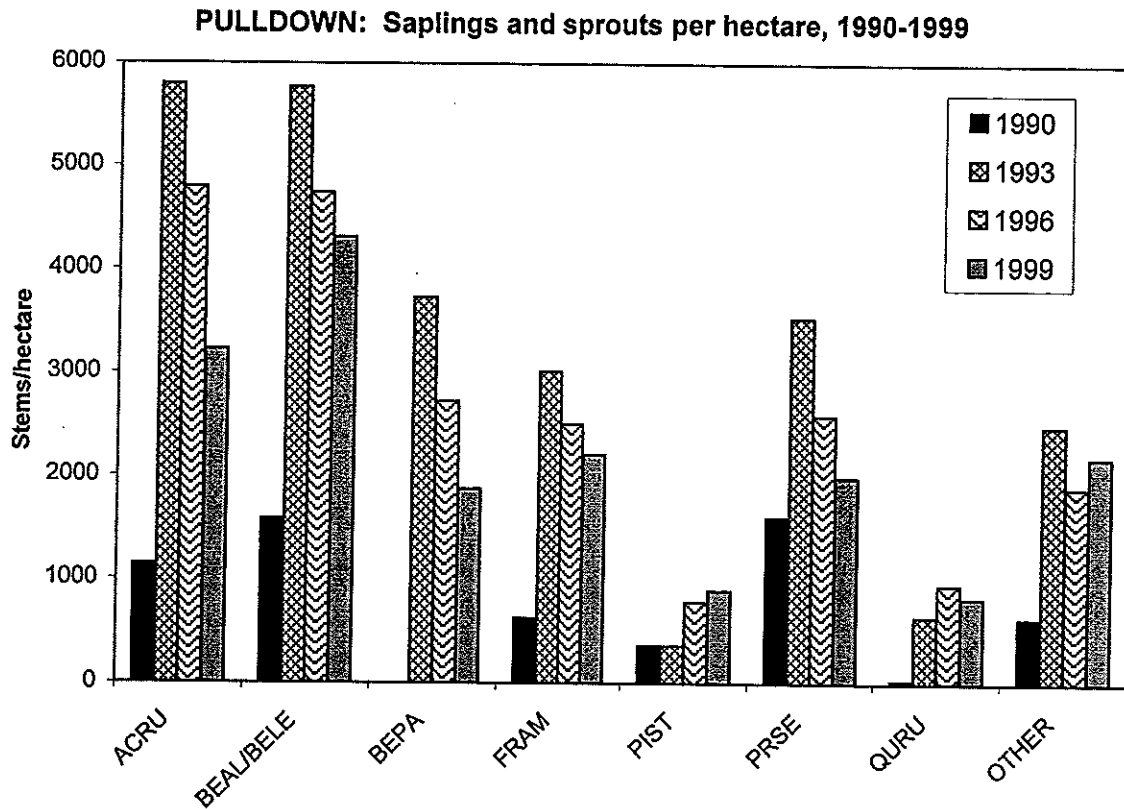
Figure 1. Regeneration density (stems/ha) in the pulldown and control plots, 1990-1999, by species. Species codes: ACRU = *Acer rubrum*; BEAL = *Betula alleghaniensis*; BELE = *B. lenta*; BEPA = *B. papyrifera*; FRAM = *Fraxinus americana*; PIST = *Pinus strobus*; PRSE = *Prunus serotina*; QURU = *Quercus rubra*. OTHER includes *Acer saccharum, Carya glabra, C. ovata, Castanea dentata,Cornus alternifolia, Fagus grandifolia, Ostrya virginiana, Populus tremuloides, Prunus pensylvanica, Quercus alba, Salix sp.,Sorbus americana,* and *Tsuga canadensis*.

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Table 1. Relative density of different regeneration types in the experimental pulldown, 1990-1999.

	PULLDOWN (% stems)				CONTROL (% stems)			
	1990	1993	1996	1999	1990	1993	1996	1999
Advance regeneration	100.0	29.7	29.2	28.4	100.0	91.2	58.5	50.0
New saplings		27.1	31.6	32.5			1.4	3.7
Seedling Sprouts		22.6	22.2	23.7		8.0	13.4	20.1
Tree Sprouts		20.3	15.4	10.8		0.9	26.8	23.9
Sprouts of sprouts		0.1	0.3	3.5				0.7
Unknown sprouts		0.2	1.3	1.2				1.5
Total (absolute values per hectare)	5958	25292	20931	17500	3250	4708	5917	5583

Advance regeneration = any stem, seedling or sprout origin, that was present in 1990 (before the manipulation). This includes stems that were smaller than 30cm in height at the onset of the study.

New saplings = seed-origin stems that germinated after the 1990 manipulation.

Seedling sprouts = stems sprouting from trees <5 cm dbh (often much smaller).

Tree sprouts = stems sprouting from trees >5 cm dbh

Sprouts of sprouts = stems sprouting from other sprouts

Unknown sprouts = stem sprouting from an unknown stem of origin

Ingrowth into the >5 cm diameter class
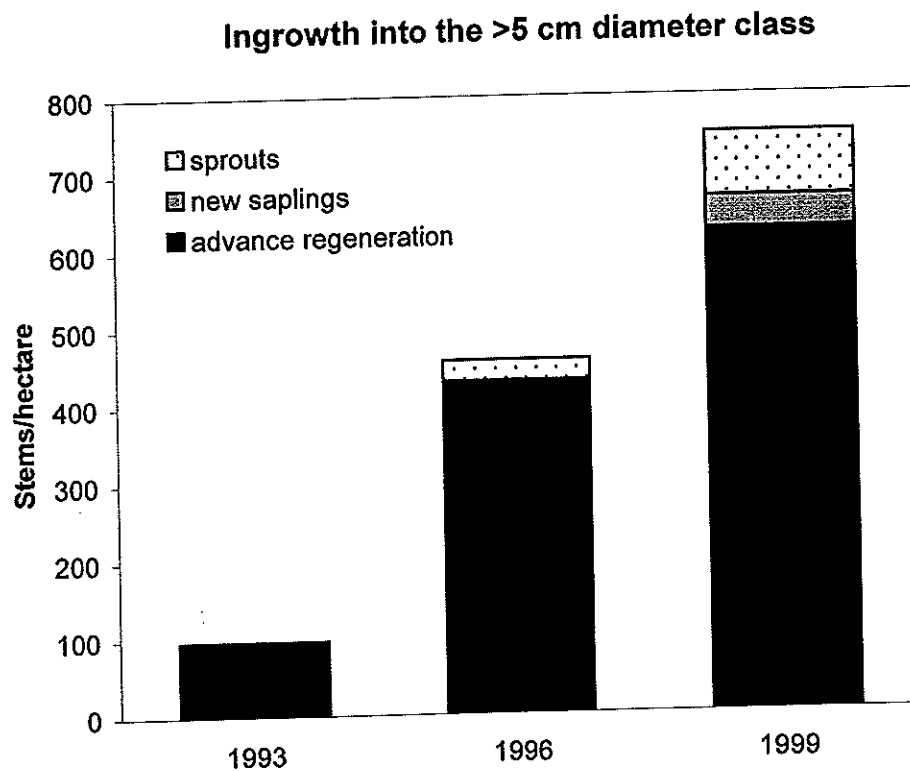
Figure 2. Ingrowth into the >5cm dbh size class, by regeneration type. While sprouting was important in initial maintenance of canopy cover of the experimental site, successful ingrowth is dominated by advance regeneration.

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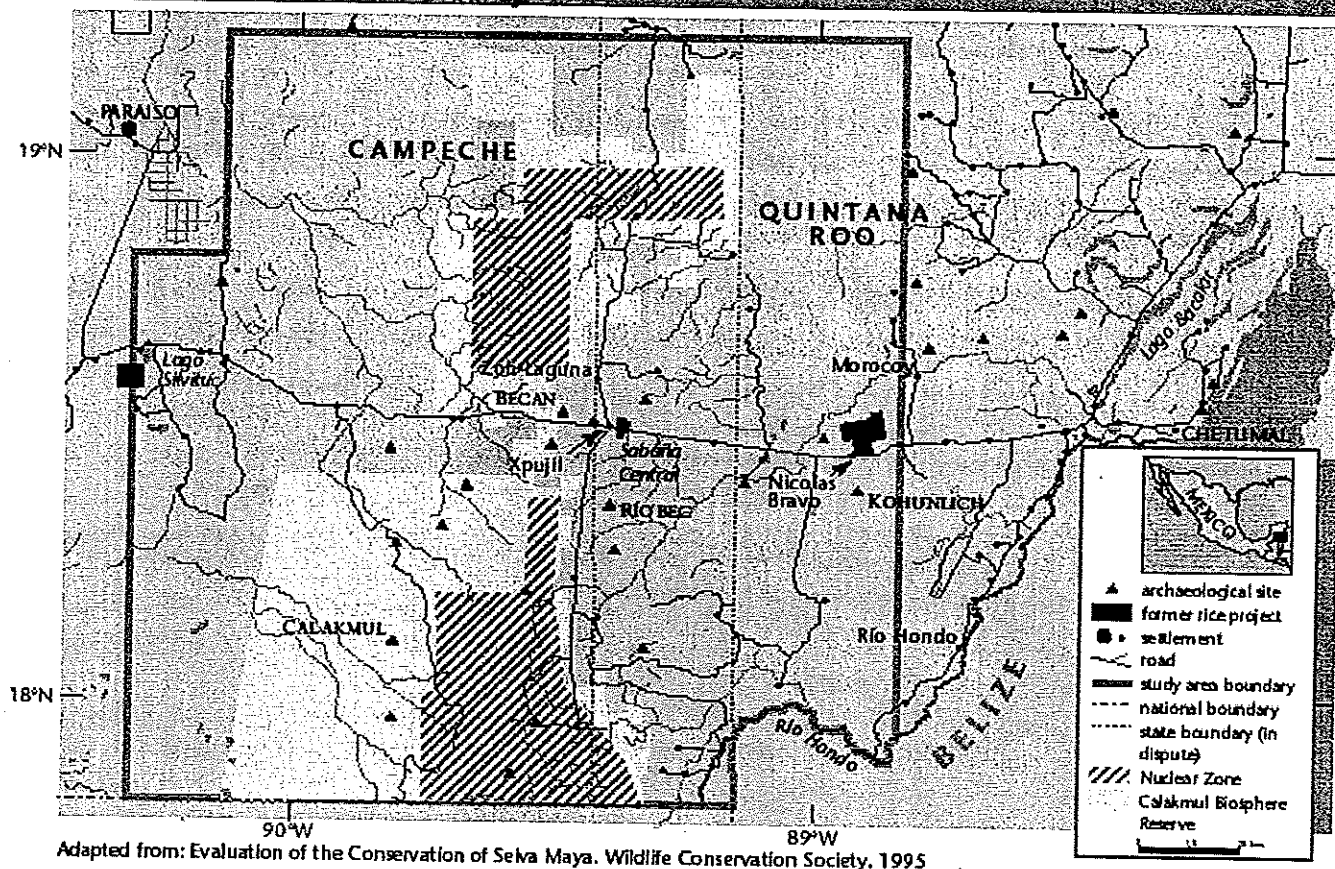Adapted from: Evaluation of the Conservation of Selva Maya. Wildlife Conservation Society. 1995

Figure 1. The Southern Yucatan Peninsular Region, showing the study area boundaries, major cultural features and the Calakmul Biosphere Reserve (established 1989).

percent vegetation cover. Land-cover and roads are being digitized using ArcView GIS software. Currently, about 80% of the photos have been digitized.

Preliminary observations suggest that agricultural activity was concentrated around older towns on the eastern and western edges of the study region, with little agricultural development elsewhere. Some of the central area with no signs of human use is now part of the Calakmul Biosphere Reserve. The eastern half of the study area (originally the main highway extended only across the eastern half of the region) contains a systematic grid of roads, presumably used for logging access. Many of these roads were faint in the photos and do not appear on current maps of the region.

We plan to relate the broad patterns of land-cover in 1969 to prior logging activity and the more recent patterns of land-cover obtained from the satellite imagery. This data set will provide a more complete understanding of the spatial extent of mid-century logging and the beginning of major deforestation and settlement in this region.

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, personal communication], 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), chloroform ($CHCl_3$), carbon tetrachloride (CCl_4), PCE (C_2Cl_4), and halon-1211 ($CBrClF_2$), as well as hydrogen (H_2), CO, methane (CH_4), nitrous oxide (N_2O), and sulfur hexafluoride (SF_6), all on a per capita basis. The results of this study confirm the accuracy of the above listed inventories for the New York City – Washington, D.C. corridor.

The seasonal character of the urban/industrial emissions for the New York – Washington, D.C. corridor are calculated as functions of CO and PCE releases. Seven cases are considered: all data; northwest winds only (NW); southwest winds only (SW); day (6 am to 6 pm); night (6 pm to 6 am) ; high U* (>0.2 m/s); and low U* (<0.2 m/s) (where U* = ($\sqrt{}$momentum flux)/100, a measure of how well mixed the air is). The two cases of 'northwest winds only' and 'southwest winds only' are chosen because the Harvard Forest station receives most of its air flow from the west, with the most polluted air from the southwest and the fastest winds and least polluted (background) air from the northwest. All seven cases track each other well. Only the NW case shows a tendency for non-conformity, particularly for H1211, $CHCl_3$, and N_2O. Seasonal cycles exist in the emissions of CFC12, CFC11, and H1211, with highest values consistently found in the summer and lowest in the winter. In the case of CFC12, such a cycle is to be expected given that its primary use is as a coolant in car air-conditioners which are used in the summertime. The pollution of SF_6 also appears to have a

seasonal cycle with highs in the spring and lows in the summer/fall. The high degree of similarity between CO/PCE and H_2/PCE suggests that CO and H_2 are emitted by the same primary and secondary sources. The same may be said about CFC11 and CFC12, whose ratios to PCE are strikingly similar.

The annual urban pollution emissions for each species indicate that a number of the species exhibit distinct inter-annual trends. Carbon monoxide, CFC11, N_2O, and TCE appear on the whole to be increasing. For CFC11, such a positive trend 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. Hydrogen's urban/industrial pollution emissions appear stable, and Halon-1211 and $CHCl_3$ do not exhibit any distinguishable pattern. Methane, CH_3CCl_3, PCE (in all categories except 1998 CO-all year), and SF_6 all decrease over the years 1996, 1997, and 1998.

The decline in methyl chloroform, although particularly dramatic, is tailing off slower than was estimated by inventories (Figs. A and B) [*Bakwin*, 1997; *Derwent*, 1998]. This is a noteworthy feature that will benefit modellers concerned with seasonal cycles for OH computations. A linear extrapolation from the 1994 and 1995 North America sales-derived values along with the 1996, 1997, and 1998 FACTS-based data implies that CH_3CCl_3 emissions ended in early 1999. An exponential curve through all points of the North America precipitous drop (1990-1995) and of FACTS predicts that CH_3CCl_3 emissions will not cease until as late as the year 2004. If such is the case, the CH_3CCl_3 lifetime of 4.8 years suggests that the end of the absolute CH_3CCl_3 concentrations may be anticipated by 2010, with the atmospheric OH abundance responding accordingly.

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Derwent, R. G., P. G. Simmonds, S. O'Doherty, and D. B. Ryall. 1998. The Impact of the Montreal Protocol on concentrations in northern hemisphere baseline and European air masses at Mace Head, Ireland over a ten year period from 1987-1996. Atmospheric Environment 32: 3689-3702.

Elkins, J. W., T. M Thompson, T. H. Swanson, J. H. Butler, B. D. Hall, S. O. Cummings, D. A. Fisher, and A. G. Raffo. 1993. Decrease in the growth rates of atmospheric chlorofluorocarbons 11 and 12. Nature 364: 780-783.

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United Nations Environmental Programme. 1985. Vienna Convention for the Protection of the Ozone Layer, 1987 Montreal Protocol to Reduce Substances that Deplete the Ozone layer Report, Final Report (New York), 1990 London Amendment, 1992 Copenhagen Amendment, 1997 Production and Consumption of Ozone Depleting Substances, 1986-1995, Nairobi, Kenya.

How N Partitioning Influences Leaf Photosynthesis and Carbon Gain in Dominant Tree Species in Two New England Forest Stands

G. Bauer and F. Bazzaz

Photosynthesis plays a key role in the forest carbon cycle because it represents the primary process of terrestrial productivity. At the leaf level there is a strong connection between maximum photosynthesis and nitrogen availability because nitrogen is needed for the synthesis of Rubisco and chlorophyll. This fundamental relationship has been intensively used to scale maximum rates of photosynthesis from leaf level to stand and biome level. However the general use of this photosynthesis-nitrogen relationship has widely ignored the fact that not all of the nitrogen present in a leaf or a needle is "functional", i.e., is directly involved in the primary processes of photosynthesis. At the whole plant level nitrogen is also needed to promote growth and nutrient uptake.
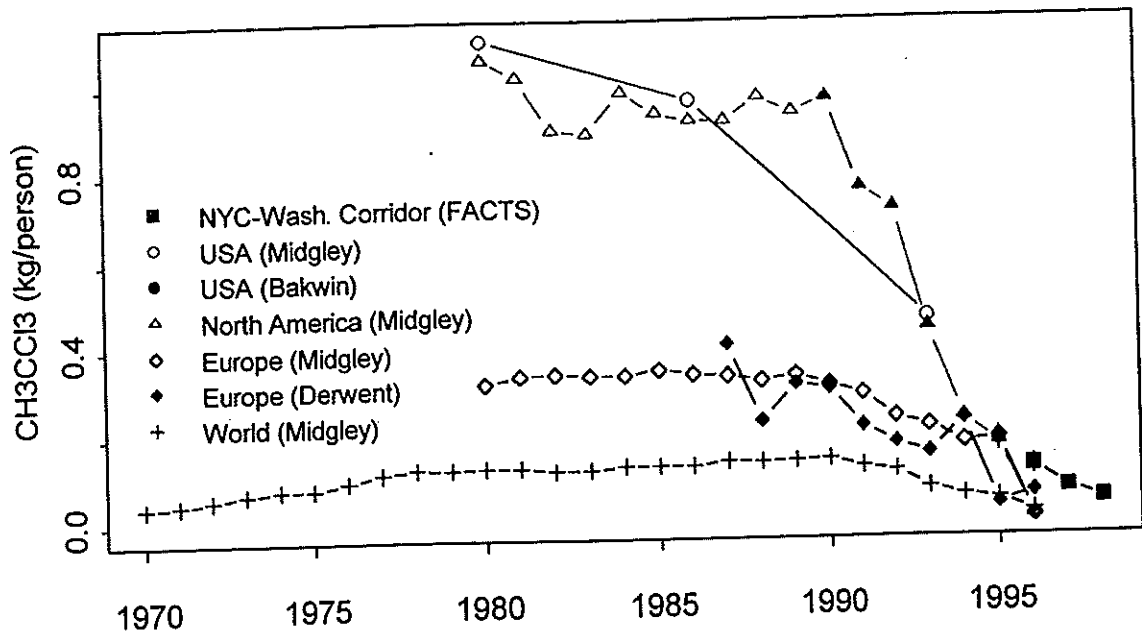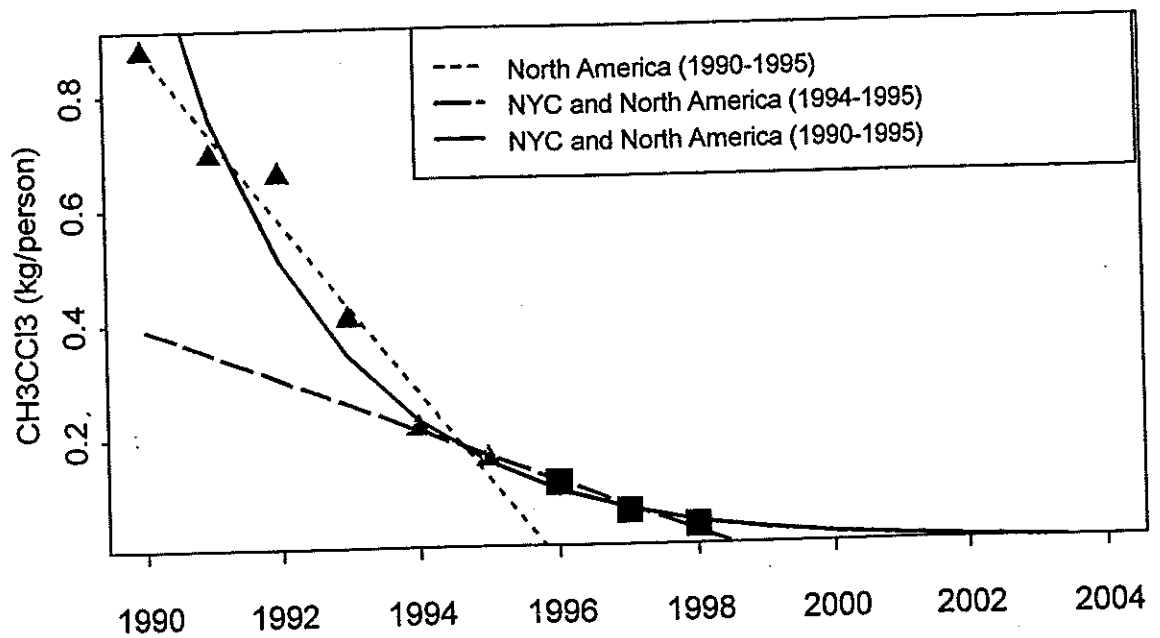
Figure A

Figure B

In this way several physiological processes compete with photosynthesis for available N. Therefore, if we want to scale photosynthesis on the basis of plant nitrogen concentration, we need to know how plant internal partitioning of N is regulated and how changing partitioning patterns affect leaf photosynthesis.

We have initiated a study in which we investigate the effects of changes in nitrogen partitioning on the photosynthesis-nitrogen relationship of forest trees. By following the seasonal dynamic of leaf photosynthesis and N partitioning we will be able to investigate whether physiologically active pools of N in the foliage can be used to scale leaf photosynthesis. Based on earlier studies carried out at the Harvard Forest we hypothesize that the photosynthesis-nitrogen relationship will change over the course of a growing season. Preliminary data from two of our study sites at Harvard Forest and Howland Forest (ME) confirmed these expectations. Individual species such as hemlock and red spruce showed a different slope in the photosynthesis-nitrogen relationship than, e.g., red oak and red maple. A comparison of protein and Rubisco concentrations for the study species supports our initial hypothesis that e.g. nitrogen investment into Rubisco is not constant across species and probably throughout the growing season. Therefore the seasonal change in photosynthetic nitrogen use efficiency has to be taken into account when scaling leaf photosynthesis to whole canopies.

Investigating the Roles of Environment and History in the Modern Distribution of the Rich Mesic Forest Community in Western Massachusetts

J. Bellemare, G. Motzkin and D. Foster

Rich mesic forests are uncommon upland communities that support numerous rare plant species and have been identified by the MNHESP as high priorities for conservation in Massachusetts (Swain 1999). However, the factors controlling the spatial distribution and species composition of this community are poorly understood. Rich mesic forest (RMF) sites are characterized by uncommon

environmental conditions, especially mesic, circumneutral soils (Weatherbee 1996), that support a unique and diverse herbaceous flora including many species that may be particularly sensitive to the impacts of past land-use (Henry *et al.* 1974, Bormann *et al.* 1979). The disturbance-sensitive nature of the herbaceous flora suggests that RMF may have occupied a more extensive portion of the landscape prior to widespread forest clearance for agriculture during the 18th and 19th C (Jenkins 1994). The RMF community is considered to be a northern variant of the Mixed Mesophytic Forest Type of the southern Appalachian Mountains, which has also been noted for its diverse herbaceous layer (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.

Evaluating the contrasting roles of historical human disturbance and environmental conditions on the spatial distribution and species composition of the RMF community is a critical aspect of understanding the causes of this community's limited distribution in the state and the rarity of many plant species associated with it. To address these issues, a broad scale survey of extant RMF sites in Franklin and Hampshire Counties, Massachusetts will be conducted to quantify environmental factors controlling the community's distribution and plant species composition. Using environmental data gathered in the broad scale survey and land-use history records from the 19th and early 20th C, a GIS model will be developed to investigate the influence of past human disturbance on the modern distribution of RMF. The model will be developed and tested for two towns in western Franklin County that are known to support numerous occurrences of the RMF community. Such an approach will lead to a characterization of RMF distribution and composition in the region, detailed information about numerous sites in western Franklin and Hampshire Counties, and increased understanding of the factors controlling species distributions and community patterns. As a result, this study will provide information that is critical for the long-term conservation and management of the RMF community.

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Swain, P. 1999. Draft of Terrestrial and Estuarine Plant Community Classifications for Massachusetts. Massachusetts Natural Heritage and Endangered Species Program. Unpublished.

Weatherbee, P. 1996. Flora of Berkshire County, Massachusetts. The Berkshire Museum, Pittsfield, MA.

based at the Harvard Forest Chronic N Experiment, where a long-term (12-yr+) of N deposition (+5 and +15 g N $m^{-2}y^{-1}$) on both coniferous and deciduous forests is underway. Our preliminary measurements (within a *Pinus resinosa* stand) demonstrate that foliar N content has significantly increased, and that this increase is accompanied by a de-coupling of the Photosynthesis-N relationship. Preliminary evidence suggests that the de-coupling is due either to increased production of non-photosynthetic proteins (e.g., Calvin cycle enzymes) or an excess production of Rubisco. The net effect of this de-coupling is that the large increases in foliar N we have observed are not accompanied with increased photosynthetic capacity. Further, we have found that needle life-span has been significantly reduced, and, even with apparent increases in foliar production (at the expense of wood production), standing leaf area has decreased. Taken together, these data suggest that potential C gain by the *Pinus resinosa* canopy has been significantly reduced by long-term N deposition.

Nitrogen Deposition and NPP in Temperate Forests: the Role of Leaf Physiology, Foliage Turnover and Canopy Structure

G. Berntson, G. Bauer and R. Minocha

There is growing evidence to suggest that the impact of N deposition on temperate forest productivity, even in the absence of N saturation, may not be as great as several studies suggest. Further, most studies of the impact of N deposition on forest processes have ignored changes that take place in the canopy. To date, there have been no empirically-based, ecosystem-scale studies of how N deposition alters canopy processes and thus the potential for C gain in forests. We initiated a study of how N deposition affects the physiology, dynamics, and structure of temperate forest canopies. We are examining how the partitioning of N within tree foliage, how it is affected by N deposition, and how these changes in N allocation relate to changes in photosynthetic capacity. In addition we are examining the effects of N deposition on foliage retention time and canopy structure in order to begin scaling changes in leaf-level processes to the entire canopy. Our study is

Data Management 1999-2000

E. Boose and J. Pallant

Over the past year, the Harvard Forest web page (http://lternet.edu/hfr) was redesigned and a new system implemented for the organization and presentation of research data on-line. The main features of this system (which is still under development) are outlined below.

An electronic Data Archive is maintained at the Harvard Forest for all scientific projects since 1988 (beginning of LTER I), as well as selected earlier projects. The Data Archive is stored as a web-compatible file system and can be viewed with a web browser such as Netscape. A copy of the Data Archive is maintained on-line as part of the Harvard Forest web page.

The Data Archive can be accessed and searched via the Harvard Forest Data Catalog (http://lternet.edu/hfr/data/catalog.html), which appears on the Data Archive homepage. The Data Catalog contains a list of research projects arranged by research category. Each project entry includes project title, list of investigators, and project code. Each entry is linked to a separate

project page, which contains additional metadata (project dates, field site, and contact person), a project Overview, and (for completed projects) links to Data and Metadata files. All files in the Data Archive are stored in plain ASCII or HTML format (except for spatial data, which are stored in ArcView or Idrisi format). A few projects are maintained on web servers at allied institutions, with links from the Harvard Forest web page. Permanent copies of the Harvard Forest web page, including the entire Data Archive, are created annually and stored at the Harvard Forest and an offsite location.

Selected metadata for each project, including project title, investigators, keywords, and project code, can be searched on-line via the LTER Network Data Catalog (http://lternet.edu/DTOC). Harvard Forest metadata are stored in a separate location (http://lternet.edu/hfr/data/dtoc.html) for weekly harvesting by the Network Data Catalog.

A Projects database is also maintained offline for Data Management purposes. For each project, this database contains the metadata described above (project code, title, list of investigators, contact person, keywords, dates, and field site) as well as project status and access codes for relevant materials in the Document and Sample Archives. The Projects database is used to track the progress of current research projects and to ensure that files in the Data Archive are updated in a timely manner.

Archive Projects at Harvard Forest, 1999-2000

J. Burk

For the past year, archive responsibilities have been divided among the following areas: archive and records management, historical research, and administrative projects. The following is a summary of the major archive related projects.

To continue the effort to make backups of crucial Harvard Forest historical records, a large microfilm project was recently completed. The material which was duplicated included all forest inventory records from 1907 through 1992, 1938 Hurricane historical information and salvage data, plantation, nursery, Cabot Foundation and case history files, outlot records for the Pisgah, Matthews Plantation, Schwartz Tract, and Tall Timbers properties, and cutting summaries. The microfilm rolls, along with those for the stand records and 1830s map series, are stored in the Shaler Hall vault, with duplicates at the Harvard University Archives in Cambridge.

In conjunction with the renovation of the Shaler Hall basement, all of the historical reprint collections were collated, sorted and inventoried. A large library of Harvard Forest reprints from the 1900s to the present was established in the basement in archival folders and new cabinets, arranged in chronological order to facilitate access by researchers. During the sorting and purging process, a considerable amount of material was relocated to appropriate individuals and institutions, including Harvard Forest and collaborative researchers, the Arnold Arboretum, the University of Southern Maine Map Library, the Arctic Institute at the University of Edmonton, the Raup and Zimmermann families, and Ann Lewis at the University of Massachusetts Department of Natural Resources.

New material continued to strengthen the Archive holdings. Over 150 towns from the Massachusetts 1830s series were added to the map collection, and an updated and reformatted map catalog was printed. The extensive physiology research collection, including film logs, photographs, figures, and slides, of Dr. Martin Zimmermann was incorporated into the archive research file collection. Important historical photographs and slides were obtained from the Massachusetts DEM office in Clinton, David Tatlock, Larry Buell, and Albert Upham. Additions were made to the research, publication, and sample archive collections on a regular basis.

The Archives continued to be an important element of the Harvard Forest, as the material and facilities were used on a daily basis by staff, collaborators, local residents, and local organizations such as the Metropolitan District Commission, Massachusetts Department of Environmental Management, Worcester Eco-Tarium, and North Quabbin Greenway planners.

Witness Tree Research from Early New England Town Records

J. Burk, E. Largay, G. Motzkin and D. Foster

The surveyor notes in early New England city and town records offer a valuable source of information about presettlement forest composition at the township level. The most comprehensive records are found in early land abstracts, usually known as proprietor books; in some towns tree species citations have totalled 2000 or more. When early land data is unavailable, information has been collected from highway and boundary surveys from town record compilations. In instances where no data was found for a particular town, this indicates that either the early records were lost or destroyed, or surveyors did not cite individual tree species in their lot or road surveys.

Prior to 1999, New England witness tree data had been collected for Vermont, north-central Massachusetts, the northern and southern Berkshires, Cape Cod, and parts of New Hampshire. In the past year, additional data has been gathered from New Hampshire and all regions of Massachusetts not covered in past studies. In Massachusetts, J. Burk and E. Largay have compiled data from several sources, including records at the Massachusetts Archives, county registries of deeds, and individual town halls and libraries. Detailed proprietor data was found for the Connecticut River Valley towns, much of Hampden County, southern Worcester County, and the eastern communities. Information from central Berkshire and western Franklin and Hampshire Counties was not as comprehensive and was mainly compiled from road surveys. The biggest gap in information was eastern Berkshire County. At the New Hampshire State Library, J. Burk gathered proprietor data for 20 towns in the south-central region, with the most detailed records found in the Concord-Manchester area and along the Connecticut River. This information was used by C. Cogbill as part of a manuscript for the Rhodora Symposium.

Once all remaining data for Eastern Massachusetts is compiled, the next states to be addressed will be Connecticut and Rhode Island. All information will be sorted by state and county and archived at the Harvard Forest as a resource for use in present and future studies.

Nitrogen Deposition Influences Regeneration of Coniferous and Broad-Leaved Tree Species In Contrasting Stand Types

S. Catovsky and F. Bazzaz

Despite increasing levels of nitrogen deposition at temperate latitudes, no studies to date have considered how this perturbation will alter temperate forest species composition. Nitrogen deposition may affect mixed forests in particular due to differences in nutrient use patterns between evergreen coniferous and deciduous broad-leaved species. To examine how nitrogen deposition may alter the composition of mixed conifer broad-leaved forests, we investigated regeneration responses of both types of species to increasing nitrogen, and additionally compared these responses across coniferous (hemlock) and broad-leaved (red oak) stand types. We addressed nitrogen effects on two critical components of forest regeneration dynamics: (1) development of an understory seedling bank, and (2) seedling responses to canopy gap formation. We applied nitrogen (0, 2.5, 7.5 g m^{-2} yr^{-1}) both to replicated understory plots in three hemlock and three red oak dominated stands, and to seedlings growing in high light conditions in soil from each stand. In both cases, we examined seedling survival and growth for three coniferous and three broad-leaved species over two years.

Nitrogen differentially influenced species' regeneration patterns, although the nature of these effects depended on light environment. In the understory, changes in seedling bank structure were driven primarily by differential seedling emergence and survival, with nitrogen decreasing red maple and red spruce abundance, and increasing birch relative abundance (Fig. 1). These changes were particularly significant in hemlock dominated stands. Under gap conditions, nitrogen predominantly increased seedling growth, with early-successional broad-leaved species responding most strongly, and coniferous species remaining relatively unresponsive (Fig. 2). In this case, seedlings were generally more responsive to nitrogen on soil from red oak stands. Thus, increasing nitrogen deposition will alter the composition of mixed temperate forests. However, given that seedling responses to nitrogen were contingent on prevailing light and soil conditions,

FIG. 1. Effects of nitrogen addition on development of under-
story seedling bank: seedling survival (± 1 SEM) (pooled across
months) in hemlock (a) and red oak (b) stands. Values above
each species represent slope coefficients calculated using trans-
formed data. Slopes significantly greater than zero (p<0.05) are
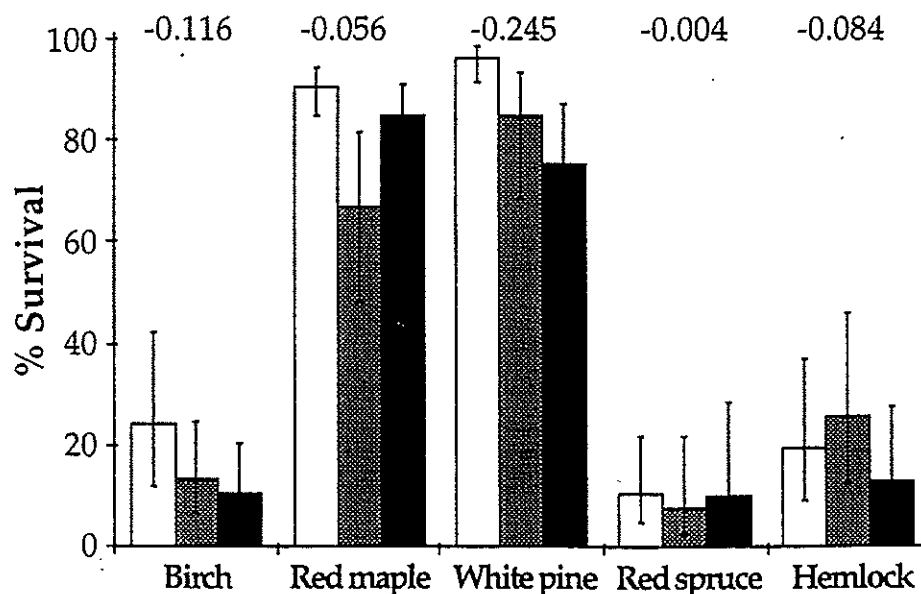shown in bold and with an asterisk.
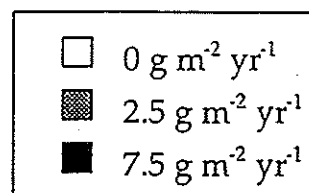
a) Hemlock stands

b) Red oak stands

Catovsky and Bazzaz
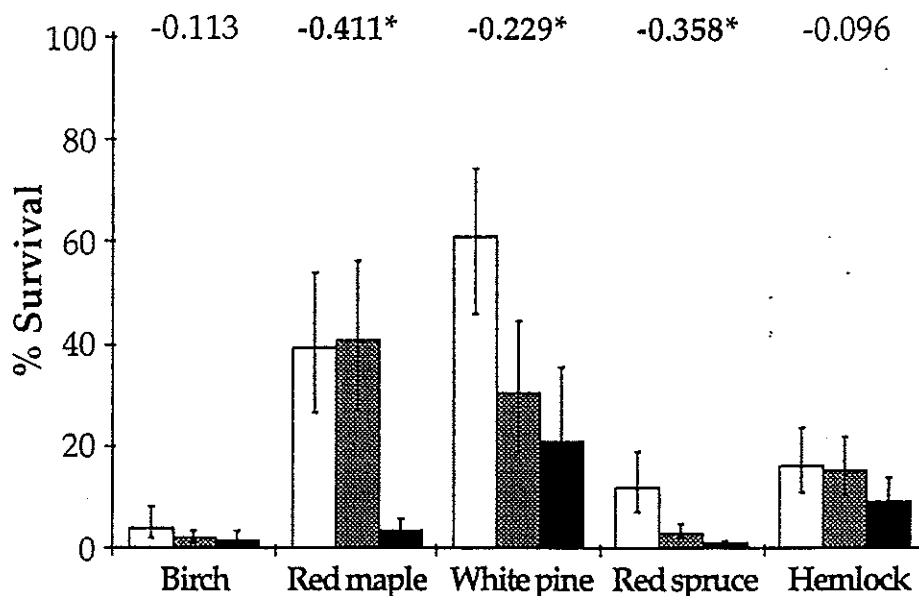
FIG. 2. Effects of nitrogen addition on seedling responses to gap formation: seedling growth (± 1 SEM) pooled across stand types. Values above each species represent slope coefficients calculated using transformed data. Slopes significantly greater than zero (p<0.05) are shown in bold and with an asterisk.

Legend:
- □ 0 g m^{-2} yr^{-1}
- ▦ 2.5 g m^{-2} yr^{-1}
- ■ 7.5 g m^{-2} yr^{-1}

Catovsky and Bazzaz
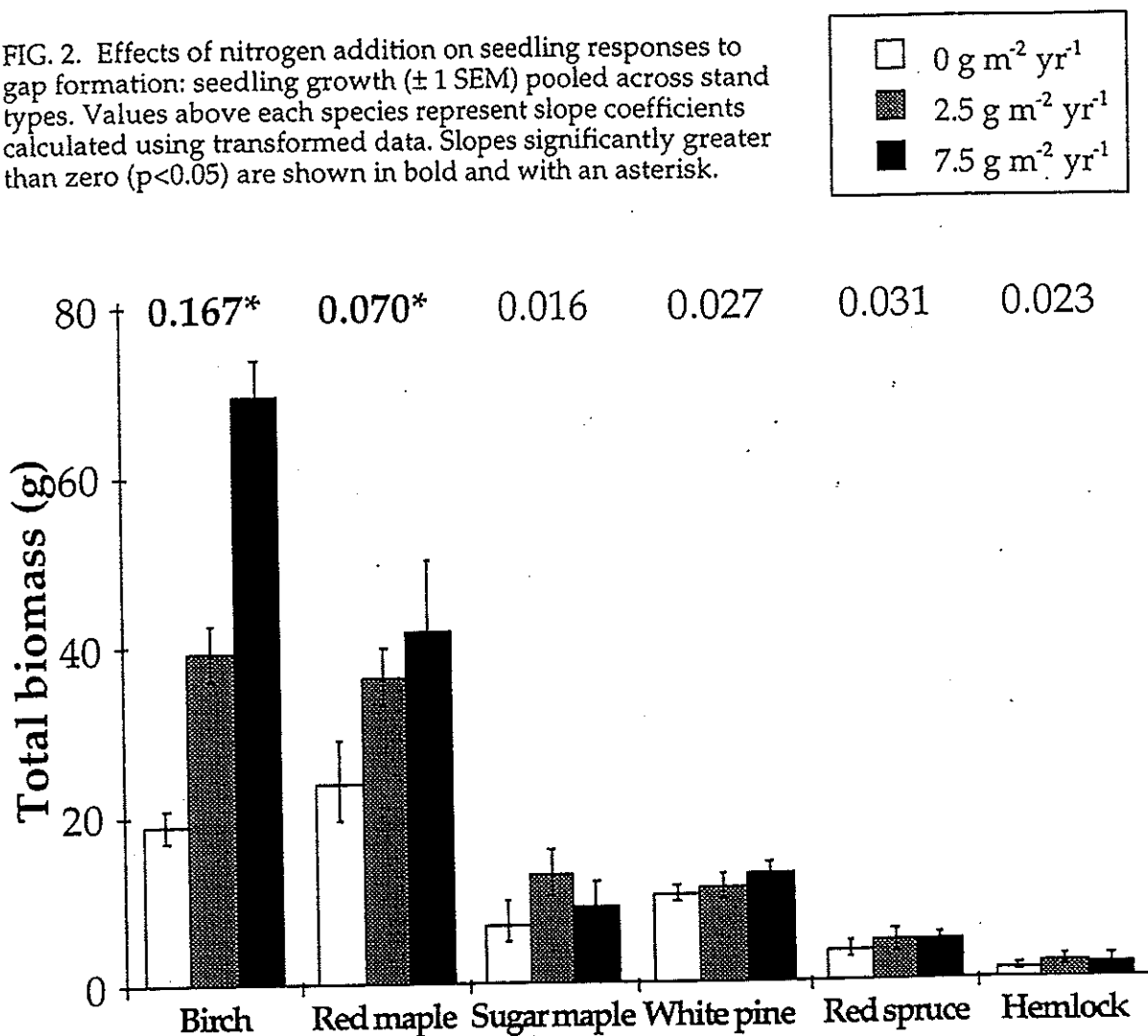
the exact nature of the change will depend on both current forest stand composition and future patterns of disturbance.

Changes in Drought Response Strategies with Ontogeny in *Quercus rubra*: Implications for Scaling from Seedlings to Mature Trees

J. Cavender-Bares and F. Bazzaz

We investigated scaling of physiological parameters between age classes of *Quercus rubra* by combining *in situ* field measurements with an experimental approach. In the *in situ* field study, we investigated changes in drought response with age in seedlings, juveniles, and mature trees of *Quercus rubra*. Throughout the particularly dry summer of 1995 and the unusually wet summer of 1996 in New England, we measured water potential and gas exchange of plants at three sites at the Harvard Forest in Petersham, MA. In order to determine what fraction of the measured differences in gas exchange between seedlings and mature trees was due to environment versus ontogeny, an experiment was conducted in which seedlings were grown under light and soil moisture regimes simulating the environment of mature trees.

Photosynthetic capacity of mature trees was three-fold greater than seedlings during the wet year and six-fold greater during the drought year (Fig. 1). The seedling experiment demonstrated that the difference in photosynthetic capacity between seedlings and mature trees is comprised equally of an environmental component (50%) and an ontogenetic component (50%) in the absence of water-limitation (Fig. 2).

Photosynthesis was depressed more severely in seedlings than in mature trees in the drought year relative to the wet year, while juveniles showed an intermediate response. Throughout the drought, predawn leaf water potential of seedlings became increasingly negative (-0.4 to -1.6 MPa), while mature trees became only slightly more negative (-0.2 to -0.5 MPa). Again, juveniles showed an intermediate response (-0.25 to -0.8MPa). During the wet summer of 1996, however, there was no difference in predawn leaf water potential between seedlings, juveniles and mature trees (Fig. 3). During the dry summer of 1995, seedlings were more responsive to a major rain event than mature trees in terms of water potential, suggesting that the two age classes depend on different water sources.

In all age classes, instantaneous measurements of intrinsic water use efficiency (WUE_i), defined as assimilation rate (A) divided by conductance (g), increased as the drought progressed, and all age classes had higher WUE_i during the drought year than in the wet year. Mature trees, however, showed a greater ability to increase their WUE_i in response to drought. Integrated measurements of water use efficiency (WUE) from carbon isotope ratios ($\delta^{13}C$) of leaves and estimated Δ values of leaf carbon (air $\delta^{13}C$ – leaf $\delta^{13}C$) indicate higher WUE in mature trees than juveniles and seedlings. Differences between years, however, could not be distinguished probably due the strong bias in $\delta^{13}C$ towards fractionation at the time of leaf production, which was prior to the onset of drought conditions in 1995.

From this study, we arrive at two main conclusions: 1) Different age classes *of Quercus rubra* use different strategies for responding to drought: Seedlings resist drought by closing stomata early in the day at the expense of carbon uptake; mature trees avoid drought conditions by accessing deeper water reserves and adjusting water use efficiency, sacrificing carbon gain only marginally. 2) Only through studies which separate environmental differences from ontogenetic differences can parameters measured on seedlings be scaled to mature trees.

Consequences of CO_2 and Light Interactions for Leaf Phenology, Growth, and Senescence in *Quercus rubra*

J. Cavender-Bares, M. Potts, E. Zacharias and F. Bazzaz

We investigated how light and CO_2 levels interact to influence growth, phenology, and the physiological processes involved in leaf senescence in red oak *(Quercus rubra)* seedlings.

Fig. 1
(A) Weekly photosynthetic rates and (B) whole plant photosynthesis throughout the 7 week period of simulated autumnal senescence (N=60). Dashed and solid lines represent sun and shade plants, respectively. Error bars are +/- 1 SE. The ratio of whole plant photosynthesis under elevated CO_2 to that under ambient CO_2 (E/A) is shown for the same time period in the inset to B. Closed circles depict shade plants, and open circles depict sun plants.
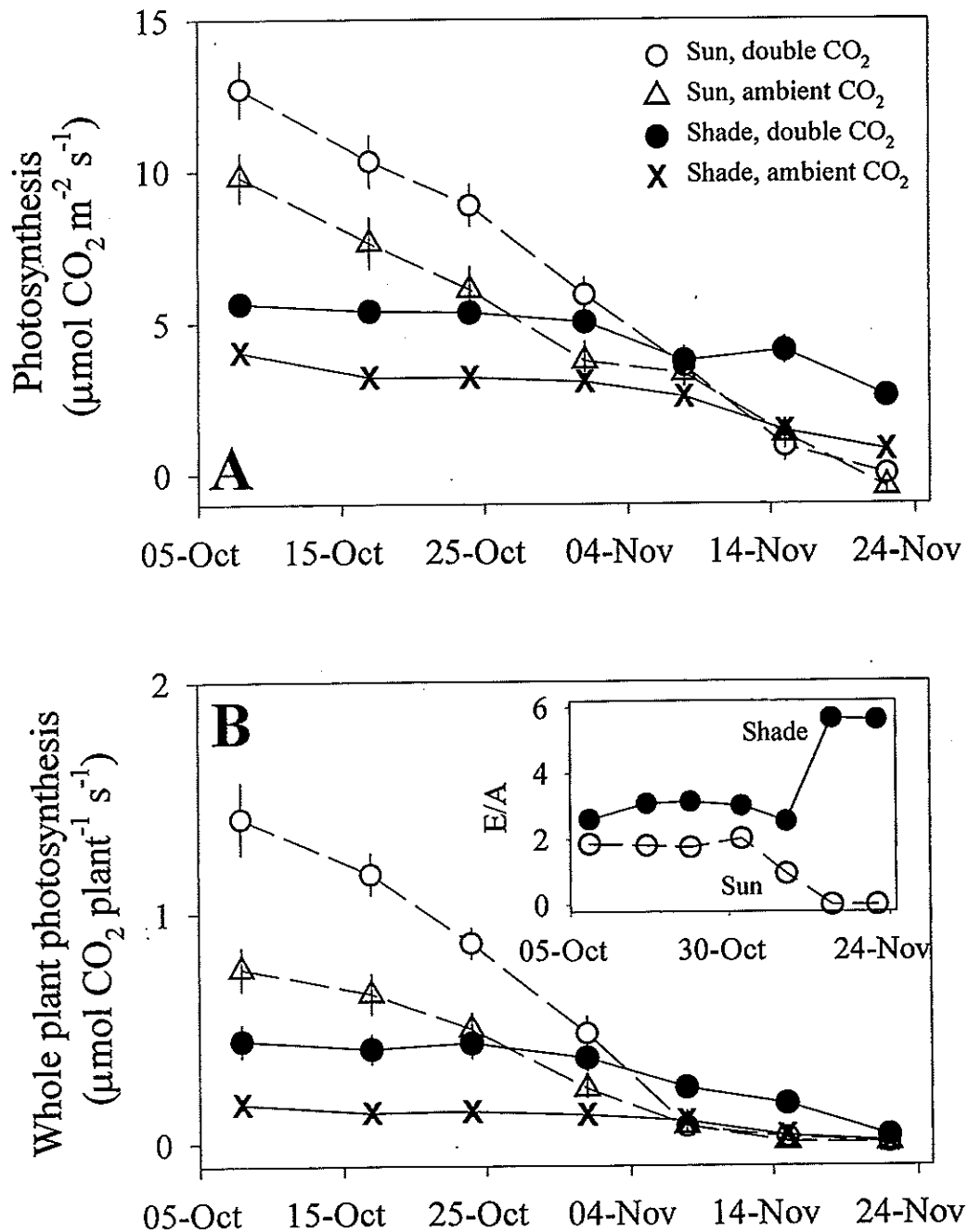
Fig. 2

(A) Chlorophyll content throughout the course of autumnal senescence (N=12); symbols are the same as in Figs. 2 and 3. Measurements in August prior to the onset of senescence are shown before the break in the x-axis. (B) Nitrogen concentration of leaves (g N [100 g leaf]$^{-1}$), measured in August before the onset of senescence, during senescence, and after all leaves had turned brown. Leaves had completely senesced by December. Treatments are shown as different if P < 0.05 (Scheffé's post-hoc multiple comparisons). Error bars are +/- 1 SE.
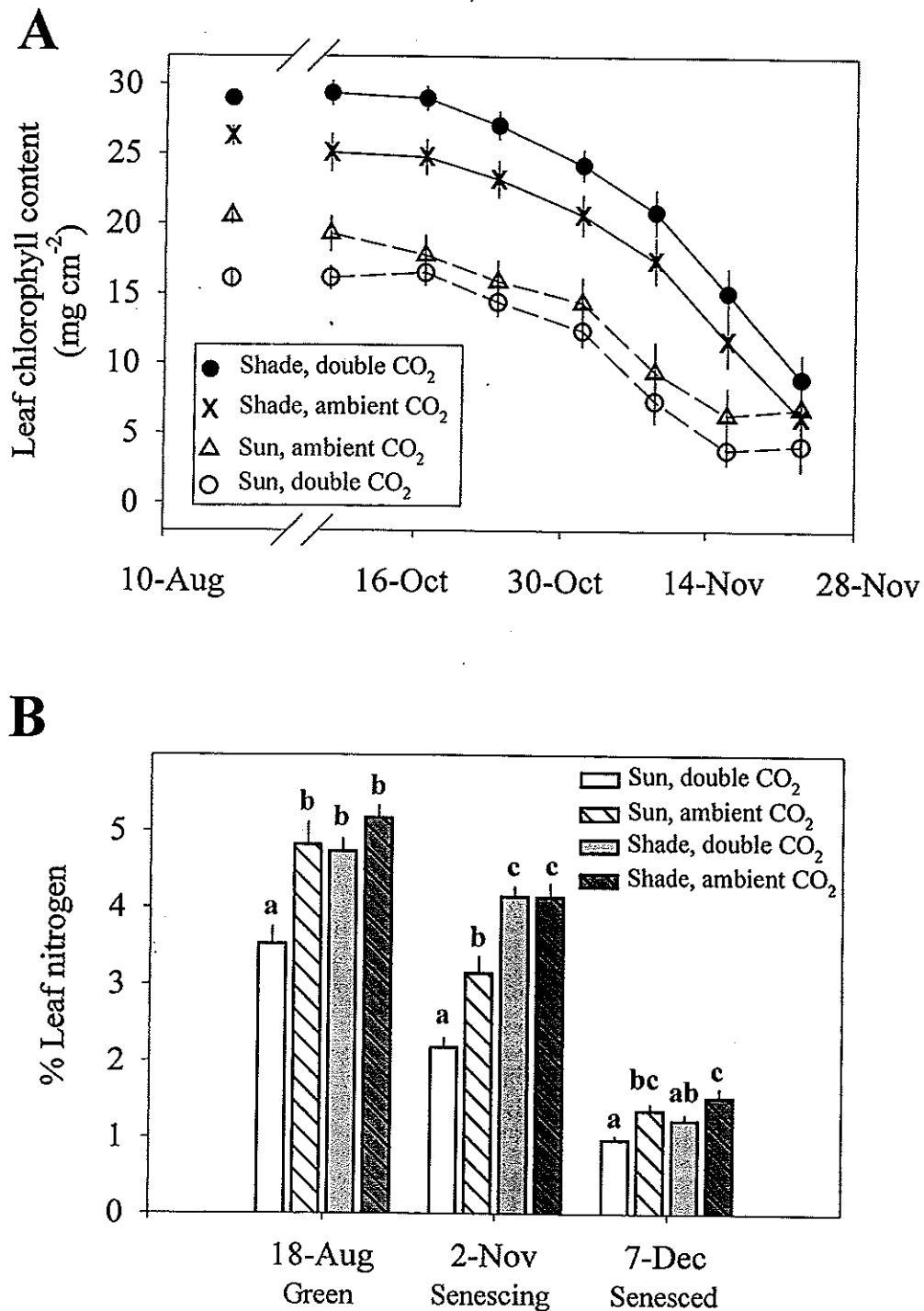
Fig. 3 Predawn (upper panels) and midday leaf water potentials (lower panels) for seedlings, understory juveniles, and mature trees during the dry and the wet summer. Measurements were taken at three different sites on Prospect Hill at the Harvard Forest on the same days and on the same individuals as in Fig. 4. Error bars are +/- 1 SE.

Cavender–Bares and Bazzaz
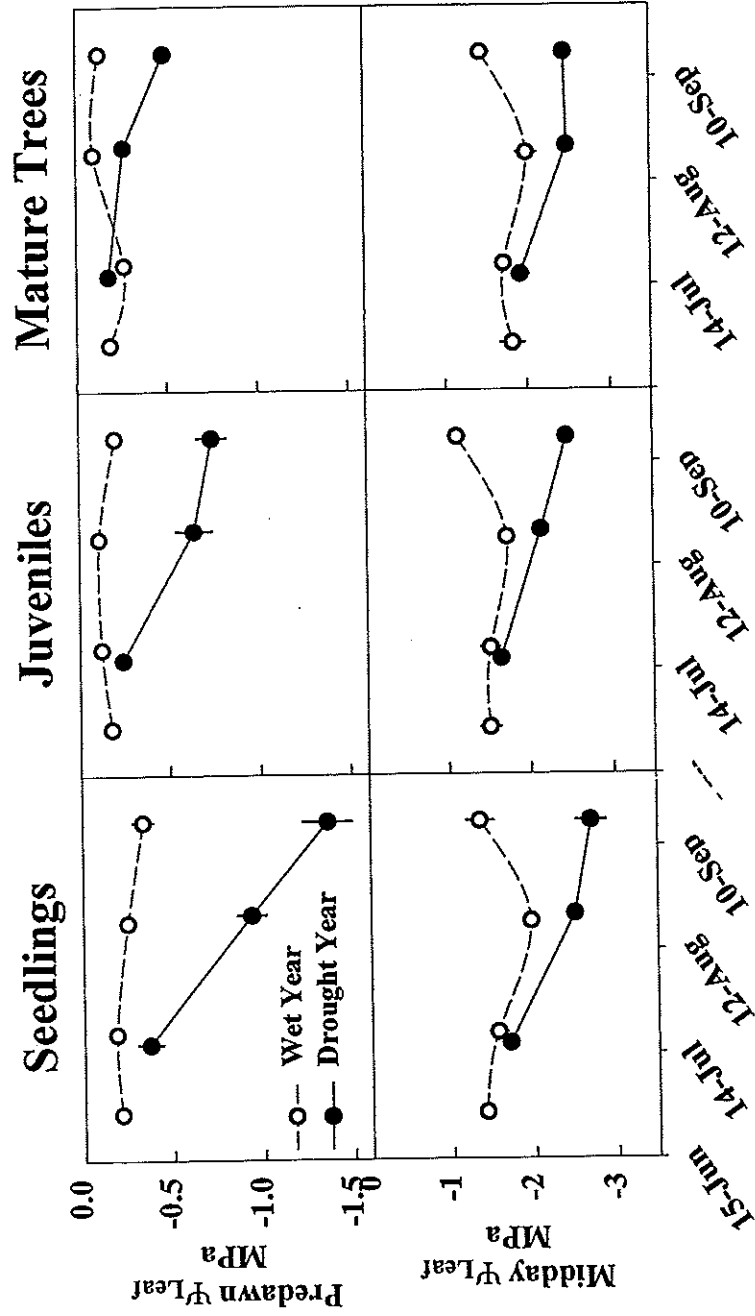
We grew plants in high and low light and in elevated and ambient CO_2. At the end of three years of growth, shade plants showed greater biomass enhancement under elevated CO_2 than sun plants. We attribute this difference to an increase in leaf area ratio (LAR) in shade plants relative to sun plants as well as to an ontogenetic effect as plants increased in size, the LAR declined concomitantly with a decline in biomass enhancement under elevated CO_2 (Fig. 1).

Elevated CO_2 prolonged the carbon gain capacity of shade grown plants during autumnal senescence, thus increasing their functional leaf lifespan (Fig. 3). Prolongation of carbon assimilation, however, did not account for the increased growth enhancement in shade plants under elevated CO_2. Elevated CO_2 did not significantly alter leaf phenology (Fig. 2). Nitrogen concentration of both green and senesced leaves was lower under elevated CO_2 and declined more rapidly in sun leaves than in shade leaves (Fig. 4B). Similar to nitrogen concentration, the initial slope of A/C_i curves indicated that Rubisco activity declined more rapidly in sun plants than in shade plants, particularly under elevated CO_2 (Fig. 5). Absolute levels of chlorophyll were affected by the interaction of CO_2 and light, and chlorophyll content declined to a minimal level in sun plants sooner than in shade plants (Fig. 4A). These declines in nitrogen concentration, in the initial slope of A/C_i curves, and in chlorophyll content were consistent with declining photosynthesis, such that elevated CO_2 accelerated senescence in sun plants and prolonged leaf function in shade plants. These results have implications for the carbon economy of seedlings and the regeneration of red oak under global change conditions.

Energy Flows in Peatlands with Heat and Water Loading: a Mesocosm Approach

J. Chen, S. Bridgham, J. Pastor, J. Weltzin, X.Wang, C. Harth, B. Dewey, J. Keller and K. Updegraff

Feedbacks between biotic processes and climate are one of the largest unknowns in the climate change debate. One of the direct consequences of global climate warming is alteration of energy balances of ecosystems, which in turn can produce significant effects on physical and ecological processes. Understanding underlying mechanisms and specific feedbacks of each energy term, hence, is vital in explaining overall responses of an ecosystem (e.g., productivity and stability). A full-factorial design was constructed in 54 mesocosm plots by manipulating heat loading (3 levels) and water table (3 levels) of two dominant peatlands in southern boreal forest with three replications. Our central hypothesis is that **climate forcing of heat loading and water-table depth determine plant community and ecosystem structure in northern peatlands, which in turn have a feedback effect on the thermal and radiative energy budgets of the system.**

Energy fluxes of net radiation (Rn) and soil heat (G) and vertical soil temperatures (Ts) at 5, 10, 25, and 40 cm in all 54 plots were continuously measured every 20 second and their averages stored at 30-min intervals since October, 1998 using an automated energy budget system (Fig. 1) to detect underlying mechanisms causing temperature changes. Cover of vascular plants, and cover and vertical growth of *Sphagnum* were measured during the summer of 1998, and weekly snow depths were measured throughout the snow season. Data from January 1 through December 31, 1999 are included in this report.

We found no significant difference in Rn ($P<0.02$) within any treatment but among treatments. Large differences in G and Ts were recorded between fens and bogs at several temporal scales from hours, days, and seasons, suggesting energy balance of two ecosystems have distinctive vegetation-energy feedback. This conclusion is also supported by significant linear correlation between energy terms (Rn & G) and vegetation characteristics (plants, thatch, snow, and *Sphagnum*). In general, fens were warmer than the bogs at all depths and they also thaw earlier in spring.

Bogs appeared to be more sensitive than fens in Rn, G, and Ts. One important founding of this experiment is that heat loading produced the greatest effect during the winter and spring, with smaller difference in the fall. During the winter, soils of heated plots were often cooler than unheated plots, likely caused by reductions of snow cover. This is especially true with high water
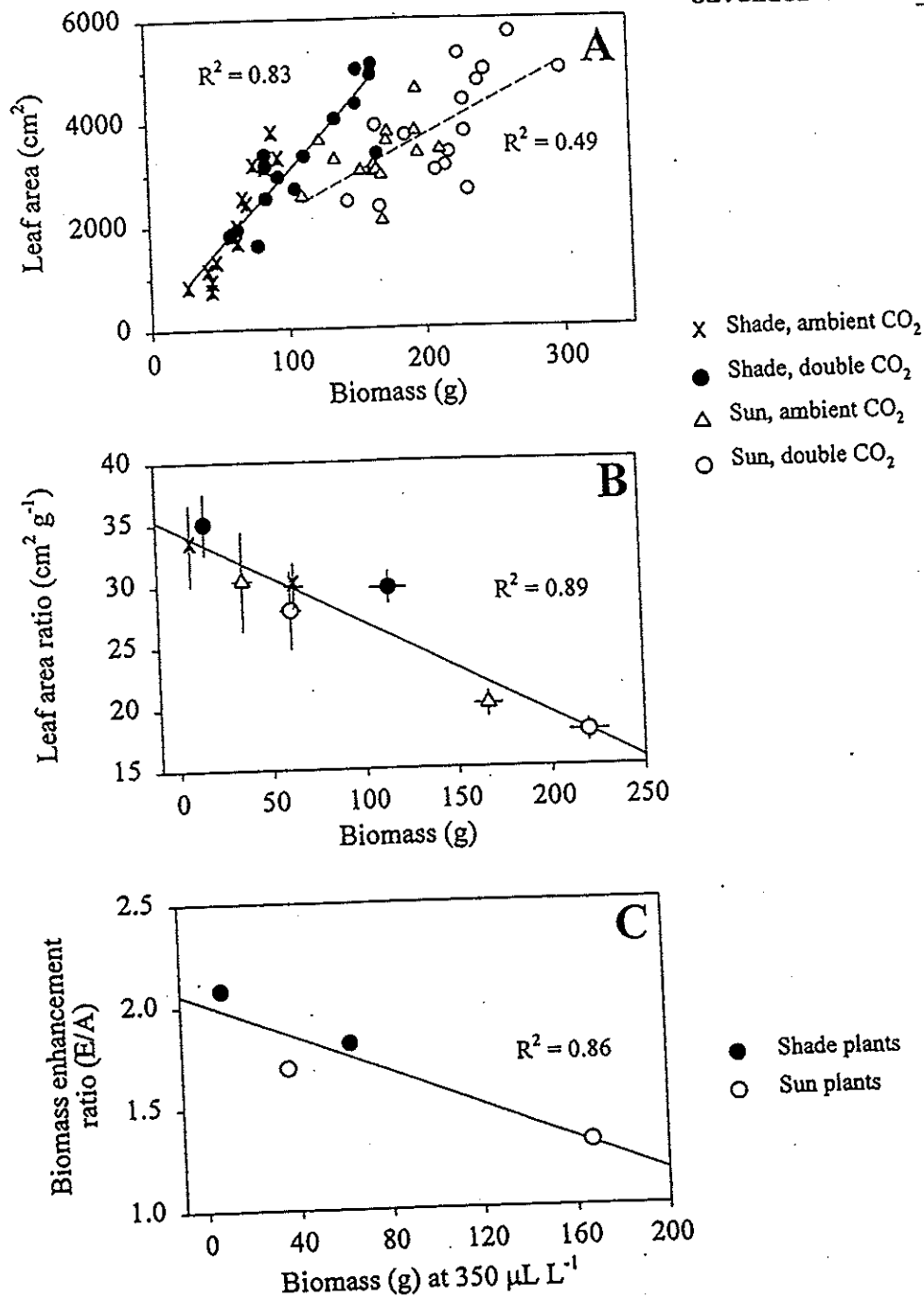
Fig. 1
(A) The relationship between leaf area and biomass for all plants at the end of the third year of growth. There were significant differences in slopes between contrasting light treatments, but not between slopes of contrasting CO_2 treatments. Therefore, regression slopes are shown only for sun and shade treatments with the CO_2 treatments pooled. Shade plants had significantly higher leaf area per unit biomass than sun plants. (B) Treatment means of leaf area ratio at the end of the second and third years of growth showing a decline in LAR with size. In both (A) and (B), Xs are shade plants in ambient CO_2, closed circles are shade plants in elevated CO_2, open triangles are sun plants in ambient CO_2, and open circles are sun plants in elevated CO_2. Error bars in B are +/- 1 SE. (C) The biomass enhancement ratio (E/A; ratio of biomass under elevated CO_2 to biomass under ambient CO_2) plotted against biomass under ambient CO_2 for years two and three. This shows that E/A declines as plants get bigger, indicating a strong ontogenetic effect. Open circles depict sun plants, and closed circles depict shade plants.

Timing of Leaf Emergence
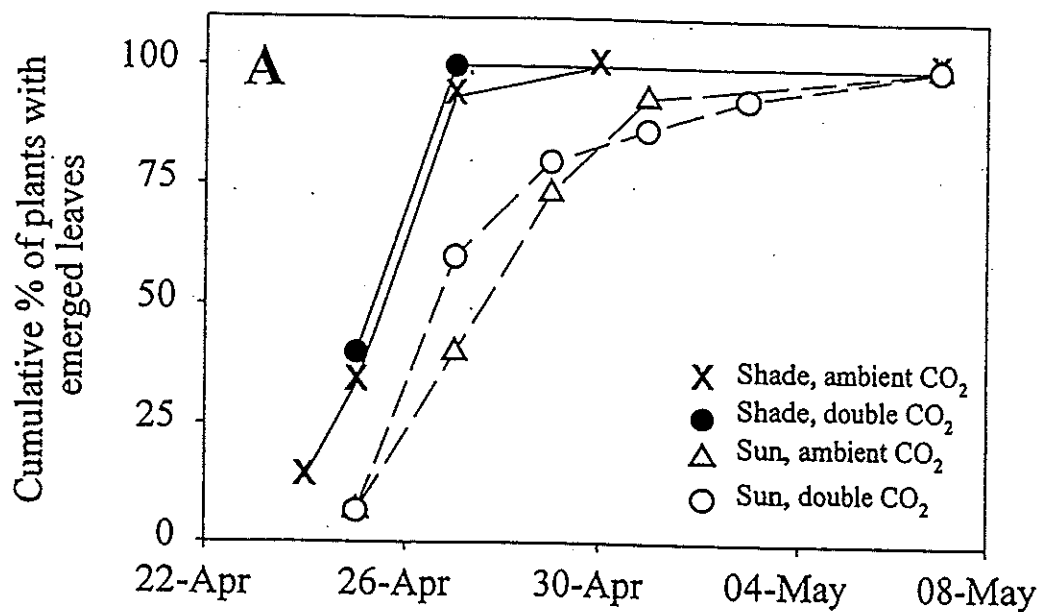
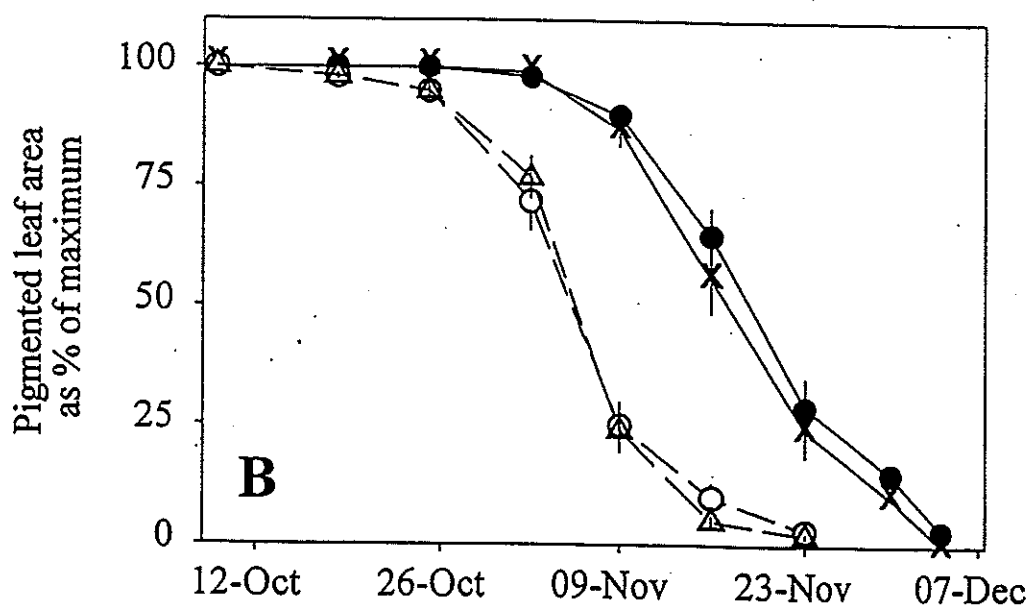## Timing of Leaf Senescence

Fig. 2
(A) Timing of spring leaf emergence as shown by the cumulative percentage of plants with emerged leaves and (B) timing of leaf senescence measured by the pigmented leaf area as a percentage of maximum (N=60). Dashed and solid lines represent sun and shade plants, respectively. Symbols are the same as in Fig 1A and B. Error bares in B are +/- 1 SE.
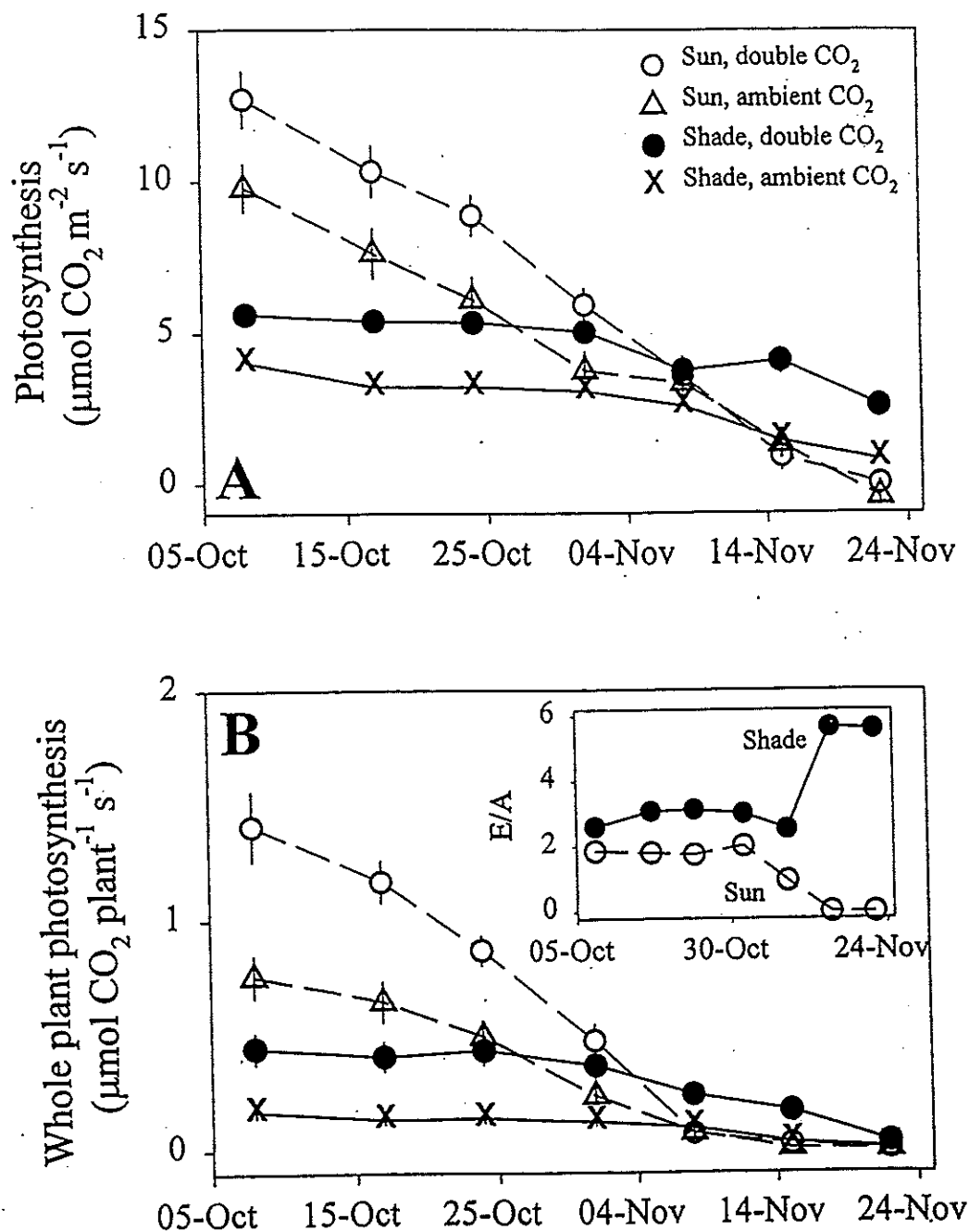
Cavender-Bares et al.

Fig. 3

(A) Weekly photosynthetic rates and (B) whole plant photosynthesis throughout the 7 week period of simulated autumnal senescence (N=60). Dashed and solid lines represent sun and shade plants, respectively. Error bars are +/- 1 SE. The ratio of whole plant photosynthesis under elevated CO_2 to that under ambient CO_2 (E/A) is shown for the same time period in the inset to B. Closed circles depict shade plants, and open circles depict sun plants.
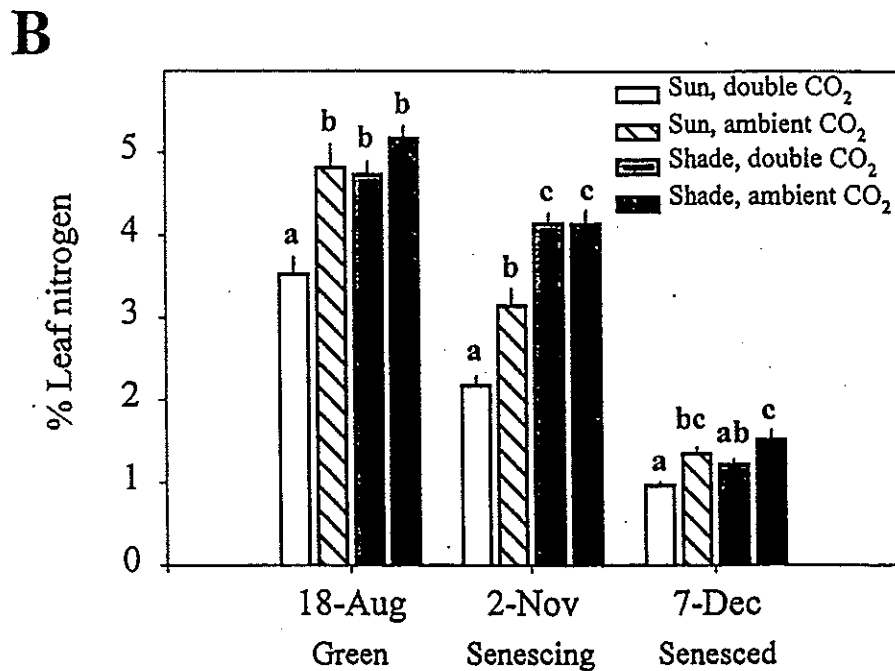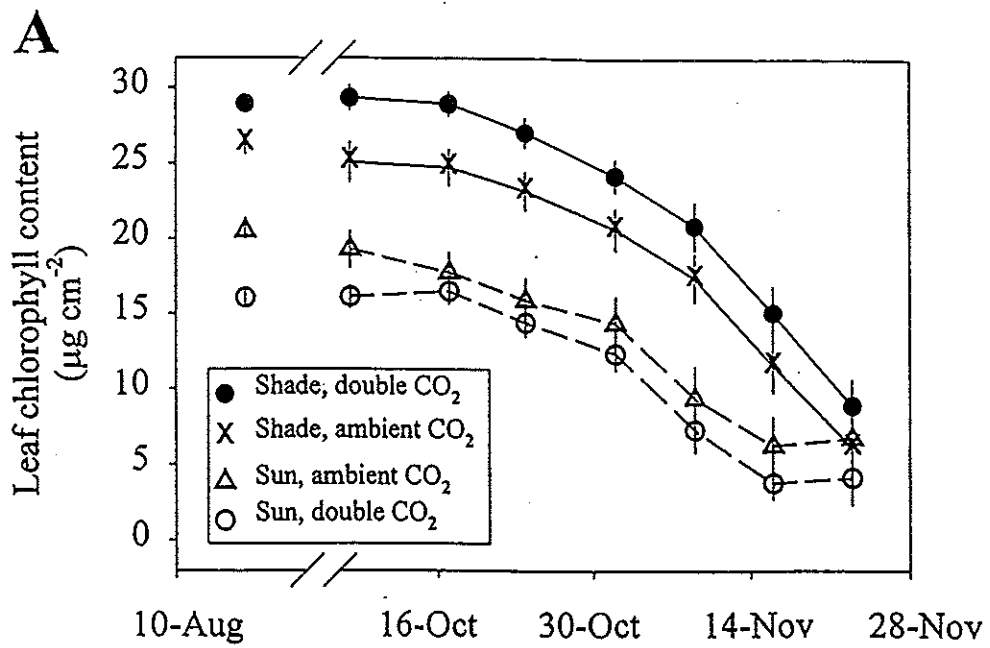
Cavender—Bares et al.

Fig. 4

(A) Chlorophyll content throughout the course of autumnal senescence (N=12); symbols are the same as in Figs. 2 and 3. Measurements in August prior to the onset of senescence are shown before the break in the x-axis. (B) Nitrogen concentration of leaves (g N [100 g leaf]$^{-1}$), measured in August before the onset of senescence, during senescence, and after all leaves had turned brown. Leaves had completely senesced by December. Treatments are shown as different if P < 0.05 (Scheffé's post-hoc multiple comparisons). Error bars are +/- 1 SE.
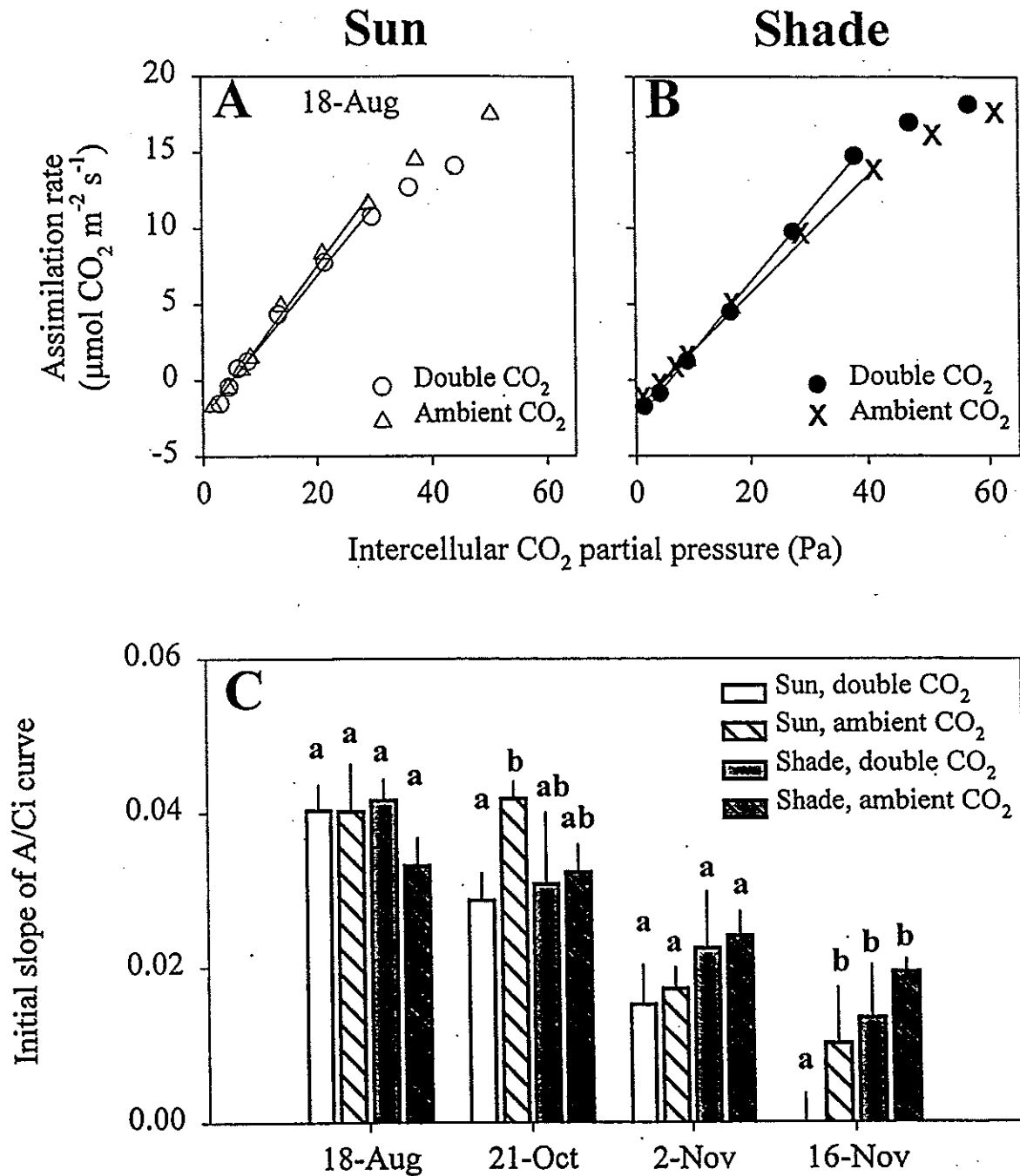
Cavender-Bares et al.

Fig. 5
Representative A/C$_i$ curves for all treatments, measured in August prior to senescence for (A) sun plants and (B) shade plants. Initial slopes were used to indicate Rubisco activity. There were no significant differences between slopes prior to senescence. (C) Means of initial slopes of A/C$_i$ curves, measured in August and at three time points throughout the

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Laptop Computer

ENC 16/18

MD9-cable

CR10

AM416 (30) diff

AM25T (24 diff)

Marine Battery (12 v)

charger

110V

Q7.1 PAR

4 Ts 4 Ts 4 Ts 4 Ts 4 Ts 4 Ts

5 H 5 H 5 H 5 H 5 H 5 H

Ts: Soil temperature s at 5, 10, 20, & 50
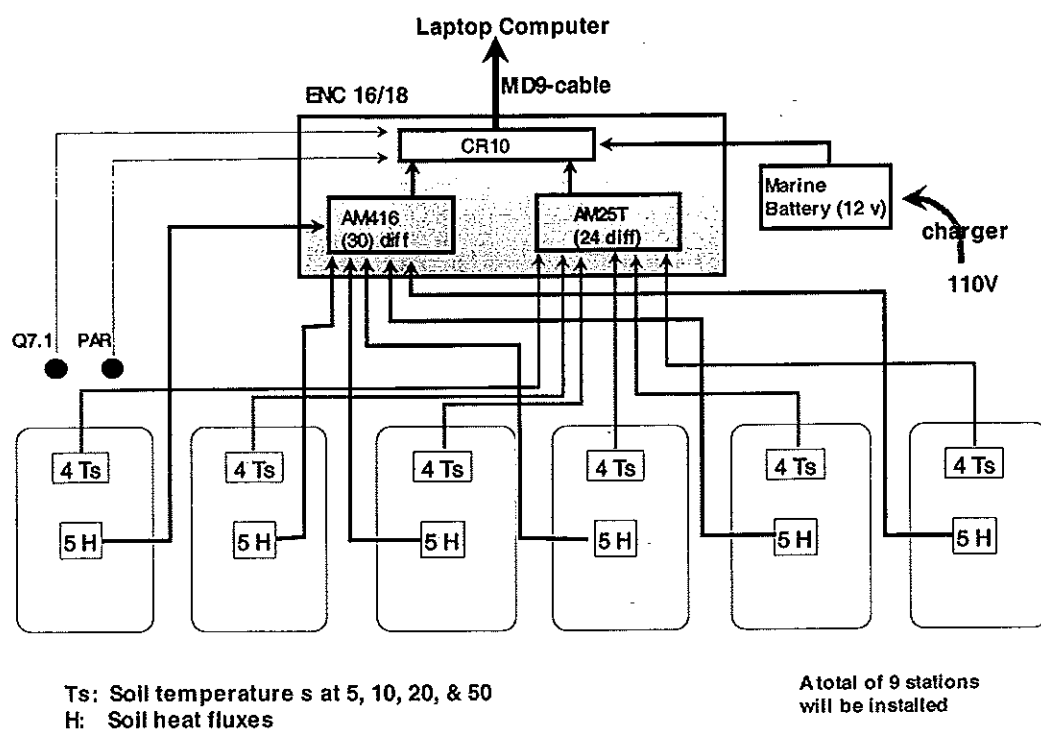H: Soil heat fluxes

A total of 9 stations
will be installed

Fig. 1. Experimental setup of the mesocosm experiment to automatically measure energy terms and vertical temperatures of 54 mesocosm plots in bogs and fens at 30 min intervals.

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table in fens. In the spring, we detected the highest temperature differences between heated and unheated plots, with very strong water table interactions (Fig. 2). Ts at 40 cm in heated plots were >0 °C in early March, 20 to 40 days before unheated plots reached the same level in April. Finally, heat loading elongated the growing season by 10-30 days (i.e., 20-25% increment) depending on the loading level and water table.

In summary, our results suggested that global warming can cause soil cooling during the winter. Such unexpected effects will likely happen in the southern-edge of snow zones in temperate areas, or in years when snow fall is significantly less (or more). Results from 1998 have triggered many critical questions and research topics. For example, if the length of growing season is increased, would ecosystem productivity be increased at the same level? Obviously, our future challenge lies in linking the biophysical changes to ecological processes such as canopy dynamics, decomposition, and gas exchange in hope that a responsive model under a changed climate can be developed.

Interaction of Forest Floor Leachate Organic Matter with Mineral Surfaces

J. Chorover, M. Amistadi and E. Davidson

Experiments were conducted to compare the affinity and reactivity of three different minerals for natural organic matter (NOM) in forest floor leachate (FFL) from hardwood and pine stands at the Harvard Forest, Petersham MA (Chorover and Amistadi, 2000). The FFLs were acidic (pH 4) with ionic strengths of 1.4 mM (hardwood) and 1.1 mM (pine), and they contained larger organic molecules (weight average molecular weights [Mw] = 5-6 kDa) than has been reported recently for surface waters using similar methods. A synthetic diluent solution was prepared to match the inorganic chemistry of the FFL and to provide a range of initial dissolved organic carbon (DOC) concentrations (0 to 140 g C m^{-3}) for reaction with goethite (α-FeOOH), birnessite (δ-MnO$_2$) and smectite (montmorillonite, SWy-2) in suspension, and in corresponding blanks.

A variety of macroscopic and spectroscopic methods were employed to show that reaction with the three minerals resulted in distinctly different NOM adsorption, fractionation and transformation patterns. Goethite exhibited a steep initial slope in the adsorption isotherm and a maximum retention of 10.5 g C kg^{-1}. The isotherm for montmorillonite was more linear, but equal amounts of C were adsorbed to goethite and montmorillonite (per unit sorbent mass) at maximum DOC (Fig. 1). Whereas preferential uptake of high Mw, aromatic constituents via ligand exchange was observed for goethite, compounds of lower than average Mw were retained on montmorillonite and no preference for aromatic moieties was observed (Figs. 2-3). In addition, infrared spectroscopic (FTIR) data indicate that montmorillonite exhibits a higher affinity than goethite for aliphatic constituents of NOM. Birnessite, which has an isoelectric point of pH < 2, retained low amounts of organic C (< 2 g C kg^{-1}) but showed the highest propensity for oxidative transformation of the NOM (Fig. 4). Oxidation of NOM was coupled to reduction and solubilization of Mn(IV) and Fe(III).

The data indicate that, upon contacting mineral soils, dissolved NOM is fractionated into adsorbed and soluble forms in a manner that is highly dependent on mineral surface chemistry. The *affinity* of a given clay for organic C does not itself provide a satisfactory measure of which NOM constituents are adsorbed versus which remain in solution. Therefore, mineralogy can strongly impact (i) the types of organic molecules that are sequestered in subsurface mineral soils and (ii) the organic chemistry of drainage waters. This work also emphasizes the fact that abiotic redox transformation reactions must be considered in studies of NOM interaction with Fe(III) and Mn(IV) containing solid phases. These reactions contribute to the oxidative degradation of NOM and result in the transient accumulation of kinetically-active reducing power (e.g., Fe(II) and Mn(II)) in the soil solution, even under oxic conditions.

Chorover, J. and M. K. Amistadi. 2000. Reaction of forest floor organic matter at goethite, birnessite and smectite surfaces. Submitted to *Geochim. Cosmochim. Acta*.
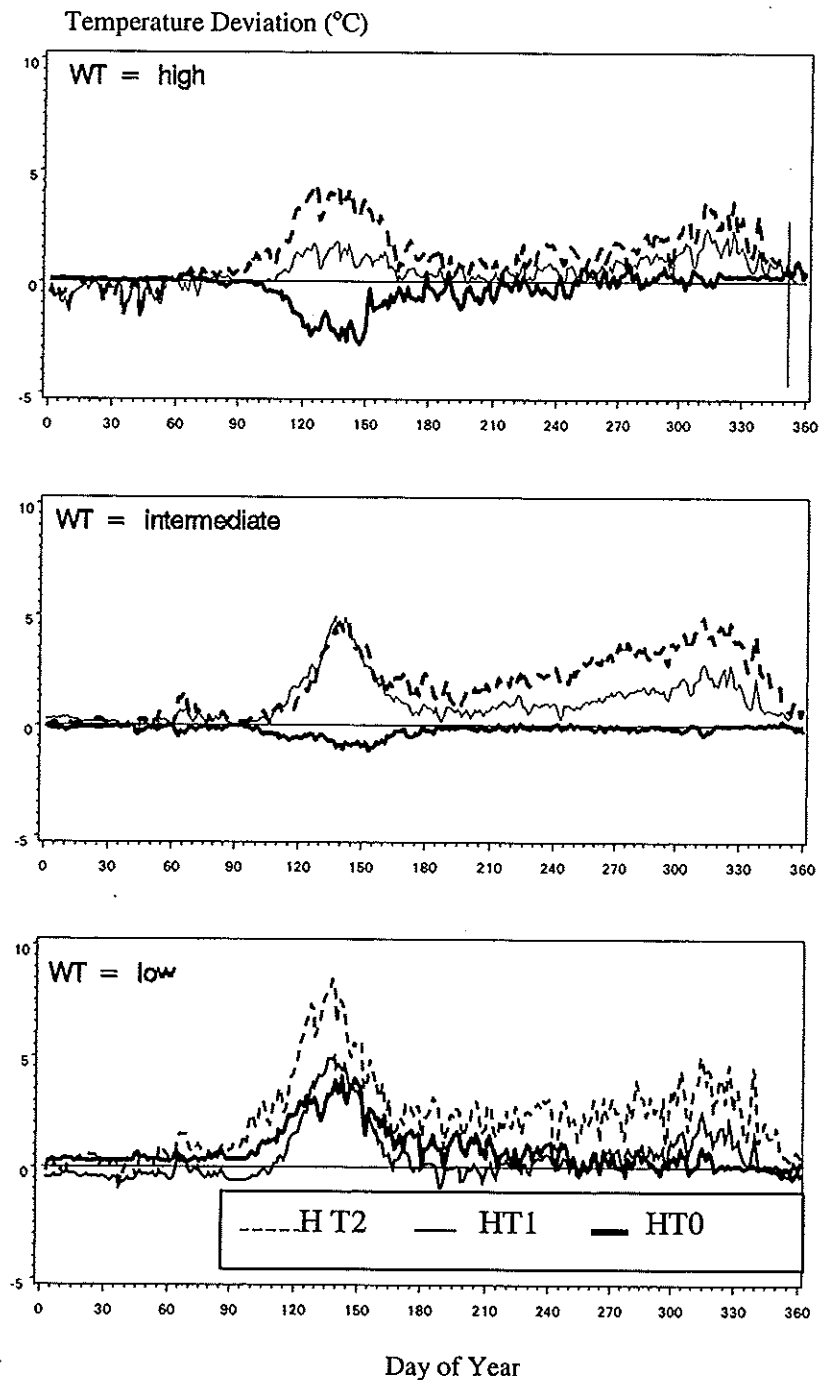
Temperature Deviation (°C)

Fig. 2. Soil temperature (10 cm) deviation (°C) from the mean (i.e., average temperature of plots without heat loading, HT) in all fens that were treated with high, intermediate, and low water tables (WT). Heated plots (HT1 and HT2) were cooler during the winter than unheated plots (HT0); and most temperature effects were in spring. Water treatments in the summer have resulted in temperature deviation throughout the year.
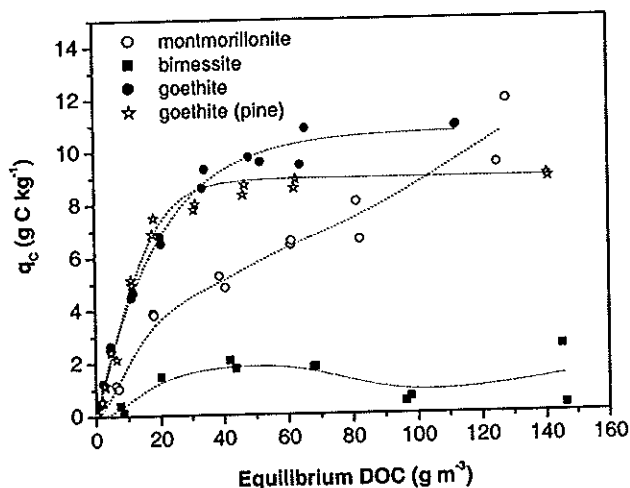
Chen et al.

Figure 1. Adsorption isotherms for FFL NOM on goethite, montmorillonite and birnessite in the dark at pH 4 (C basis). Oak FFL NOM is used for comparison across mineral types, whereas the effect of FFL source (oak versus pine) is assessed using goethite as a common adsorbent.
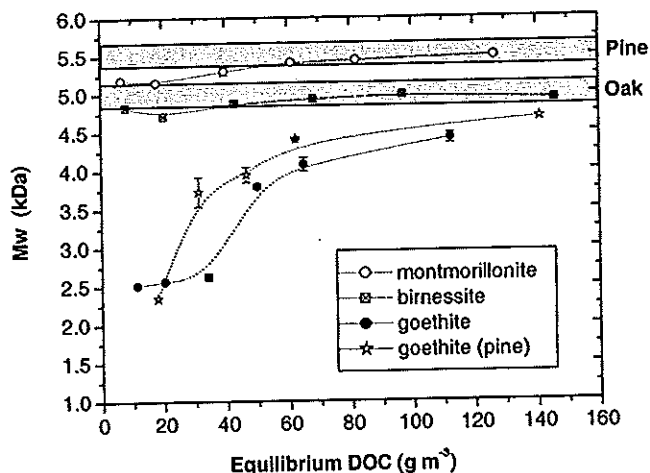

Figure 2. Effects of reaction with mineral surfaces on weight average molecular weight (Mw) of dissolved NOM as measured by HPSEC. Grey band represents the mean ± 95% confidence interval for Mw of unreacted NOM. Oak FFL NOM is used for comparison across mineral types, whereas the effect of FFL source (oak versus pine) is assessed using goethite as a common adsorbent.
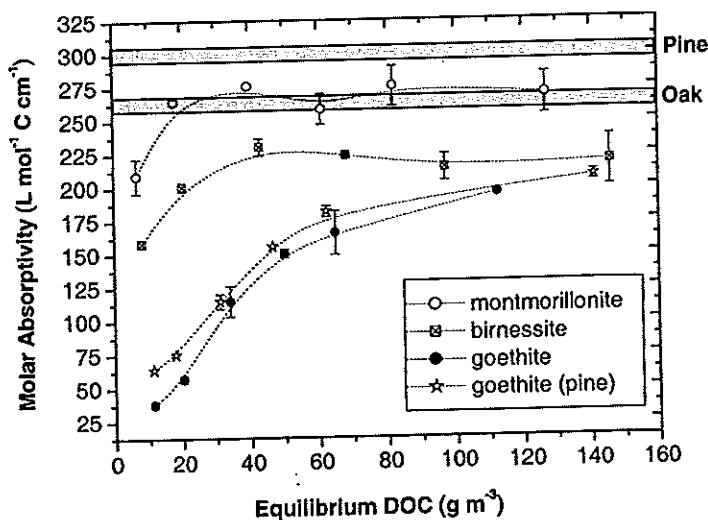

Figure 3. Effects of reaction with mineral surfaces on molar absorptivity (ε) of dissolved NOM as measured by UV absorbance (280 nm) normalized by DOC. Grey band represents the mean ± 95% confidence interval for ε of unreacted NOM. Oak FFL NOM is used for comparison across mineral types, whereas the effect of FFL source (oak versus pine) is assessed using goethite as a common adsorbent.
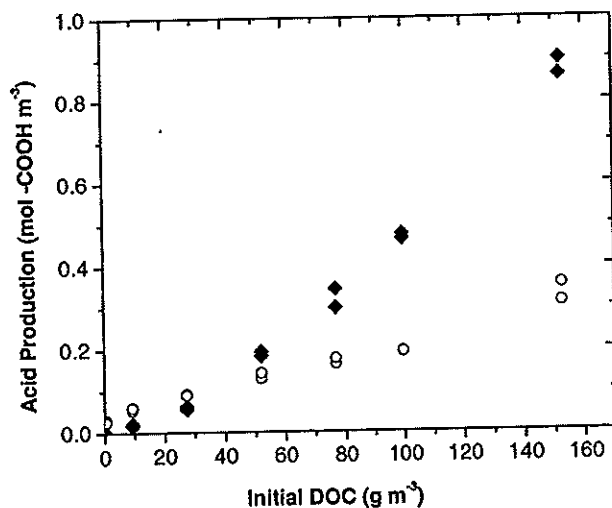

Figure 4. Concentration of formic and acetic acids in suspension supernatant solutions (oak FFL NOM) after 17 h reaction time in the dark with birnessite versus initial DOC concentration. Units on the y-axis are moles of carboxylic acid per cubic meter of suspension. These acids were not present at detectable concentrations in the unreacted blanks or in montmorillonite suspensions.

Vegetation and Climate History from Northern New England in Relation to the Little Ice Age

S. Clayden, D. Foster, J. McLaughlin, D. Koester, S. Barry, D. Francis, B. Wolfe and E. Doughty

Paleoecological evidence indicates that the forests of New England were changing in composition before European arrival. In particular, several pollen records from lakes in the Northeast show declines in beech and hemlock coincident with a period documented in historical and dendroecological records known as the Little Ice Age (~1450-1850). This interval is characterized by highly variable conditions, with greater frequencies of long cold winters, and short cool summers. Cooler temperatures alone are not consistent with declines in beech and hemlock, both northern temperate tree taxa. Other related factors, including moisture, may contribute to these species decline. In order to comprehensively investigate this pre-settlement vegetation trend, we are analyzing the paleo record of multiple proxy indicators of climate from several sites in New England, spanning both latitudinal and topographical gradients. Fine-resolution pollen and charcoal analyses allow us to reconstruct vegetation and fire histories, while independent climate proxies - fossil diatoms, chironomids, and stable isotopes - are indicative of aquatic and hydrological conditions.

Levi Pond in Groton, Vermont was selected as the northernmost study site. The land outside of the village of Groton, settled in the late 1700's, was considered too rocky to farm and the major cultural impacts on this landscape have been logging, and the railroad. Today Levi Pond is surrounded predominantly by red spruce, hemlock, white pine, white birch, and red and sugar maple.

Pollen analysis of the top one meter of sediment from Levi Pond representing the last 3000 years, indicates a gradual increase in spruce to the present (Fig. 1). Beech and hemlock decline coincident with settlement, while birch increases. The diatom record shows changes coincident with the long-term increase in spruce, settlement, logging activity, and more recent development of camps around the site. The fossilized remains of chironomid insects reflect lake-water surface temperatures. In combination with information gained from stable isotope analysis on the lake and catchment hydrological balance, these indicators will provide independent climate assessments in relation to the Little Ice Age. At this site, the pollen record shows declines in beech and hemlock that follow the Little Ice Age period.

Foliar Decomposition After Hemlock Woolly Adelgid Infestation in Eastern Hemlock Ecosystems

R. Cobb, S. Currie and D. Orwig

The hemlock woolly adelgid (HWA), an aphid like forest pest introduced from Asia, is spreading virtually unrestricted through the eastern hemlock (*Tsuga canadensis*) range in northeastern North America. *T. canadensis* does not appear to have any resistance to HWA, nor has an effective natural HWA predator been identified in this region. This epidemic has the potential to dramatically alter the ecosystem function of *T. canadensis* forests and may influence nutrient cycling in subsequent stands. A recent study by Jenkins *et al.* (1999) suggested that changes in decomposition rates may be partially responsible for alterations of ecosystem function in HWA infested stands. Decomposition of foliar litter plays a critical role in the assimilation and release of elements through forest ecosystems. Decomposition rates are closely associated with foliar quality and a growing body of knowledge suggests that insect attack can alter foliar chemistry. Understanding decomposition in HWA attacked ecosystems will be critical for determining how this infestation alters the function of *T. canadensis* ecosystems.

The objectives of this study are: (i) to determine if HWA attack influences decomposition by directly altering foliar quality, and (ii) to determine if HWA attack influences decomposition by altering microclimate. To accomplish this we designed an 18-month *in situ* decomposition study. We placed two sets of mesh bags containing *T. canadensis* foliage on the soil surface at each of eight study sites (see Orwig *et al.*, this volume). One set of bags contained foliage from yet uninfested stand at Harvard Forest while the second contained foliage from the individual study site.

Fig. 1. Pollen diagram from Levi Pond, Groton, Vermont. Spruce (*Picea*) gradually increases over the last 3000 years, while hemlock (*Tsuga*) and beech (*Fagus*) decline clinicident with settlement indicators: ragweed (*Ambrosia*) sorrel (*Rumex*) and grass (Poaceae).
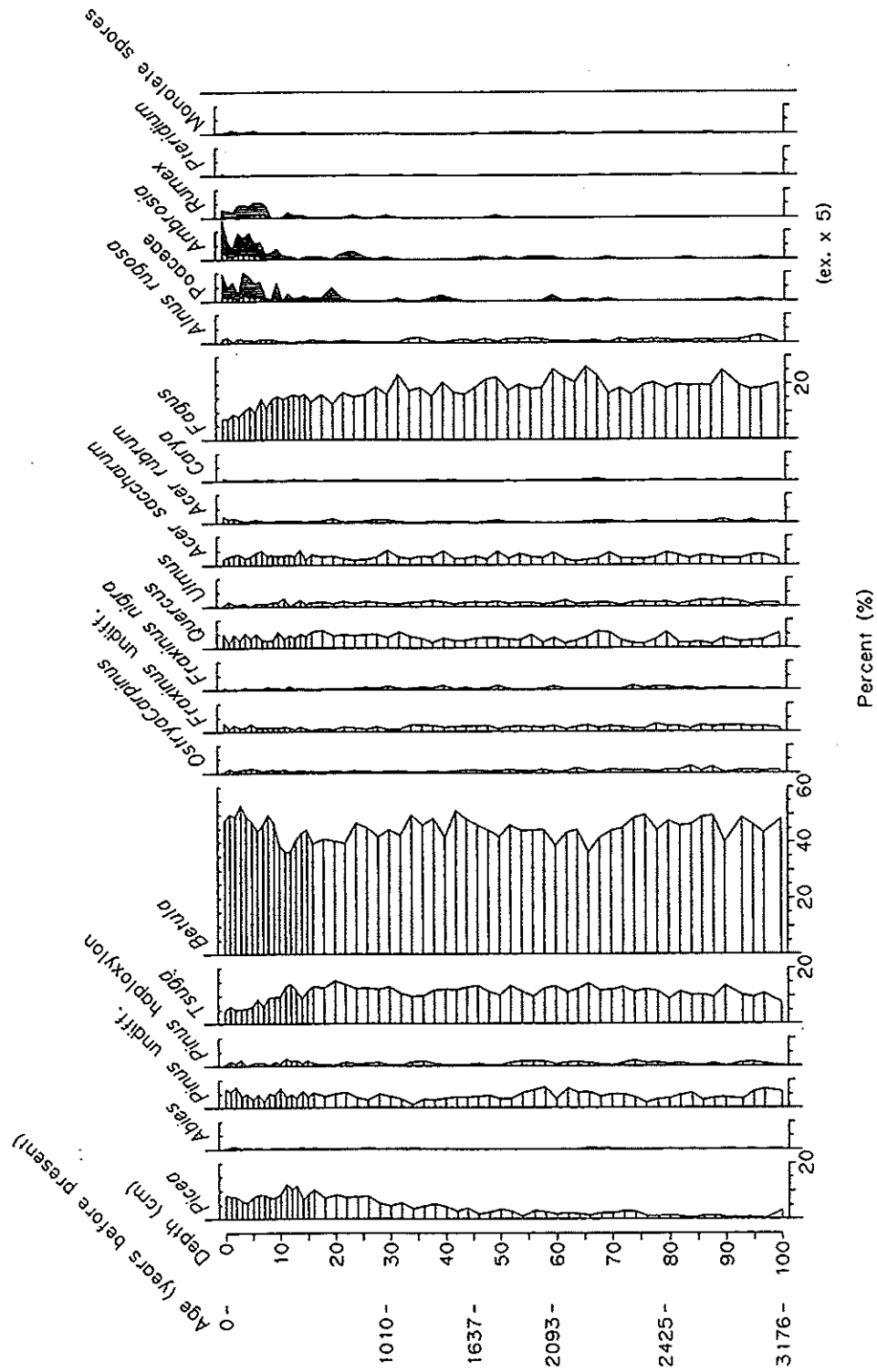
Clayden et al.

Six-month results indicate that HWA attack is slowing decomposition in stands with severe and moderate infestation levels. Although the trend was more pronounced in the severely infested sites compared to the moderately infested sites, decomposition was indistinguishable between the two types of litter. This suggests that microclimate is having a much greater influence on decomposition than initial foliar quality. Although soil temperatures are similar between all sites, the severely and moderately attacked stands have lower soil moisture. These results suggests that dry soil is limiting the establishment of fungal hyphae and microbial communities on soil surface foliage and is thus slowing decomposition in these sites.

Jenkins, J.C., J. D. Aber, and C. D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Can. J. For. Res. 29: 630-645.

Diurnal to Interannual Scales of Variability in Ambient Methane Measured at the Harvard Forest NIGEC Tower, Petersham, MA, Redux

P. Crill and K. Bartlett

Since late 1991, we have made more than 190,000 discrete analyses of ambient methane (CH_4) concentrations. Our automatic gas chromatographic system samples every 6-15 minutes (every 15 minutes since 1996) and samples are compared to working standards calibrated against NOAA-CMDL standards. The observation mixing ratios ranged from 1.709 to 2.471 ppmv, a difference of 762 ppbv. The daily averages varied from 1.765 to 2.045 ppmv (Fig. 1), with monthly medians varying over a much narrower range, 1.79- 1.88 ppmv.

Seasonal trends in the monthly medians are evident in each of the years that we sampled (Fig. 2). The minima occurred in spring and summer and the maxima in fall/winter. Minima appear to be due to increases in photochemically produced tropospheric oxidants before biogenic sources warm enough to produce sufficient CH_4 to significantly affect ambient mixing ratios.

Significant variability in seasonal amplitude and timing is present from year to year.

Long term trends in the data were masked by the occurrence of one to three day events of higher mixing ratios when ambient CH_4 would increase by more than 200 ppbv over background levels. Variability in ambient CH_4 mixing ratios is correlated with wind direction, with highest average mixing ratios occurring during time periods when air reaching the tower is from the southerly and southwesterly directions (Shipham et al., 1998b). Examination of the lowest 10% quantile of the CH_4 data reveals a long term increasing trend in these "background" data (Fig 3) of 4.3 ppbv per year in the monthly medians from November 1991 to December 1997, with an r^2 of 0.35, in general agreement with observed global clean air trends. Similar calculations using the upper 10% of the data suggest that there is little long term increase ($r^2 = 0.0002$) and that there are no strong trends in the most polluted air reaching the tower.

The sporadic high CH_4 events at the tower occur more frequently in the winter and thus have a striking effect upon the amplitude and the shape of the seasonal CH_4 signal. Seasonal trends in median values are more clearly revealed through examination of trends in the highest and lowest 10% quantiles of the data, which differ both in magnitude and timing (Fig. 4). Median values for the lowest 10% exhibit a seasonal amplitude of roughly 33 ppbv with maxima in late winter, February and March. Monthly medians of the top 10% exhibit a seasonal amplitude of 113 ppbv.

A diurnal signal is also evident in the data after the inter-annual and seasonal signals are removed (Fig 5). Diurnal maxima occur at night and minima during the day differing by about 12 ppbv. Again there appear to be seasonal differences in both the amount of diurnal variation and the times of daily maxima (Shipham et al., 1998a). Mixing ratio maxima occur near or just after sunrise in the spring and summer, but much closer to sunset in the fall and winter months.

Shipham, M.C., K.B. Bartlett, P.M. Crill, R.C. Harriss and D. Blaha. 1998a. Atmospheric methane measurements in central New England: An analysis of the long term trend and the seasonal and diurnal cycles. J. Geophys. Res. 103: 10621-10630.

HARVARD FOREST CH4
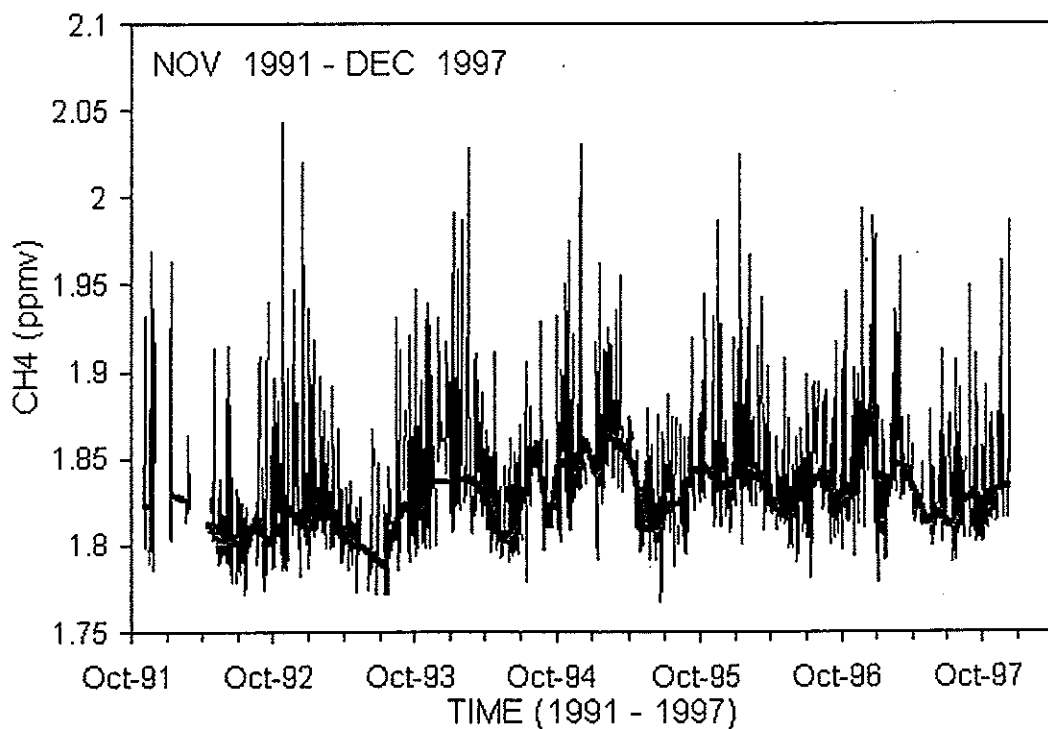## DAILY AVERAGES AND MONTHLY MEDIAN

NOV 1991 - DEC 1997

Fig. 1. Daily averaged CH_4 ambient mixing ratios.

HARVARD FOREST CH4
MONTHLY MEDIAN

| —■— 1992 | —□— 1993 | —▼· 1994 | —▽· 1995 | · •· 1996 | -⊖- 1997 | —▲· 1998 | —— mean |

Fig. 2. Monthly median CH_4 mixing ratios.

HARVARD FOREST CH4
long-term trends - Medians
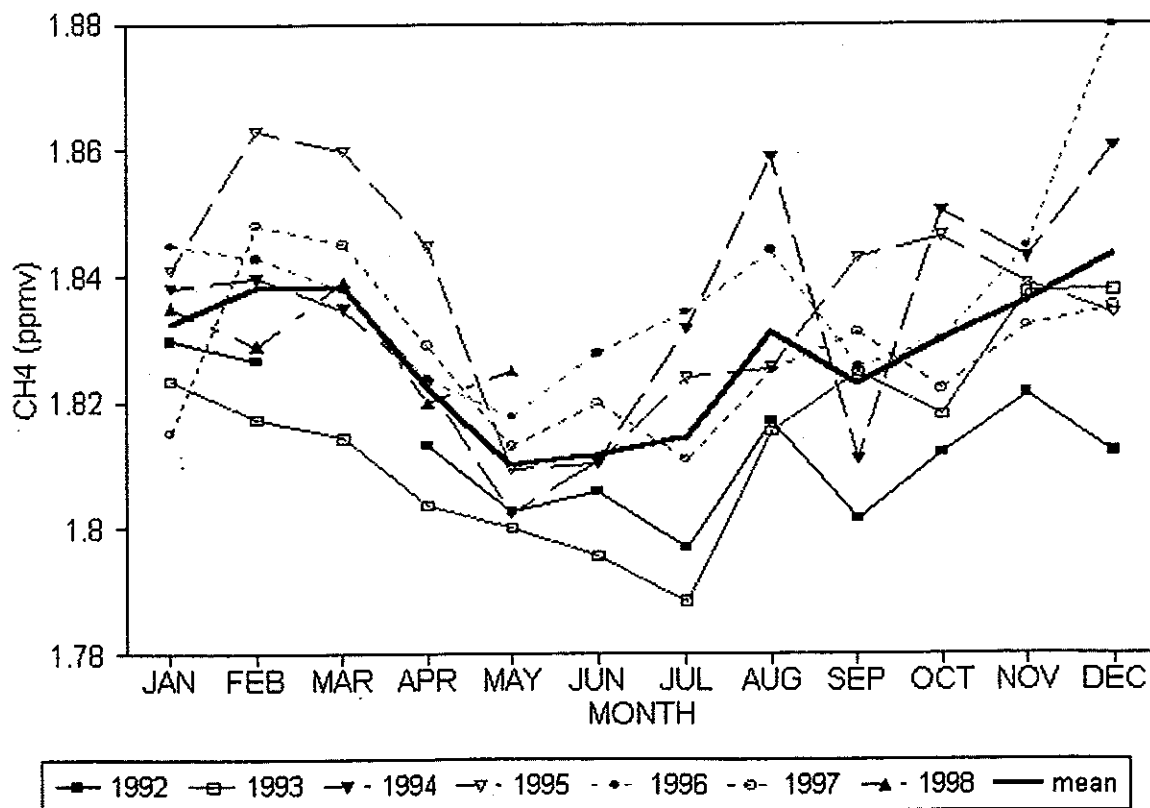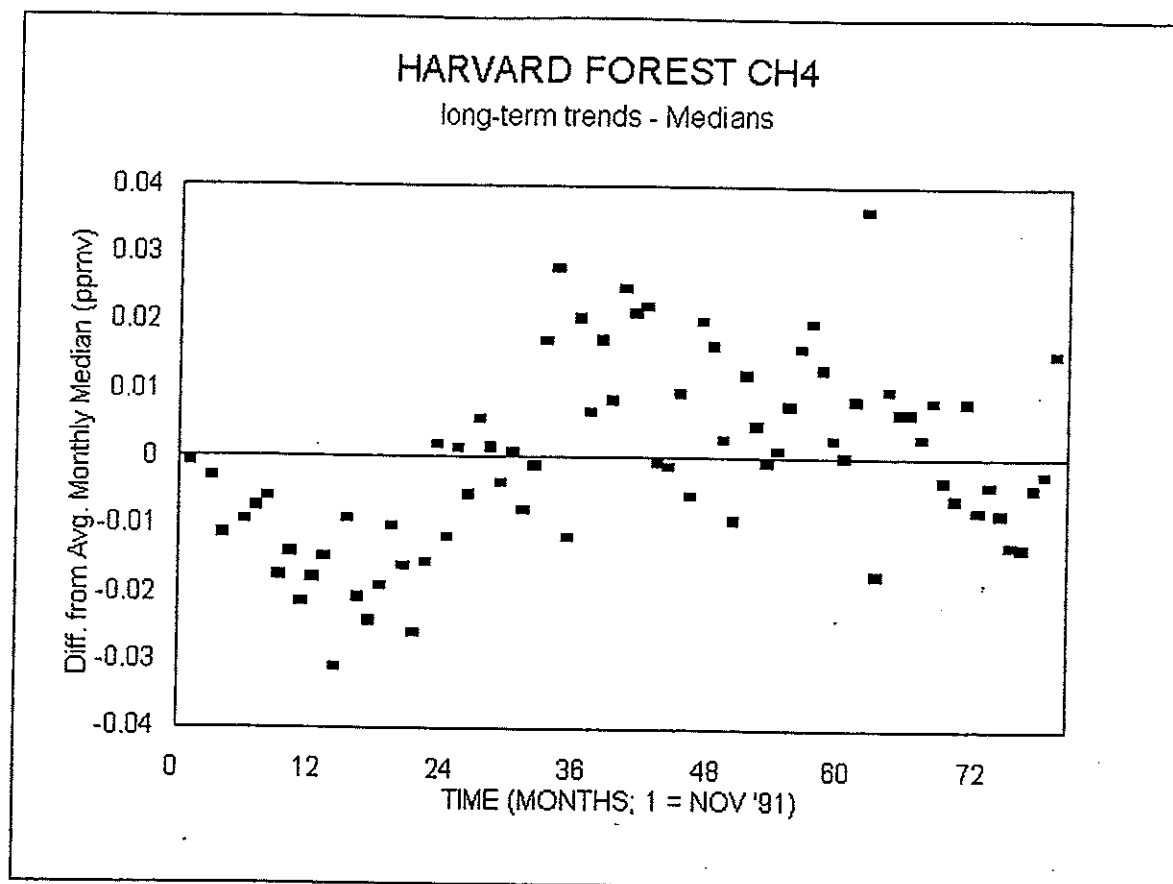
Fig. 3. Difference of the monthly median CH_4 mixing ratios from the long term (1991-1997) monthly median.

Harvard Forest, Petersham, MA
3-PT RUNNING AVG. OF MONTHLY MEDIANS
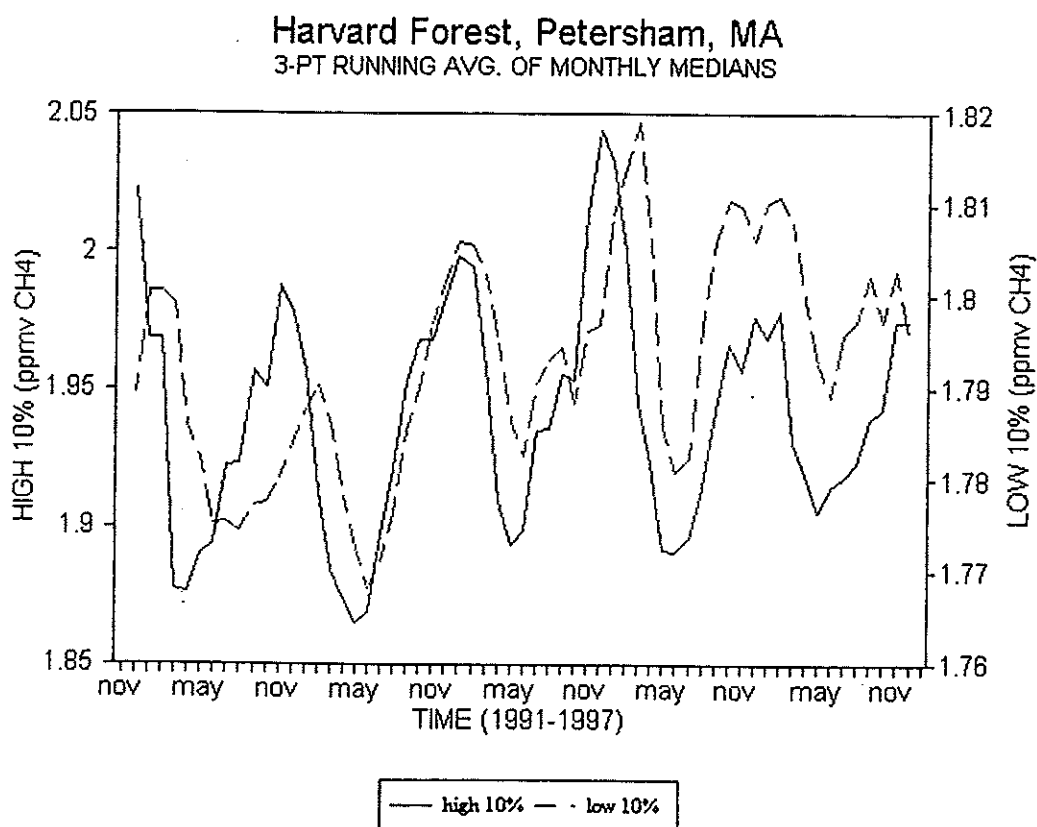

high 10% —— · low 10%

Fig. 4. Smoothed (3-month running average) monthly medians of the highest and lowest 10% quantiles of all the data.

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SEASONAL DIURNAL CHANGE - 1992-1996
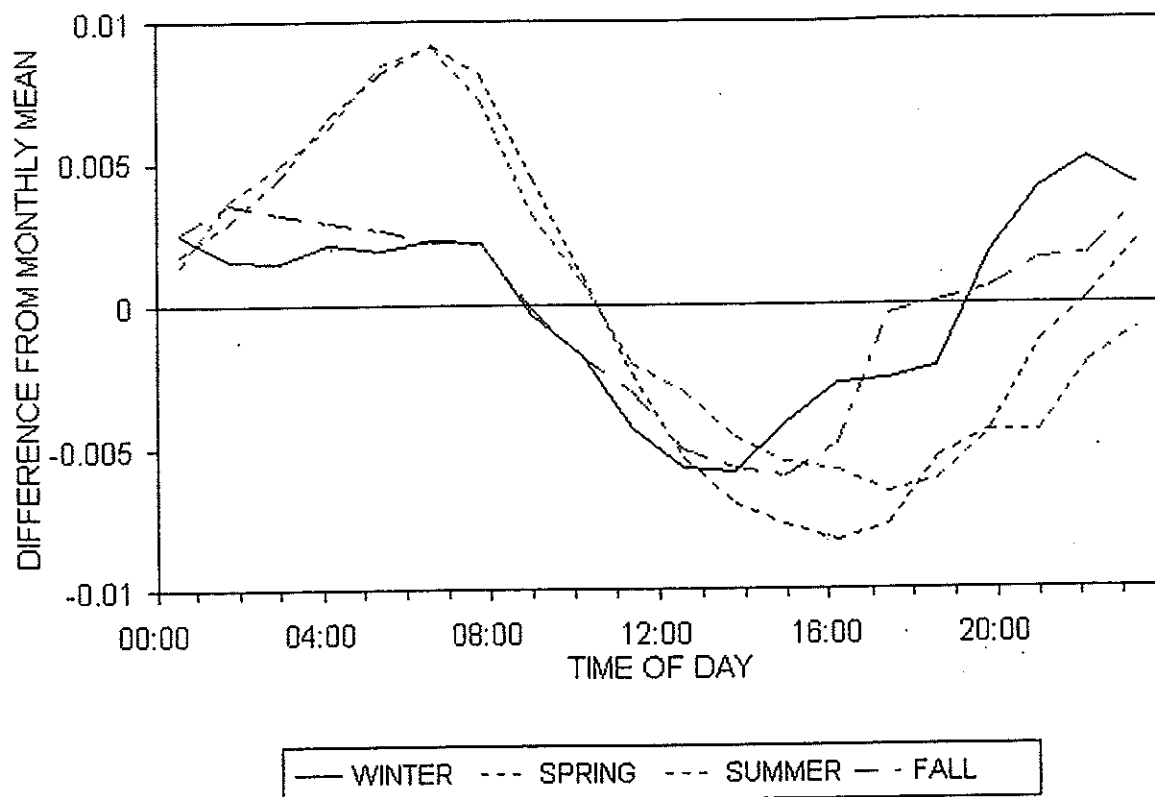## corrected for annual change

Fig. 5. Detrended seasonal diurnal changes in ambient CH_4 mixing ratios.

Crill and Bartlett

Shipham, M.C., P.M. Crill, K.B. Bartlett, A.H. Goldstein, P.M. Czepiel, R.C. Harriss and D. Blaha 1998b. Atmospheric methane measurements in central New England: An assessment of regional transport from surrounding sources. J. Geophys. Res. 103: 21985-22000.

Immobilization of Nitrate and Nitrite in Temperate Forest Soils: Microbial and Abiotic Processes and Potential Interaction

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

Biotic and abiotic mechanisms by which inputs of inorganic-N are converted to organic-N and retained in soil were investigated using ^{15}N in sterilized and live soils. Soils were obtained from areas outside the chronic N deposition plots at Harvard Forest. Samples of the control and sterilized organic soil were analyzed immediately after ^{15}N addition and 24 hours later to determine ^{15}N incorporation of nitrate or nitrite into inorganic and organic soil-N pools.

Up to 80% of ^{15}N-nitrite was not recoverable immediately after addition to sterilized organic soils, while 10-20% loss was observed in control soils (Fig. 1). About 30-50% of the nitrite was recovered in an organic fraction during the 24 hour incubation in both live and irradiated soils, indicating an abiotic process, such as nitrosation of soil organic matter, may be responsible for this immobilization (Azhar *et al.*, 1986). Although sterilization by autoclaving or γ-irradiation did not significantly affect the relative percentages of label recovered in inorganic and organic pools, autoclaving reduced overall recovery of ^{15}N immediately upon addition. We suspect conversion to gaseous N may account for the N loss observed when nitrite was added to both control and sterilized soils.

Added ^{15}N-nitrate was recovered largely as-is (>60%) in all soil treatments and less than 8% was recovered as organic-N with no significant changes after 24 h incubation (Fig. 2). Less than 1% of ^{15}N-nitrate was recovered as ammonium and we have not included this pool in the figures for sake of simplicity. Similar amounts of ^{15}N were recovered in the organic pool in sterilized and control soils, however organic N retained in the soil after mineral-N extraction and mineral nitrogen in the extract did not sum to the total ^{15}N added to the sample (Fig. 2). We report a substantial fraction of nitrate (30 to 50%) was not recovered as inorganic-N or insoluble organic-N. The deficit N, we believe, was removed from the soil by the mineral-N extraction but was not in the form of nitrate, nitrite or ammonium. We have termed this fraction "soluble-N" and suspect it may be organic, but have not made a direct determination of the form of N in this pool.

Substantial ^{15}N added as nitrate was calculated (by difference) to be in the soluble-N pool in both control and sterilized soil, with no differences observed over the course of the incubation period. This suggested that the nitrate immobilization process into this pool might be abiotic. Sterilization of soil may lead to changes in soil properties that enhance the conversion of nitrite and nitrate to nitrogen gasses or unknown N forms. Hence, artifacts of sterilization are a concern, but nevertheless, these results show that an unidentified process of abiotic immobilization of nitrate to form organically bound N may be important in organic layers of temperate forest soils. These findings support observations by Berntson and Aber (2000) that show nitrate immobilization, as measured by disappearance of ^{15}N-nitrate from soil cores, was best described by 2 kinetic rates. An immediate, (<1 h) rapid rate accounting for up to 80% of nitrate immobilization and a much slower rate approximating what has traditionally been attributed to microbial nitrate immobilization.

E.S. Azahar, R. Verhie, M. Proot, P. Sandra and W. Verstraete (1986). Binding of nitrite-N on polyphenols during nitrification. Plant and Soil 94: 369-382.

G. M. Berntson and J.D. Aber (2000). Fast nitrate immobilization in N saturated temperate forest soils. Soil Biology and Biochemistry 32: 151-156.
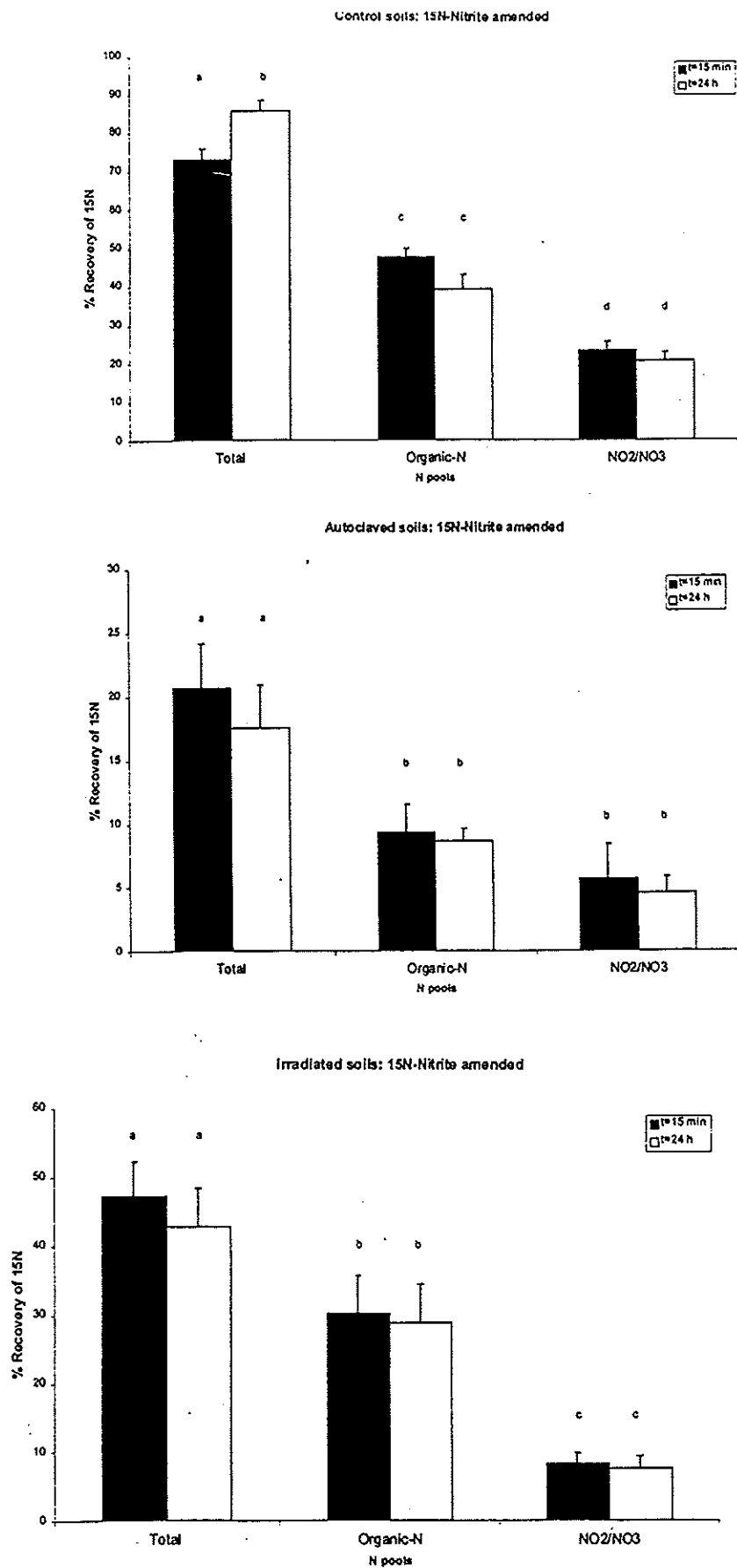
Dail et al.

Fig. 1 Percent recovery of ^{15}N added as nitrite to (a) control, (b) autoclaved and (c) γ-irradiated organic soils. Mean % recovery reported (n=3) and error bars are 1 S.D. of mean. Statistically significant differences between means at α=0.05 (t-test) reported as different letters above consecutive bars. Total = total ^{15}N recovered in soil immediately after addition (t=15 min.) or after 24 h incubation at 20°C. Organic-N = [15]N remaining in soil after mineral-N extraction. NO2/NO3 = mineral-^{15}N in soil extract (some nitrite was oxidized to nitrate during the incubation period).
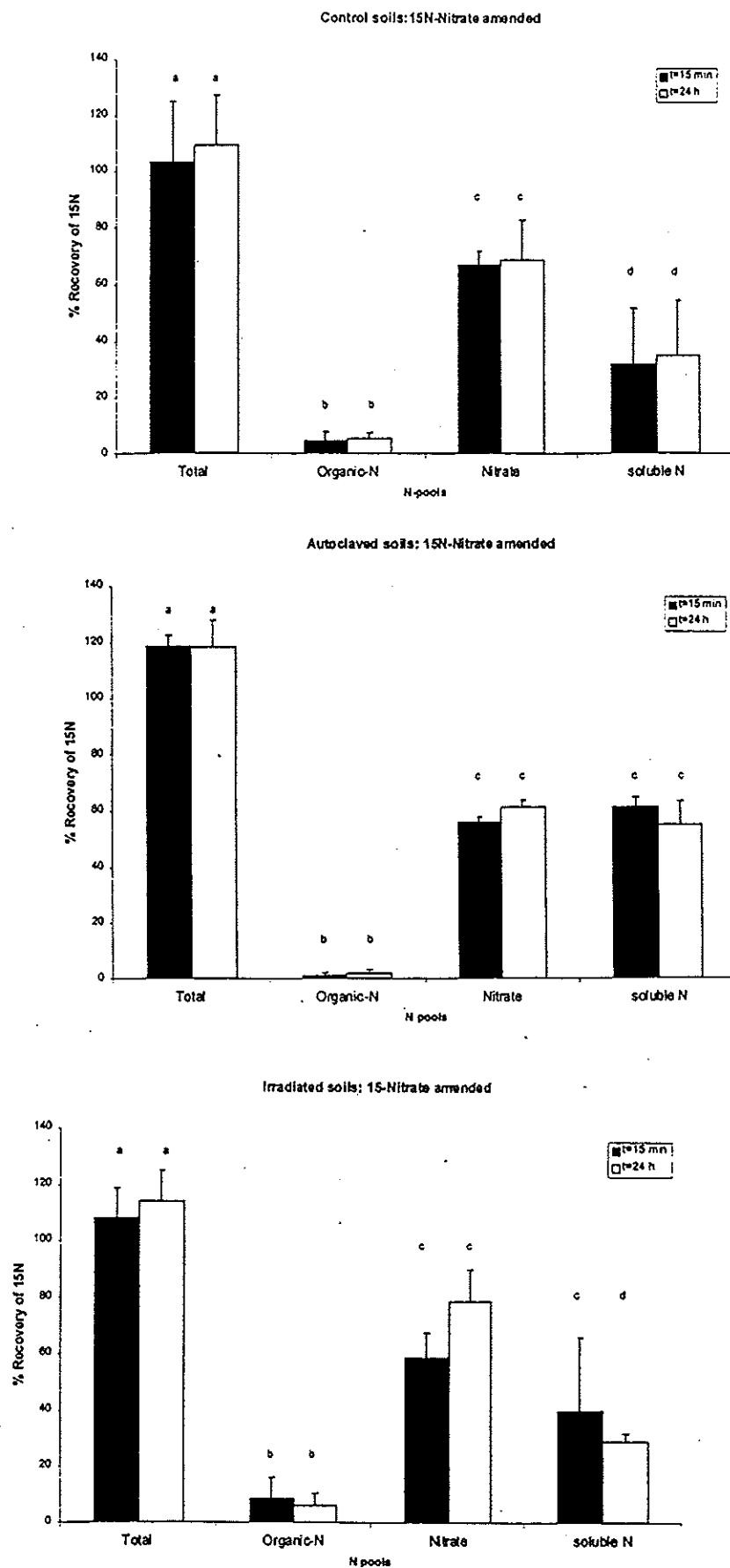
Dail et al.

Fig. 2 Percent recovery of ^{15}N added as nitrate to (a) control, (b) autoclaved and (c) γ-irradiated organic soils. Mean % recovery reported (n=3) and error bars are 1 S.D. of mean. Statistically significant differences between means at $\alpha=0.05$ (t-test) reported as different letters above consecutive bars. Total = total ^{15}N recovered in soil immediately after addition (t=15 min.) or after 24 h incubation at 20°C. Organic-N = [15]N remaining in soil after mineral-N extraction. Nitrate = [15]N recovered in form added. Soluble N = difference between total recovery and mineral N forms; SD calculated by propagation of error method.

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, B. 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 to 1993 by Knute Nadelhoffer and coworkers. These samples were analyzed for chemical structural information by solid-state ^{13}C and ^{15}N NMR and molecular level detail by pyrolysis GC/MS. Results were used as a control to compare samples of green leaf material and soils that were collected by Nadelhoffer and coworkers in 1999 and analyzed by the same analytical techniques to determine the effects of heavy N fertilization. Additionally, samples collected in 1999 from control, low N and high N plots were compared to separate changes associated with forest changes and N fertilization.

^{13}C NMR spectra from all 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 out. 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 and 3).

Of particular interest are the effects of N fertilization on leaf growth 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 (Fig. 1). However, most of these additional structures are removed by lipid extraction (Fig. 2) indicating that the structures may be associated with easily removable/degradable components such as chlorophyll and other extractable lipid compounds. Increased levels of lignin (90-160 ppm) and aliphatic amide carbons (160-190 ppm) are also observed in the NMR spectra of the leaf samples from high N plots relative to control samples (Fig. 1). Spectra of 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 (Hardwood shown, Fig. 3). This indicates that the rate of decomposition has decreased with increased N fertilization, supporting results of a litter decomposition study performed by Magill and Aber (1998). Pyrolysis GC/MS results (in progress) provide additional details such as the presence of phytadienes, derived from chlorophyll and aid in the understanding of changes that are occurring in the Chronic N plots.

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

Relationships Among Woodland Vegetation and Land-Use History, Cape Cod National Seashore, MA

R. Eberhardt, D. Foster, G. Motzkin, J. Harrod and B. Hall

Human land-use affects the composition, structure, and landscape pattern of vegetation worldwide, and human disturbance history must be considered when interpreting modern vegetation and developing conservation objectives and strategies. The specific effects of land-use history on modern vegetation are poorly understood because land-use history is complex, poorly documented and often correlated with environmental gradients. In this study we are examining relationships among modern woodland vegetation and land-use history on 5100 ha of glacial outwash deposits on Cape Cod National Seashore in southeastern Massachusetts. Like previously-studied sand plains in the Connecticut Valley (Motzkin, *et al.* 1996, 1999), relatively homogeneous site conditions and the availability of detailed historical information make the study area particularly appropriate for evaluating the effects of land-use history on vegetation. The
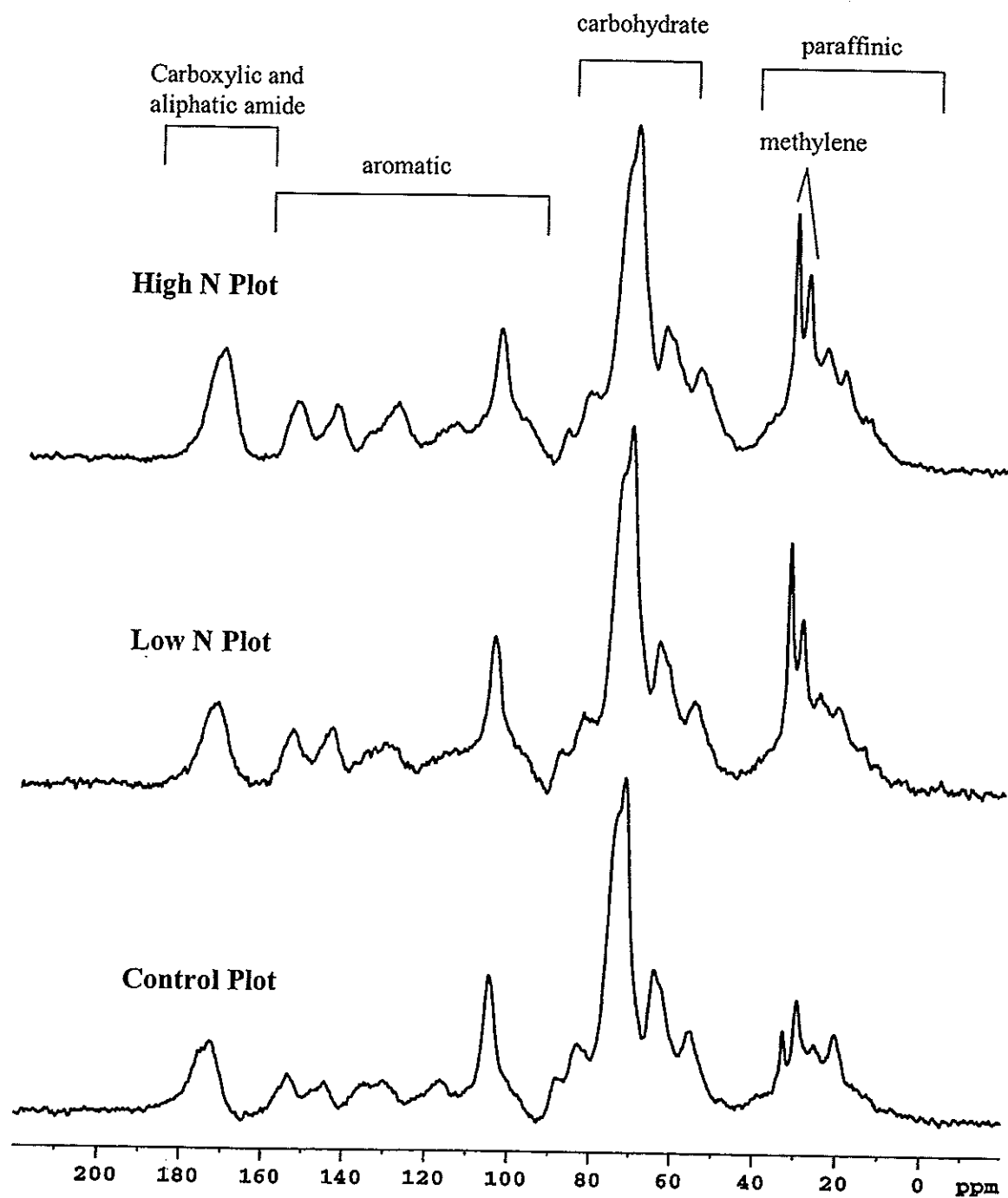
Figure 1. Black oak green leaf samples collected in 1999 from Chronic N high N, low N and control plots.
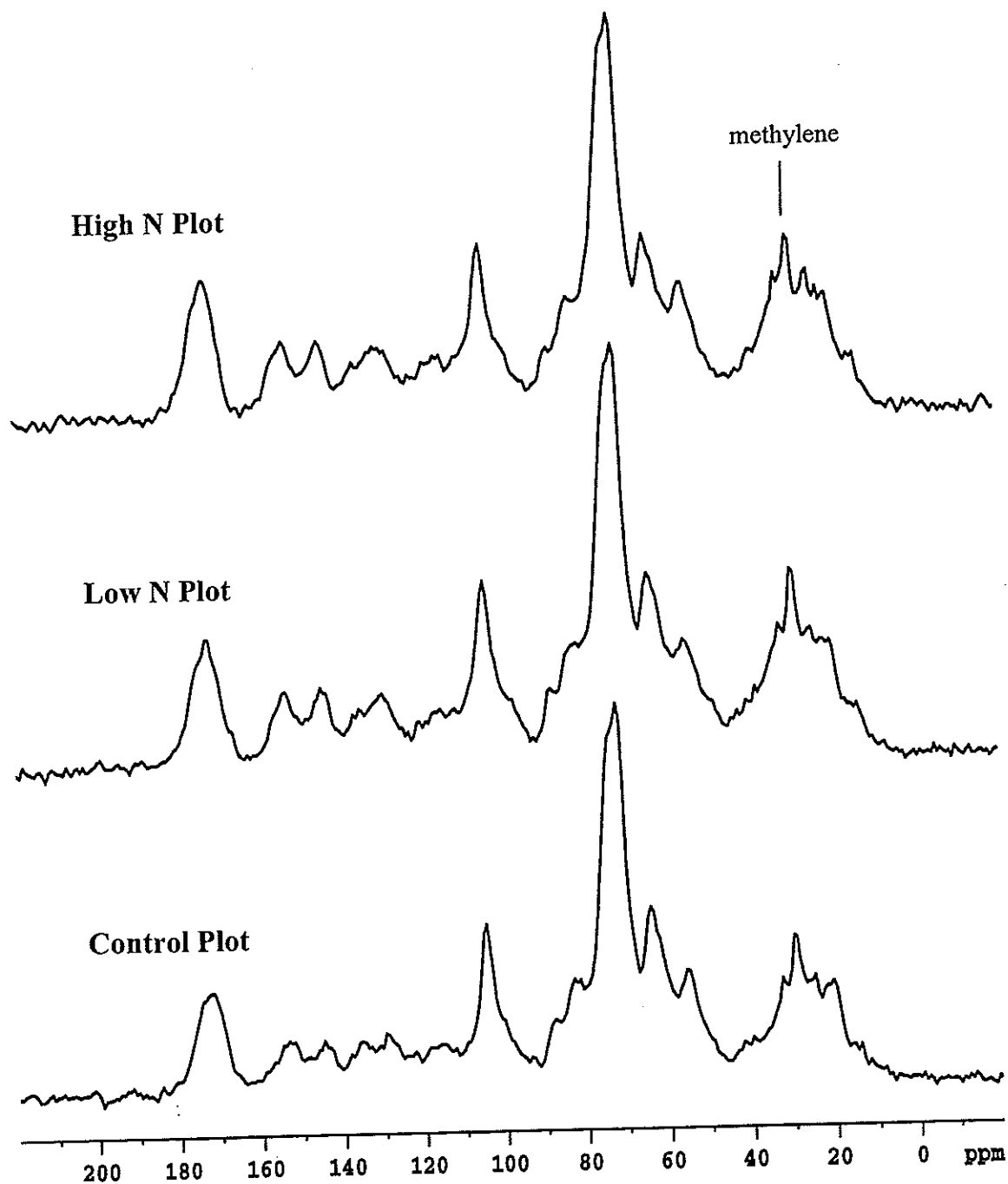
Figure 2. Lipid extracted black oak green leaf samples collected in 1999 from Chronic N high N, low N and control plots.
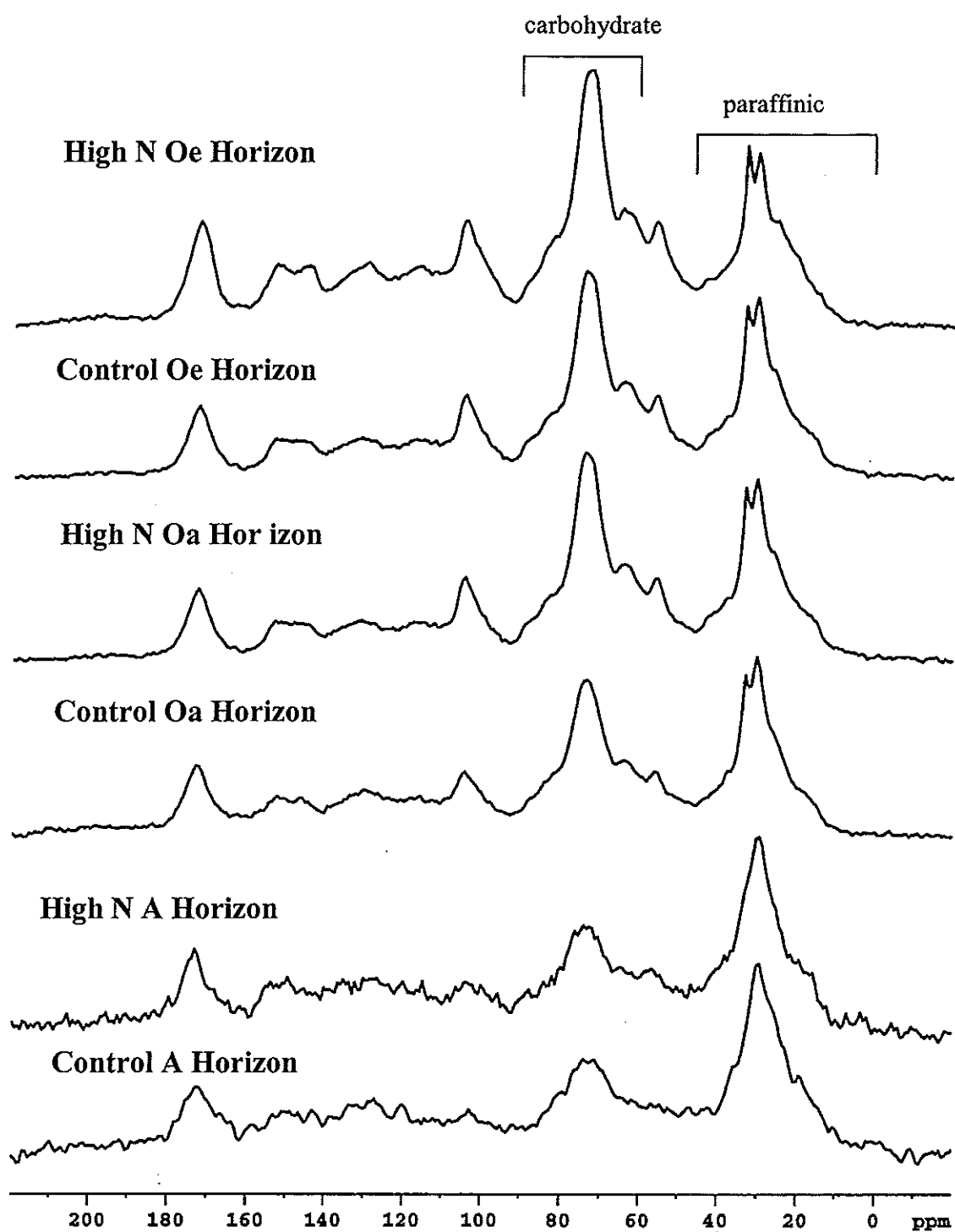
Figure 3. Soil samples collected in 1999 from hardwood Chronic N high N and control plots.

conservation significance of the site also provides an opportunity to inform management efforts.

Colonists settled outer Cape Cod by 1644, and US Coast and Geodetic Survey maps suggest that agriculture/open land covered approximately 48 % of the study area during the mid-nineteenth century. Land abandonment and reforestation followed: based on 1938 aerial photographs, agriculture/open land covered approximately 15 % of the study area by the mid-twentieth century. Using historical maps and the presence/absence of plow (Ap) horizons, we have grouped randomly-selected modern vegetation plots (n = 91) into four broad categories of historical land-use (cultivated/improved pasture, unimproved pasture/open, woodlot, and military use). Overall variation in species composition relates significantly to variation in land-use history (Fig. 1), with common understory species occurring preferentially in certain land-use categories (Fig. 2). Preliminary results indicate that *Deschampsia flexuosa, Arctostaphylos uva-ursi, Prunus serotina, Amelanchier* spp. and *Trientalis borealis* occur more frequently in former croplands or improved pastures, *Smilax rotundifolia* and *Myrica pensylvanica* concentrate in former umimproved pastures or open areas, and clonal ericaceous shrubs favor former woodlots. This study illustrates that land-use history can exert a dominant effect on modern vegetation in coastal New England and must be considered when developing conservation objectives and management guidelines.

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

Motzkin, G., W.A. Patterson III, D.R. Foster. 1999. A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. Ecosystems 2: 255-273.

Songbird Nest Predation in Eastern Oak Forest: Variations with Nest Height

. R. Field

Predation is a major cause of nest failure for many open-nesting forest bird species. Understanding the ecology of nest predation is important for conservation and management of forest birds. Although songbirds nest throughout the vertical layers of a forest, little is known about predation in the higher strata. Research on nest predation at different heights of vegetation has been limited to ground or shrub levels. Few studies have examined predation events at bird nests above 2-3 m.

One potential predator, the white-footed mouse (*Peromyscus leucopus*), is omnipresent in the mixed oak forests and a capable climber. However, we know little about mice as predators of songbird nests, especially those in the canopy and subcanopy. Pervious studies of nest predation often used artificial nests baited with quail eggs. Because mice have difficulty depredating the relatively large quail eggs, their role as a potential predator throughout the forest may have been underestimated.

In the summer of 1999, I continued a study of predation of songbird nests in the mixed oak stands of Harvard Forest and the northern Quabbin Reservation. The objectives of this study are to estimate nest predation rates in the vertical layers of a mixed oak-forest and evaluate the role of mice as potential predators of those nests. The work is being done in parallel with C. A. Langtimm's study of population estimates and vertical distribution of *P. leucopus*.

In 1997, I conducted point count at 2 sites on Prospect Hill area of Harvard Forest. I identified 35 species of birds on the study plots, 25 of which were known or probable breeders. Among those were species that tend to nest on the ground, in shrubs or low branches, in subcanopy trees, and higher into the canopy. In 1998 and 1999, I expanded the study to sites at the Tom Swamp forest and the north Quabbin Reservation (near Gate 19). With the help of summer technicians from the Harvard Forest program, Research Experience for Undergraduates in both 1998 and 1999, we conducted bird surveys at all three sites (1998 only), and artificial nest
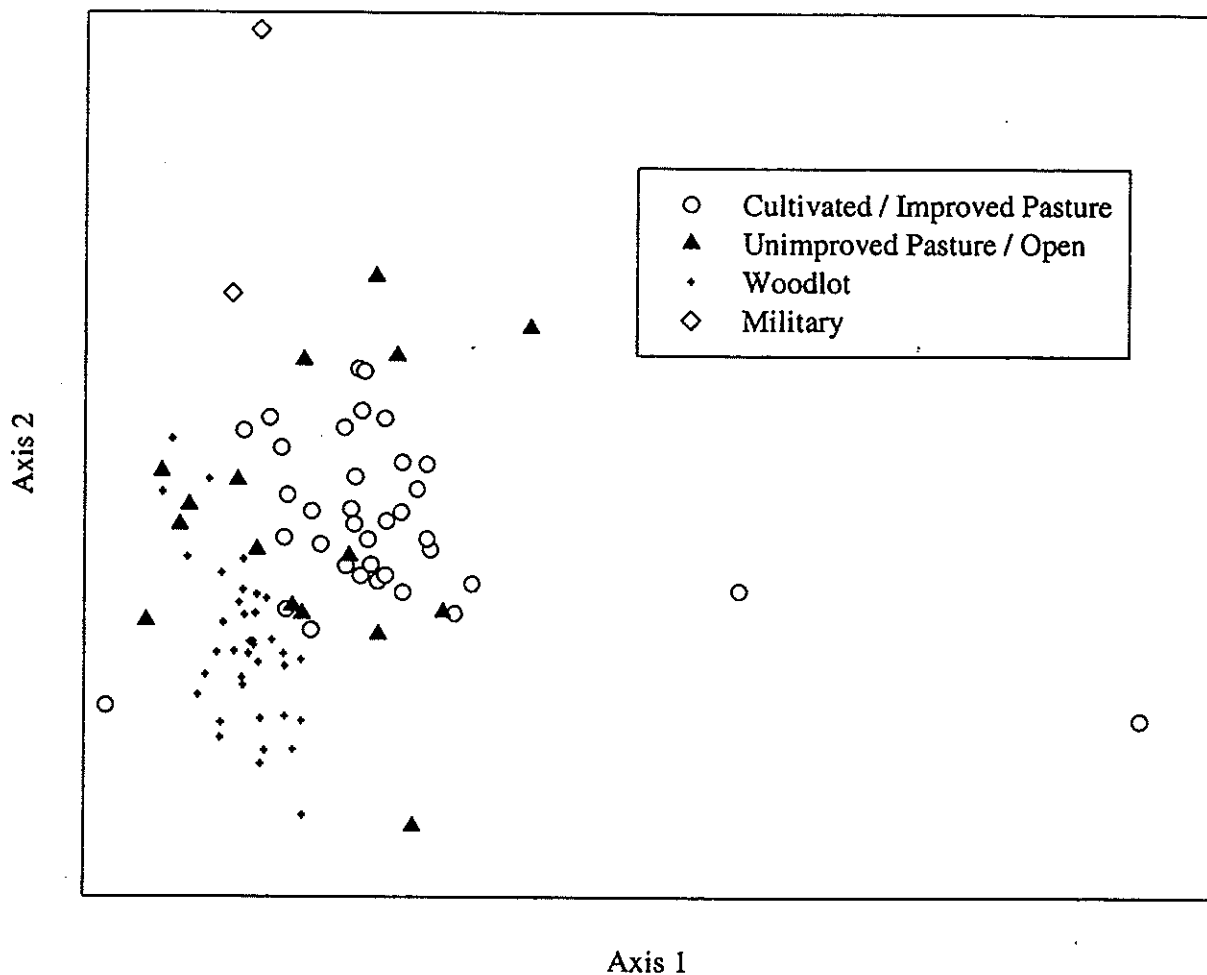
Figure 1. Categories of historic land-use of Cape Cod National Seashore plots shown in ordination space. Proximity in ordination space indicates overall similarity in species composition. Dissimilarity matrices of species composition and historic land-use categories are significantly correlated (Mantel test: standardized r = 0.373, Monte Carlo p < 0.001).

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Figure 2. Frequency of occurrence (%) of common woodland species in plots of different historical land uses on Cape Cod National Seashore. Only species occurring in >20% of total plots are shown. Plots in areas used intensively by the military in the mid-twentieth century (n = 2) are not depicted.

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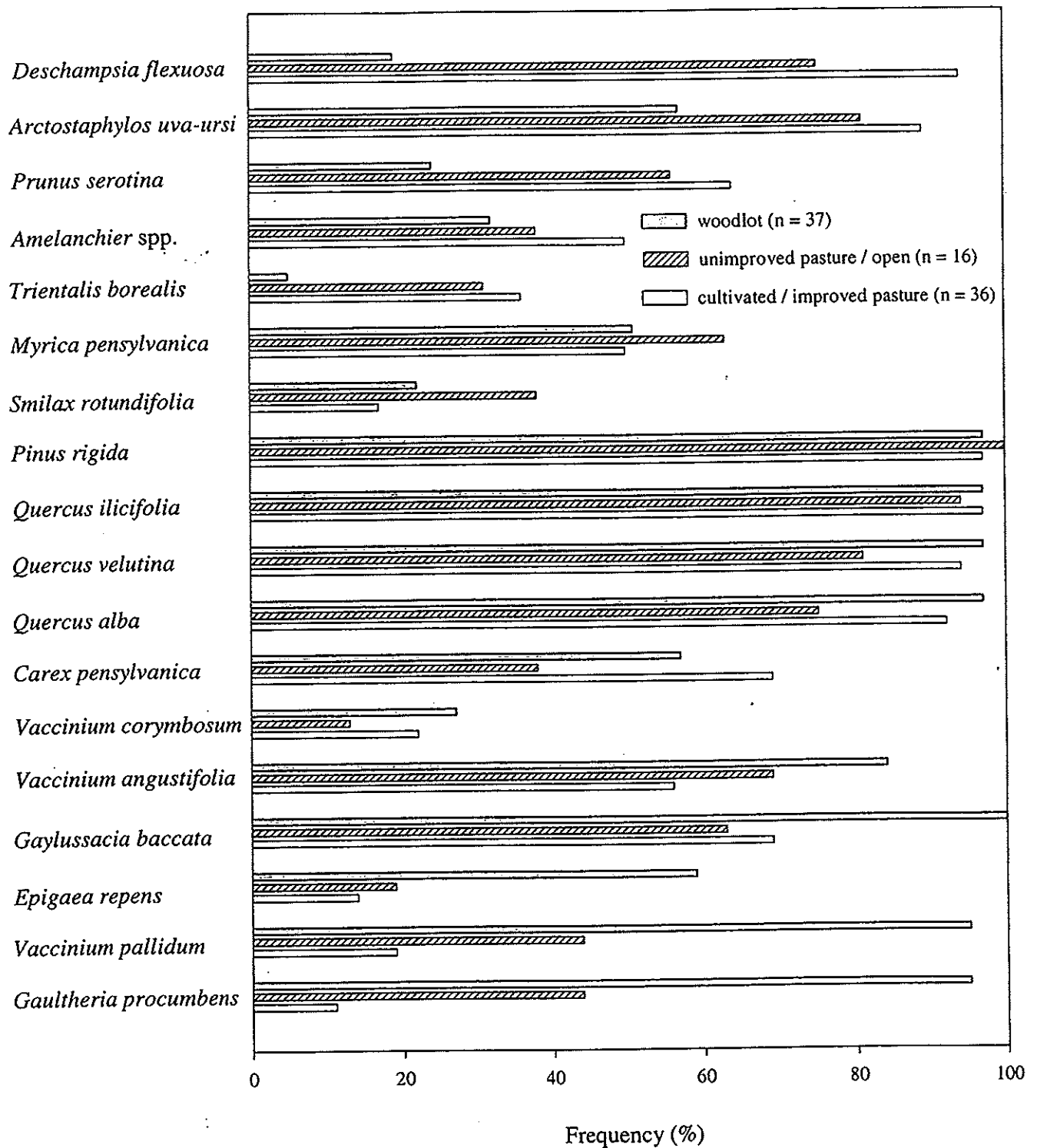experiments using plasticine eggs. Eggs made of modeling clay or plasticine have been used in nest predation studies to document potential predators based on tooth or claw marks on the eggs. Nests were placed at sites on the ground, in shrubs, in the low subcanopy (mean height of 7.4 m), and in higher subcanopy (mean height 11.3 m). In 1999, I repeated the artificial nest experiments using ground-shrub grids at the same 3 sites, but doubled the number of tree nest sites.

Results are preliminary at this time because the project will continue in the summer of 2000. The importance of a long-term study was apparent in the 1998 and 1999 data because of the variability between years. Overall nest depredation was lower in 1999 compared to 1998, with less evidence of mouse depredation at the artificial nests (Table 1). In 1998, nest predation was lowest in Tom Swamp compared to Prospect Hill and the Quabbin site. However, in 1999, depredation tended to be higher in Tom Swamp than the other 2 sites. Although numbers of depredated nests were lower in 1999, there was a similar pattern in predation rates for the 4 strata (Table 1). Ground nest predation was lowest, shrub and low subcanopy nest predation were similar, and high subcanopy nest predation was highest.

Width of incisor marks in the "depredated" plasticine eggs for both years were variable in the ground and shrub nests, indicating a diversity species. Although sample sizes were small for the higher nests, the eggs in the subcanopy were marked with only smaller incisor indentations in the range of tooth marks from museum samples for *Peromyscus*.

The lower predation rates in 1999 may have been the result of a lower population of mice in 1999 and differences in precipitation between the 2 years. Because of abundant acorns in the fall of 1999, we anticipate an increase in the mouse population in 2000 that will make the nest predation results more comparable with the 1998 season. For the 2000 season, I will repeat the artificial nest experiments for comparison with the previous 2 years.

The information from this study will help us better understand predatory risks for songbirds nesting throughout the vertical structure of New England oak forests.

Forest-Atmosphere Exchange Processes: Report on Activities 1999-2000

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

1. Introduction

We have been studying how mass and energy exchanges between the forest and the atmosphere occur, and what consequences they have on the local microclimate. Our efforts have been motivated by the following questions about flux measurements:

a) If the eddy covariance method is so good, why is the energy balance not closed?

b) Are flux and mean profiles similar across different forest canopy types?

c) Does the presence of topographically controlled local winds bias flux observations?

d) What really goes on at night (as regards CO_2 flux observations)?

Our second effort is motivated by curiosity about how representative point flux measurements can be to the wider region, and to what degree do forests alter climate:

e) What changes occur in the lower atmosphere when leaves emerge?

f) Does the occurrence of forced cumulus clouds play a pivotal role in reducing stress to the vegetation?

2. Energy balance /turbulence studies
Similarity forms in the canopy and roughness sublayers

Based on data from the EMS tower and other sites we have quantified the shape of heat, water vapor, and CO_2 flux cospectra in the roughness sublayer, just above the canopy. These are not identical to the commonly cited forms found over flat terrain. Consequently, fluxes calculated using fixed averaging intervals (the common approach) "miss" an important low-frequency contribution, but the missing flux can be estimated using a correction that depends on mean wind speed.

Previously we showed that the drag coefficient changes little as the Harvard Forest goes from leafless to the foliated state. A new result is that the profiles of σ_w and u_* (friction velocity) are *similar* within the canopy for each state, if a foliage-weighted canopy thickness z_c,

Table 1. Comparison of predation rates (percentages) for artificial nest
experiments in 1998 and 1999 at two sites in Harvard Forest and one site
in the Quabbin Reservation. Total number of nests (N) are shown in parentheses
for each group with the first number the 1998 sample size and the
second number the sample size for 1999.

	1998	1999
SITES (N=64, 96)		
Prospect Hill	68.8	19.8
Tom Swamp	56.3	26.0
Quabbin Reservation	76.6	20.8
STRATA		
Ground (N=84, 108)	63.1	13.0
Shrub (N=84, 108)	69.0	27.8
Low Subcanopy (N=12 , 36)	66.7	25.0
High Subcanopy (N=12 , 36)	83.3	30.6
OVERALL PREDATION RATE (N=192, 288)	67.2	22.2

Field

which depends on the *profile* of vegetation in the canopy, is used for the vertical scale. This similarity extends to a variety of broadleaf forests; a different but still similar profile occurs for conifers (Fig. 1). There is a general expression for the displacement $d/h = 0.38 z_c$ for broadleaf forests, and this replaces the commonly used $d/h = 0.75$, where h is canopy top height.

DRAINO-99. On calm nights, many observers find that local CO_2 buildup in the canopy, even when combined with the direct flux measurement, lead to unrealistically low estimates of ecosystem respiration. This problem may be the result of averaging the eddy flux improperly, or as Lee (1998) is the most recent to suggest, the local drainage flows may advect the "missing" CO_2 away. Drainage circulations are notoriously difficult to observe, and they rarely occur as sustained flows. Such flows at the forest floor are further complicated by the presence of tree trunks and subcanopy vegetation. In DRAINO-99, we deployed instruments at the EMS for four months to observe subcanopy flows. Five sonic anemometers (four 2-D and one 3-D) were deployed at 1.5 m around the EMS tower. Fast-response observations of [CO_2] and specific humidity were made with the 3-D anemometer. An acoustic sounder operating at canopy height from a nearby scaffolding tower reported wind speeds and turbulence intensity at 25m intervals up to 750m. Ongoing continuous measurements at the EMS tower include those from 3-D sonic anemometers at 30m, 18m and 11m, the radiative budget components, and temperature, CO_2 and H_2O profiles. On two nights, we observed the motion of neutrally buoyant bubbles along the forest floor. Preliminary results include: a) Understory flows are most frequently decoupled from the flow above (see "snapshot", Fig. 2); b) On average, nighttime flows are from Prospect hill or the nameless hill to the west of it. From the bubble observations, we observed that these topographic flows are not sustained; c) The diurnal cycle of understory wind speeds peaks in the early afternoon, in phase with temperature. We are currently studying the occurrence of gravity waves inside the canopy and in the stable boundary layer above at night. In future, analysis of the acoustic sounder record will also allow us to model the effect of Prospect Hill on HF fluxes.

3. Climatalogical Studies

Climatological studies. At Worcester MA, we calculated R, a relative humidity and B', a tendency Bowen ratio, based on T_{max} and q, the daily average specific humidity. R goes through a minimum near the time of leaf emergence at Day of year 116. At extremes of R, $\partial R/\partial t = 0$, and $L\partial q/\partial t = R\,\varepsilon\,(C_p\,\partial T_{max}/\partial t)$, and it follows that $B' = 1/(R\,\varepsilon)$, where $\varepsilon = [L/C_p]\partial q_{sat}/\partial T$, with $q_{sat}(T, p)$ the saturation specific humidity at given temperature and pressure. $B = 1/\varepsilon$ is the "equilibrium" flux Bowen ratio. Previously it has been argued that evaporation only proceeds at near to the equilibrium rate because fluxes are converging beneath a rigid lid, but we found that only 5% of surface fluxes are trapped in the mixed layer in long-term averages. There is another mechanism to maintain R nearly steady during the growing season. The agent seems to be the appearance of boundary layer cumulus clouds (BlCu), a result that came from analysis of a composite of case studies.

Composite study. Following a typical frontal passage, the mixed layer (sfc to 1500 m) functions as a heat and moisture reservoir, as local and regional warming and moistening modify the overlying air mass. The presence of forests locally modifies these air masses through evapotranspiration (ET). Increased BL humidity reduces the vapor pressure deficit (VPD) and surface temperature, and this facilitates the formation of Blcu. A composite of the BLcu sequences showed a rapid drying and cooling of the mixed layer followed by a gradual warming and moistening over a period of 4-5 days. Budgets of the temperature and humidity tendencies showed that, during days 2-5 of the sequence, the mixed layer (ML) grows rapidly into the previous days' residual layer. The entrainment terms (heat and moisture) contribute only 10-20% to the daily ML heat and moisture tendency after the first day. The presence of active cumulus clouds modulates the exchange of mass, heat, and moisture between the ML and free atmosphere above, maintaining an approximate mixed layer equilibrium at constant R.

Lee, X. 1998. On micrometeorological observations of surface-air exchange over tall vegetation. Ag. Forest. Met. 91: 39-49.
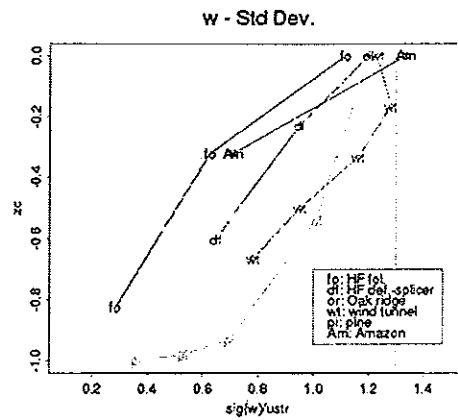
w - Std Dev.

Fig. 1 Scaled profiles of σ_w at several forests. Height is given by the cumulative fraction of foliage, z_c.

Draino99 8 / 13 / 1999   14.5 LST

Draino99 8 / 21 / 1999   1 LST
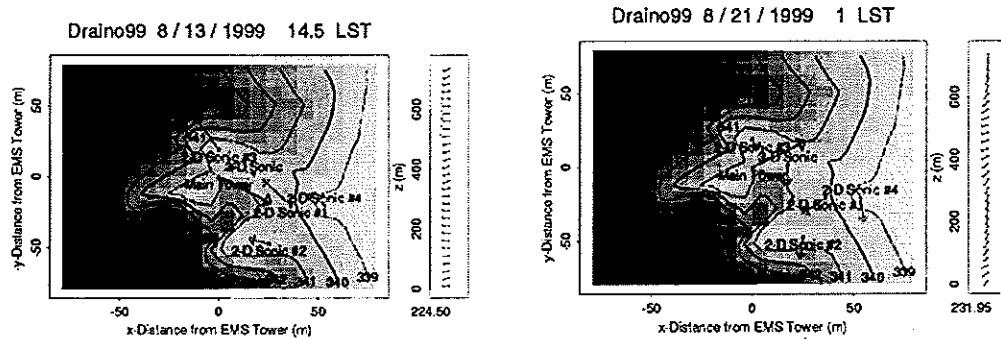
Fig. 2 Wind observations at the EMS site. Contours are in meters. Vectors for the understory anemometers are scaled such that 100m on the map is equivalent to 1 m/s. For the tower wind at tower top (bold arrow), 100m is equivalent to 5 m/s. The barbs on the vertical profile follow meteorological practice, indicating 2.5 m/s steps in increasing wind speed.

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A New Approach to Modeling Soil Carbon Dynamics

S. Frolking

Many soil biogeochemistry models (e.g. Century, DNDC, etc.) are obliged to partition total soil organic matter (SOM) into a series of pools (e.g., fast, slow, passive), without a sound empirical methodology for doing so. This is further complicated if the models attempt to develop a vertical profile of SOM.

I am working on a new approach to this problem, building on SOM modeling work I have done for boreal forests and peatlands. In this approach, annual litter fall is deposited into a litter cohort. This cohort then loses mass, with its decomposability declining linearly with mass lost

$$\frac{dm}{dt} = -k(m) \cdot m = -\left(k_0 \frac{m}{m_0} \right) m$$

$$m(t) = \frac{m_0}{1 + k_0 t}$$

$$(1)$$

where m_0 is the litterfall, and k_0 is the initial mass loss rate for this tissue. This approach was generally successful in modeling SOM accumulation over millennia in peatlands, where annual cohorts are well-stratified. However, for forested ecosystems, litter does not remain stratified, and, when root litter inputs are considered, doesn't even begin that way. To account for this, the litter cohorts (combined above- and below-ground) will have a prescribed initial distribution, and will disperse/diffuse through the soil profile with time. Since modeling actual diffusion of SOM would involve so many unknowns (for which there are so few data) it will instead be prescribed in what may be a reasonable form. The function I am currently exploring for the SOM profile is the gamma distribution (Fig. 1a)

$$f(z; a, b) = \frac{z^{a-1} e^{-z/b}}{b^a \Gamma(a)}$$

$$(2)$$

where z is depth, and a and b are parameters. b corresponds to the decay in SOC content down the soil profile, and a relates to the skewness of the distribution. Combining these two ideas (decomposition and dispersion), the SOM would be described by a collection of annual cohorts with the following mass distribution (Fig. 1b)

$$m(z, t; a, b) = \frac{m_0}{1 + k_0 t} \cdot \frac{z^{a-1} e^{-z/b}}{b^a \Gamma(a)}$$

$$(3)$$

The total mass of any annual cohort would be given by integrating this over the depth profile and would be as in equation (1). The total SOM at any depth would be given by adding all the cohort contributions at that depth. Time evolution of the SOM distribution will be generated by making a and b functions of time.

This approach is mathematically tractable, and can be explored in very simple models initially. The model will generate profiles of SOM, decomposition, CO_2 production, and can easily be 'labeled' to generate $\Delta^{14}C$ values for SOM and CO_2 production, all of which can be tested against observation.

Carbon Exchange by an Old-Growth Hemlock Forest in the Summer of 1999: Eddy Covariance Data Compared to Model Predictions

J. Hadley and E. Huber

We measured carbon exchange near the NE corner of a ≈ 200 year old hemlock stand using eddy covariance during twelve days in mid-summer 1999. Wind was primarily from the SW, or from the main part of the hemlock stand, during 6 to 12 hours in each of three days and four nights. During these periods the average measured nocturnal ecosystem respiration (R_e) was about 4.8 μmol m^{-2} s^{-1}. Adjustments for CO_2 storage during calm periods raised this to about 6.2 μmol m^{-2} s^{-1}. An ecosystem carbon exchange model estimated R_e at about 7.3 μmol m^{-2} s^{-1} during these periods, or 17% above the measured value. An overestimate of surface soil water content could explain some of this difference. Soil water in the top 5 cm of soil was unusually low at the beginning and end of eddy covariance measurements, but two small rain events occurred in the interval, and the model estimate of soil respiration was very sensitive to surface soil moisture. Soil respiration was about 65% of estimated R_e. Overestimates of leaf area or sapwood volume could also have contributed to the apparent 17% model overestimate of R_e.

38

cohort depth distribution
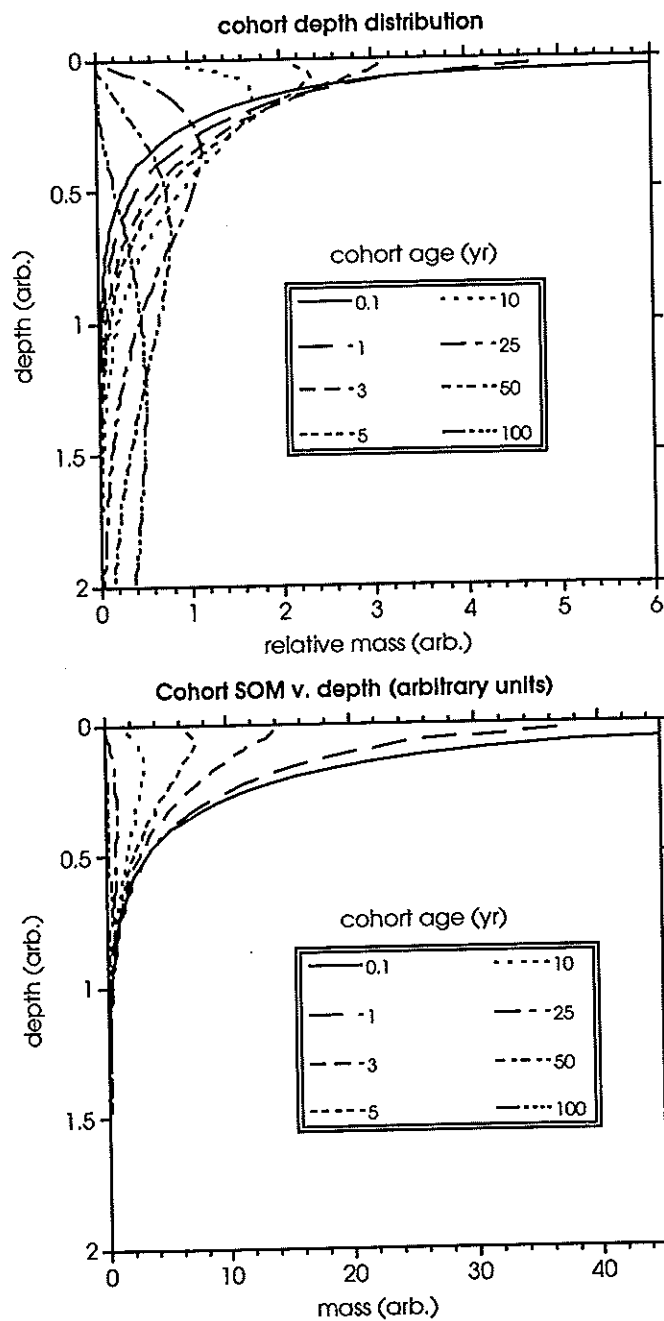
Cohort SOM v. depth (arbitrary units)

Fig. 1 – (a) Depth distribution of SOM annual cohorts, all normalized to the same mass. As cohorts age, their distribution flattens and the peak moves down the soil profile. (b) As for (a), but with declining cohort mass taken into account. These are only exploratory figures and not meant to represent any particular soil profile.

Frolking

Eddy covariance showed that R_e was higher in the hemlock forest than in surrounding hardwood forests. During the twelve-day measurement period, R_e was above 5 μmol m^{-2} s^{-1} during 46 % (19 of 41) half-hourly nocturnal periods with wind from the SW quadrant and adequate turbulence for eddy covariance measurements. In contrast, R_e was above 5 μmol m^{-2} s^{-1} only 7% of the time (6 of 82 measurements) with other wind directions. Average R_e with SW wind was more than twice Re with wind from the SE and NW quadrants (Fig. 1, p< 0.01). Average R_e during periods of NE wind was intermediate (3.8 μmol m^{-2} s^{-1}), but this included two of three extreme outliers in the data set. Without these points, R_e from the SW quadrant was over twice R_e from all other directions.(p≤ 0.002). Wind speed, momentum flux, air temperature and time of night all had small effects on R_e, but with these accounted for statistically, average R_e from the SW was still higher than from any other direction, and was greater than for SE and NW at p< 0.05.

During daylight, eddy covariance measured average C uptake of the hemlock stand at 6.3 μmol m^{-2} s^{-1}, but the carbon exchange model predicted only 5.0 μmol m^{-2} s^{-1}. The difference between measured and modeled C flux in the daytime (1.3 μmol m^{-2} s^{-1}) was very close to the nighttime difference, so an overestimate of R_e could explain both differences. Weighting the average day and night fluxes by the length of light and dark periods (≈14 and 10 hours) gave an average measured C uptake of 1.1 μmol m^{-2} s^{-1} (1.14 g m^{-2} d^{-1}) and a very small model-estimated C release of 0.09 μmol m^{-2} s^{-1} (0.09 g m^{-2} d^{-1}).

The Forest Vegetation of Cape Cod: a Regional-Historical Analysis

J. Harrod, D. Foster, G. Motzkin, B. Hall and R. Eberhardt

Our study documents changes in land use and forest cover in Cape Cod, MA over the past 400 years and evaluates influences of historical land use, regional position, and geologic substrate on modern forest composition and structure at landscape to regional scales. Pollen and witness tree data suggest that the Cape was largely forested

and that pitch pine and oaks were the most abundant trees at the time of European settlement in the 17th century. Fuelwood cutting and land clearance led to a rapid loss of forest cover; by the 18th C, wood shortages and severe soil erosion occurred in several towns. A landcover map from the mid-19th C shows the Cape as 49% forested, with most areas near the coast cleared and large patches of forest remaining in the interior (Fig. 1). Forest cover increased following farm abandonment and afforestation efforts, exceeding 65% in 1951, but has since decreased due to residential and commercial development, falling below 50% by 1990.

Our analysis of the modern forest vegetation, based on 270 plots, indicates that Cape-wide vegetation patterns reflect historical land use, geologic substrate, and regional position. Several species show strong spatial variation, with mesophytic trees and vines most abundant on the inner Cape and early-successional shrubs and grasses most abundant on the outer Cape (Fig. 2). Within landscapes comprised of single geologic substrates, history of past land use is the principal factor driving compositional patterns (Fig. 3). While 400 years of land use have dramatically transformed the Cape's land cover and strongly influenced distributions of individual species, modern canopy composition is strikingly similar to that inferred from 17th century witness tree data.

Differential Responses of Trees to Drought During Ontogeny in New England: a Species-By-Ontogeny Interaction

J. -S. He and F. Bazzaz

We developed a framework for scaling seedling responses to mature trees combining both environmental and ontogenetic differences between seedling and adults. We investigated how radial growth of juveniles and mature trees differ in responses to drought in temperate tree species in New England. Saplings and mature trees of four species, which ranked according to increasing shade-tolerance (successional position) as paper birch < red maple <yellow birch <sugar maple, were sampled in well drained Canton loam soil at Harvard Forest.
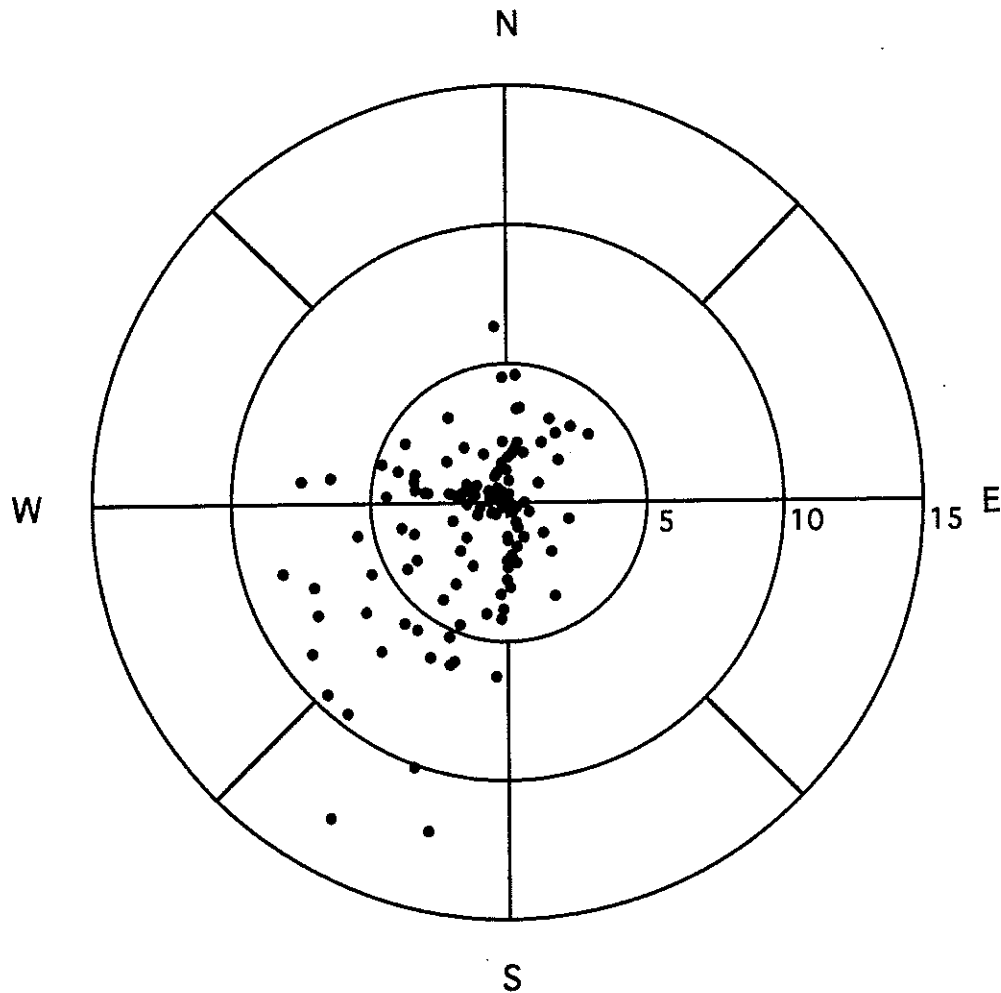
Figure 1. Measured ecosystem respiration (μmol m^2 s^{-1}) on the radial axis versus wind direction during nocturnal eddy covariance measurements. Data were collected above the canopy at 29 m height near the northeast corner of the old-growth hemlock stand between July 25 and August 6, 1999. Each point represents a single measurement over a 30-minute period. Three extreme outliers with carbon uptake rates near 20 μmol m^{-2} s^{-1} with north and northeast winds are not shown in order to show greater detail for the remaining points.

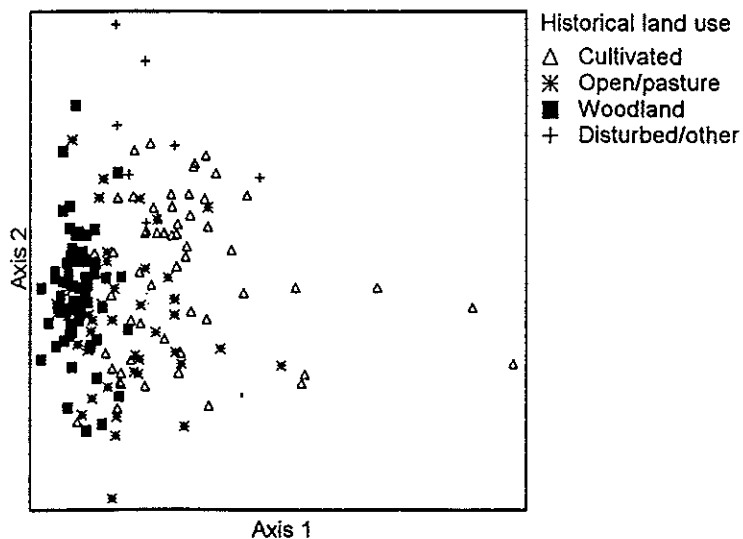Figure 1. Historical changes in forest cover (dark areas) on Cape Cod. 1830-1848 cover is based on town plans and USCGS maps; 1951 and 1990 cover are based on aerial photographs.

1830-1848   1951   1990

Figure 2. Regional variation in abundance of three species in 1999 forest plots: the mesophytic tree Acer rubrum, the grass Deschampsia flexuosa, and the dwarf shrub Arctostaphylos uva-ursii.

Acer rubrum   Deschampsia flexuosa   Arctostaphylos uva-ursii

Figure 3. Detrended correspondence analysis (DCA) ordination of species cover in 1999 forest plots from the outwash plain of Cape Cod. First axis scores reflect compositional differences between historical woodlands and more intensively disturbed areas. The second axis reflects a regional gradient from inner to outer Cape.

Historical land use
△ Cultivated
✳ Open/pasture
■ Woodland
+ Disturbed/other

Axis 2

Axis 1

Harrod et al.

Mature trees experienced differential ring-width reduction during four severe drought periods occurring from 1957 to 1995. Except for 1957, the four species have not any significant difference in their relative changes in radial growth during drought, but their relationships between ring-width index (RWI) and monthly Palmer Drought Severity Index (PDI) were varied. The late successional species (sugar maple) and mid successional species (yellow birch) had significant positive correlation with several monthly PDI in current and previous years. In contrast, early successional species (paper birch) and mid successional species (red maple) showed no significant positive correlation with monthly PDI in current or previous year. All saplings of all species exhibited significant growth reduction during 1995 drought, and showed significant interspecies difference. A relative change in radial growth of a late successional species (sugar maple) was more significant than that of the other 3 species in saplings during drought 1995 (Fig. 1). No saplings of the species showed positive correlation between RWI and monthly mean PDI of previous year. A three-way (species × ontogeny × sites) ANOVA analysis showed that the differences between saplings and mature trees in paper birch and sugar maple were significant, showing a species-by-ontogeny interaction. The result that saplings of paper birch had a less, and saplings of sugar maple had a bigger growth reduction than mature individuals suggested there is an ontogenetic shift as saplings grow to mature individuals.

Atmospheric Reactive Nitrogen at Harvard Forest: Measurements in Progress

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

Semi-continuous measurements of nitric acid (HNO_3) and nitrogen dioxide (NO_2) began at the Harvard Forest Long-Term Ecological Research site in August 1999. A dual-channel tunable diode laser absorption spectrometer (TDLAS) provides the high sensitivity (100 ppt) and fast time response (1 second) needed to record ambient variations and deposition rates by the eddy covariance method (for instrument details, see Horii *et al.* 1999). The new measurements augment the existing suite of trace gas concentration and flux measurements at the site and facilitate the detailed study of reactive nitrogen (NO_y) speciation and effects on ozone (O_3) production over seasonal and annual time scales. The measurements will continue for at least a year, providing the necessary data to assess the relative importance of HNO_3 deposition as a sink for tropospheric reactive nitrogen compared to NO_2 and Peroxyacetylnitrate (PAN). A separate abstract by Munger *et al.* (2000) presents PAN measurements. Monitored species at the site include NO_y and O_3 concentrations and dry deposition fluxes, NO_x (NO + NO_2) and PAN concentrations, non-methane hydrocarbons, and other tracers of anthropogenic pollution such as CO, CO_2, CFCs, and SF_6.

Deployment of the TDLAS instrument for unattended, continuous, outdoor operation in all seasons represents a significant breakthrough in the use of what was once a laboratory-based technique. TDLAS instruments have been used successfully at field facilities where air samples may be drawn into an indoor laboratory, outdoors for short measurement campaigns in fair weather, in mobile laboratories for limited periods, and on aircraft. The dual TDLAS at Harvard Forest has been installed in two weatherproof, temperature-regulated enclosures on the top two stages of a scaffolding tower, roughly 100 m from the main EMS tower. Maintenance includes bi-weekly retrieval of data and transport of 60 liters of liquid nitrogen to the site in order to cool laser diodes and detectors, periodic replacement of compressed nitrogen gas cylinders, and occasional refilling of trace gas reference cells. Throughout the fall season, the primary elements of the system have continued to function at the expected sensitivity levels. Work continues during the winter and spring of 2000 to reduce data dropout periods, and increase concentration and flux data coverage for both HNO_3 and NO_2.

A detailed comparison of TDLAS and slow Photolysis/O_3-Chemiluminescence NO_2 measurements is currently being conducted. This will include measurement of the Photolysis/O_3-Chemiluminescence reference gases by the TDLAS to crosscheck calibration values. Analysis of continuous 1-second NO_2 data from the TDLAS instrument will then be analyzed with 8 Hz vertical winds from the sonic anemometer to produce dry

Figure 1. Relative (%) changes in radial growth of four species from predrought to 1995 drought. Error bars represent 1SE of the mean. The significance between saplings and mature trees (Scheffé *post hoc* comparisons, * p< 0.05) are shown above each column pair. Columns with a same letter in each group (mature trees and saplings) are not significantly different at *p*<0.05, and with a different letter are significantly different at *p*<0.05 (Scheffé *post hoc* comparisons).

He and Bazzaz
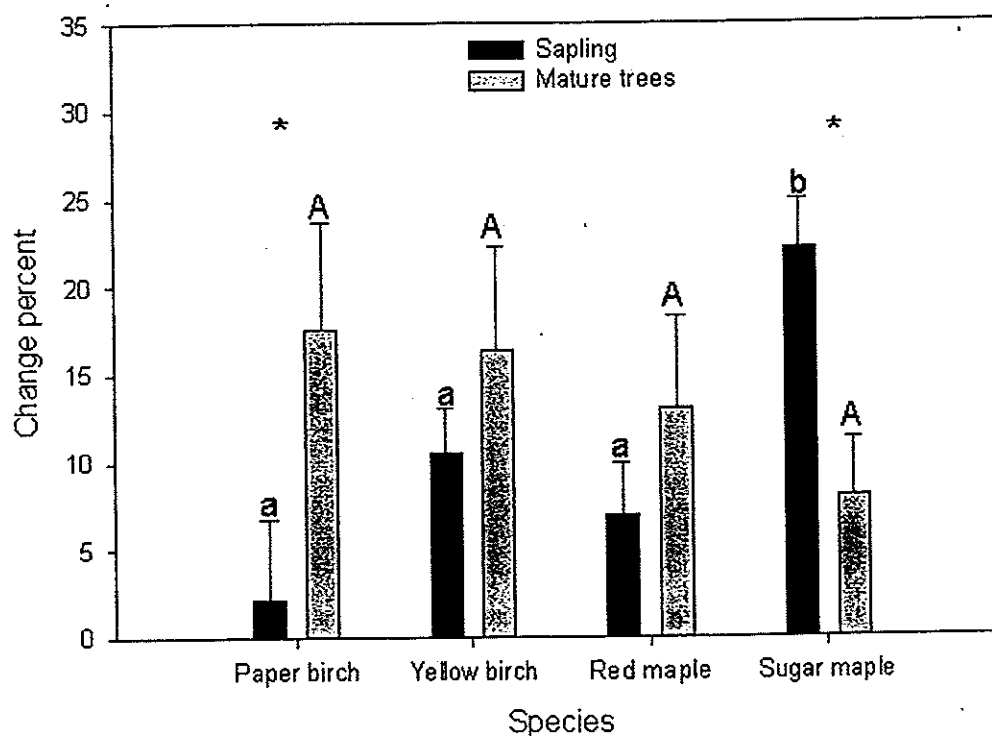
deposition flux values. The technique will then be extended to HNO₃ measurements.

Figures 1 and 2 show examples of HNO₃ and NO₂ spectra from the dual TDLAS obtained during the fall at Harvard Forest. The unambiguous detection of the particular species is evident in the match between the measured spectra and the non-linear least squares fits to tabulated spectral parameters. Longer time-averaged spectra are presented to show high signal-to-noise examples, but the usual mode of operation uses a fast spectrum accumulation time of 1 second.

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.

Munger, J. W., C. V. Horii, S. C. Wofsy. 2000. Biogenic hydrocarbons and nitrogen oxides: A forest atmosphere interaction with implication for regional air pollution, 11ᵗʰ Annual Harvard Forest Ecology Symposium Abstracts.

removed, as well as environmental protection features to be applied during the operation. The permit also requires a map depicting the spatial extent of harvest. These permits provided a data source for our study, which seeks to depict the extent and pattern of harvest as a form of disturbance in the 19-town North Quabbin region (168,300 ha). Harvest permits were reviewed and tabular and spatial data were captured on each operation since 1984.

Over the course of 16 years, preliminary data analysis indicates: 1,992 commercial harvests; average area = 16.8 ha (maximum = 338.7 ha, minimum = 0.15 ha, sd = 19.1 ha). During this time period, commercial harvest covered 33,404 ha (an average of 2,091 ha/year, in 137 operations), representing 23.3% of all forest in the north Quabbin region (Fig. 1). During this time, 3,349 ha had been harvested more than once. Mean harvest intensity was 44.8 m³/ha (7.7 Mbf/acre).

We intend to continue capturing these data over time, and to further analyze data looking for landscape patterns of this disturbance, as well as where this disturbance is not happening. These data contribute to an improved understanding of ecosystem dynamics, and further could be used in studies of carbon flux in this landscape.

Timber Harvest as a Form of Disturbance in the North Quabbin Region

D. Kittredge and D. Foster

In addition to numerous sources of natural disturbance acting on the forested landscape of southern New England, the commercial harvest of timber creates disturbance effects by removing parts of trees, reducing stand density and elevating light levels, disturbing mineral soil, and altering stand structures. Knowledge of the extent to which this form of disturbance occurs, and the typical size, frequency, intensity, and pattern of such disturbance, will contribute to an improved understanding of ecosystem dynamics in this forested region.

The commercial harvest of timber (i.e., 25 Mbf (59 m³) or more from an operation) is regulated in Massachusetts through the Forest Cutting Practices Act. An approved permit is required to conduct such an operation. These permits require information on the volume of wood

Assessing the Indirect Consequences of the Hemlock Woolly Adelgid: Ecosystem and Vegetation Response to Hemlock Logging

M. Kizlinski, D. Foster and D. Orwig

Hemlock woolly adelgid (HWA) (*Adelges tsugae*), an exotic aphid-like insect from Japan, was introduced to southern Connecticut in the mid-1980s and has since spread to central Massachusetts and continues to move northward. With no effective native predators or host resistance, HWA has left thousands of hectares of dead or dying eastern hemlock (*Tsuga canadensis*) forest. Landowners are now required to make management decisions regarding the fate of their hemlock, decisions that have not been necessary in the past. The option of logging, either before the arrival of HWA or during the early stages of infestation, presents a series of questions that have not been formally addressed. Eastern hemlock has
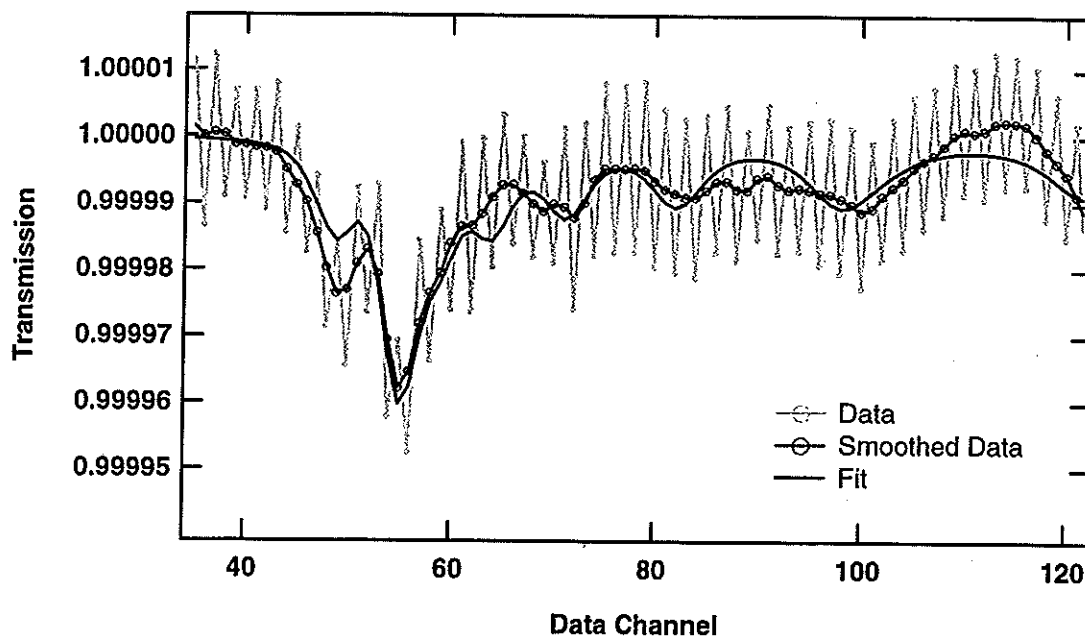
Figure 1. TDLAS HNO_3 spectrum, 1721.98 cm^{-1} to 1722.2 cm^{-1} acquired at Harvard Forest 8 October 1999. 4 hours worth of 15-second spectra have been co-averaged and ratioed against an averaged background spectrum. The fit corresponds to 345 ppt HNO_3. The sawtooth pattern in the unsmoothed spectrum does not significantly alter the retrieved concentration and is an artifact of the long average.
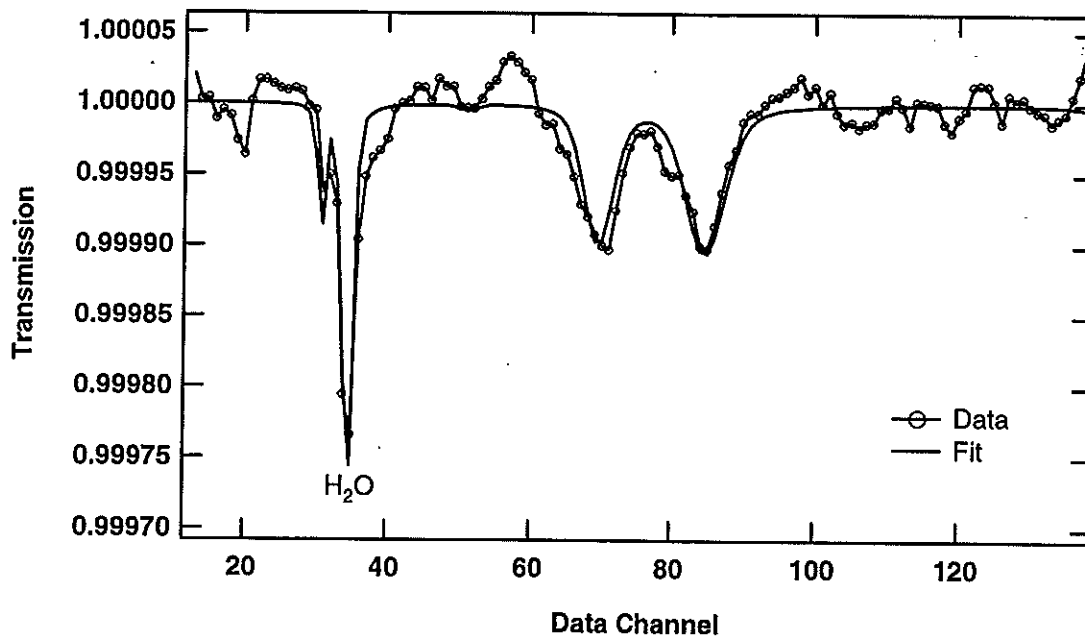
Figure 2. TDLAS NO_2 spectrum, 1593.1 cm^{-1} to 1593.5 cm^{-1} acquired at Harvard Forest 19 October 1999. 30 1-second spectra taken over the course of an hour have been co-averaged and ratioed against an averaged background spectrum. The fit corresponds to 514 ppt NO_2. The H_2O feature on the left side of the spectrum indicates a small difference between ambient water vapor during the background and signal spectra accumulation intervals. The difference is easily taken into account by including H_2O in the fit.

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timber harvest, 1984-1999
North Quabbin Region

8   0   8   16   Miles
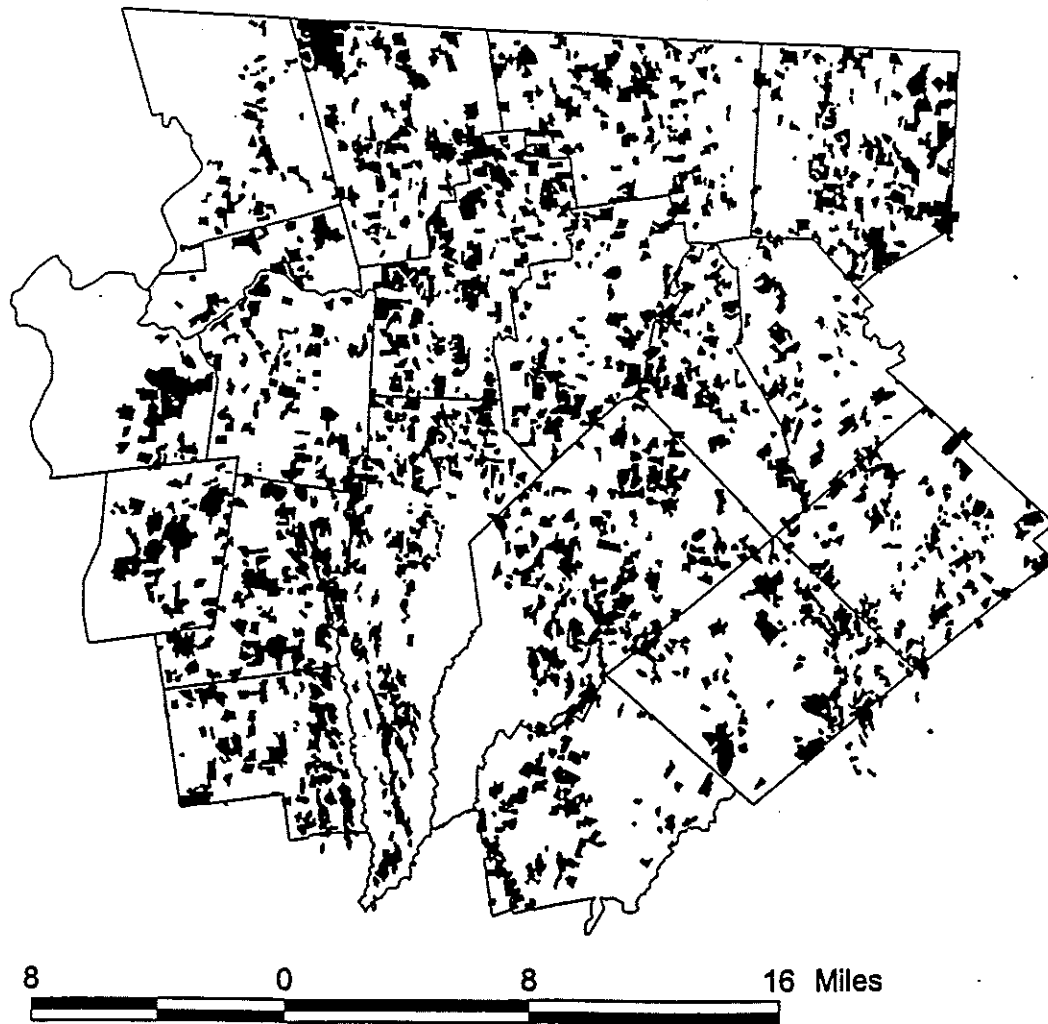
Tot84_99.shp

Study_t.shp

where Tot84_99.shp=
timber harvest locations
(n=1,992; 82,541 ac.)

Study_t.shp=
19-town study area

data: Harvard Forest, Petersham, MA

Figure 1.

not been a commercially valuable species, so information on the silviculture and management of the species and the impact of logging on ecosystem and vegetation dynamics is neither extensive nor complete. This project will address these issues, which are growing in importance as more and more hemlock stands are logged in response to HWA.
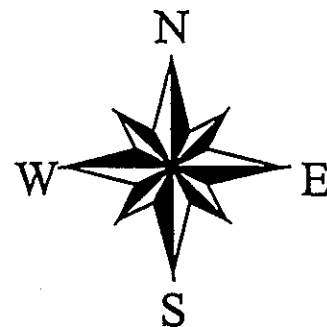
Fifteen logged stands were chosen for this study to cover the range of ages and successional states since HWA arrival and hemlock logging commenced about 15 years ago. Site selection was limited to those locations that were dominated by hemlock, were heavily logged, and are located on comparable soils. These sites represent 13 years of post-logging succession and ecosystem recovery.

Vegetation plots have been established in eight stands and data has been collected on pre-harvest stand composition and basal area, intensity of harvest, and sapling (>2 cm diameter at breast height (dbh)) density. This summer, these plots will be revisited and data on seedling and herbaceous cover will be collected. Ecosystem parameters to be measured this summer include nitrogen (NH_4^+ and NO_3^-) availability and mineralization rates, decomposition, pH, bulk density, moisture, and soil organic matter content.

By comparing the results of this study to other ongoing HWA work at the Harvard Forest, comparisons can be made between the effects of logging and 'natural' mortality of hemlock stands. Using this information, better informed management decisions can be made regarding newly infested stands, as well as those areas that face imminent infestation.

Variation in Vertical Activity of White-footed Mice in Oak Forest

C. Langtimm

A third year of study of the climbing patterns of white-footed mice, *Peromyscus leucopus*, revealed substantial annual variation in the vertical activity of this species in understory trees and shrubs. The proportions of arboreal captures at a moist site on Prospect Hill was 59% and 64% in July and September of 1997, but in June and August of 1998 proportions dropped

below 50% to 37% and 44%, and then dropped even further in June and August 1999 to only 14% and 23%. Estimates of population abundance were comparable in 1997 and 1999 and do not explain the differences in proportions between those years. 1999, however, was an extremely dry year compared to the previous years and may have had an impact on prey items accessible to mice in shrubs and trees. Arboreal captures at a more xeric site in Tom Swamp were similar in 1998 and 1999 (29% and 30% in June and August 1998 and 25% and 33% in June and August 1999), supporting the likelihood of site-specific differences in climbing activity for the species. Limited trapping in the crowns of canopy oak trees continued to document the presence of white-footed mice at higher levels of the forest, although fewer individuals were captured during the summer of 1999 than in the previous two years. The documented seasonal, annual, and site-specific variation in climbing activity of this species demonstrates the behavioral plasticity of white-footed mice to utilize all levels of the forest. This plasticity could have important implications for our understanding of their role in the epidemiology of Lyme disease, gypsy moth outbreaks, and songbird nest predation.

Does Carbon Quality Limit Soil Carbon Loss Due to Warming?

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

The soil warming experiment, designed to investigate the effects of a 5°C increase in temperature on soil processes, has been running since the summer of 1991. Over the past 9 years, CO_2 fluxes, which represent both root and microbial respiration, have been measured from April to November in heated, control, and disturbance control (DC) plots. Extensive sampling of the soil organic and mineral horizons was undertaken in 1999 to investigate soil carbon stocks. Through the examination of these data, along with the application of our knowledge of carbon cycling dynamics across ecosystems, we are refining our hypotheses of soil responses to warming.

Long-term pattern of soil respiration in response to warming – During the first five years warming increased the average annual rate of soil respiration by about 20%. After 1995, the CO_2 efflux differences between the heated plots and the disturbance controls began to decline until there were no measurable differences in 1999 (Fig. 1).

Relative effects of warming on root and microbial respiration - In a separate warming experiment, designed to investigate the relative contributions of root and microbial respiration to total soil respiration, we have consistently observed that about 20% of CO_2 efflux is contributed by root respiration, and about 80% of CO_2 efflux is the product of microbial respiration.

Estimating carbon losses from the soil in response to warming – Combining information from the CO_2 efflux measurements and the study to separate root from microbial respiration, we have estimated that 934 g C/m^2 have been lost from the soil over the first 9 years of the experiment (Fig. 2).

Comparison of soil carbon stocks in heated and DC plots in 1999 allows us to quantify carbon loss from the soils directly. Thus far we have completed this analysis for the organic horizon, and from these direct measurements we calculate a loss of carbon from the O horizon of 260g C/m^2. The carbon lost from this horizon is about 20% of its total stock.

A two-pool soil carbon concept and the potential for positive feedback – Based on results from the soil warming study, we hypothesize that there are at least two pools of soil carbon at the Harvard Forest: an easily decomposable pool rich in relatively simple carbon compounds that are readily accessible to microorganisms; and a difficult to decompose pool made up of complex ring compounds and otherwise lignified carbon. The decline in the difference between CO_2 released from the heated and DC plots in the years following 1995 may represent the exhaustion of the readily accessible pool of carbon in the heated plots. Our study causes us to suggest that while CO_2 efflux from mid-latitude forests will lose carbon in response to warming, a long-term and large positive feedback response to warming is not likely.

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_4NO_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_4NO_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_4NO_3 additions. Plots were established in two forest stands, a red pine plantation and a mixed hardwood stand, and are located in the Prospect Hill tract of Harvard Forest.

Increased soil water nitrate concentrations have been measured in the pine high N plot since 1989 and in the hardwood high N plot since 1995. In 1999, pine high N mean annual nitrate concentration was 20-fold greater than pine control; hardwood high N mean annual nitrate concentration was nearly 10-fold greater than control. Green foliage N content of the dominant species has increased dramatically with nitrogen treatments. Percent N in foliage from the high treatment plots has been measured at 80% and 25% greater than control foliage for red pine (pine stand) and black oak (hardwood stand), respectively. Changes in foliar biomass have not been significantly different overall.

Data currently under analysis include aboveground woody biomass, root biomass, root nitrogen and carbon content, soil bulk density, fungal and microbial biomass. Canopy access towers were installed in 1999 and *in situ* photosynthesis measurements are planned for the 2000 field season.

CO₂ efflux percentage increase
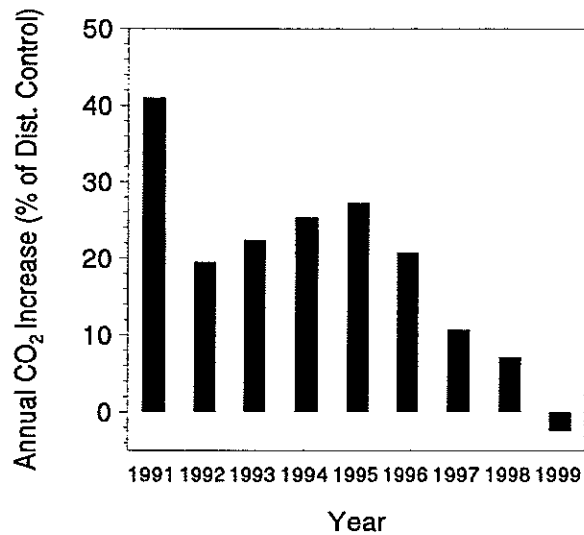
Figure 1. Annual increase in CO_2 efflux of the soil warming heated plots: percent difference when compared to disturbance control plots ((H-DC)/DC*100).

Cumulative Δ carbon released
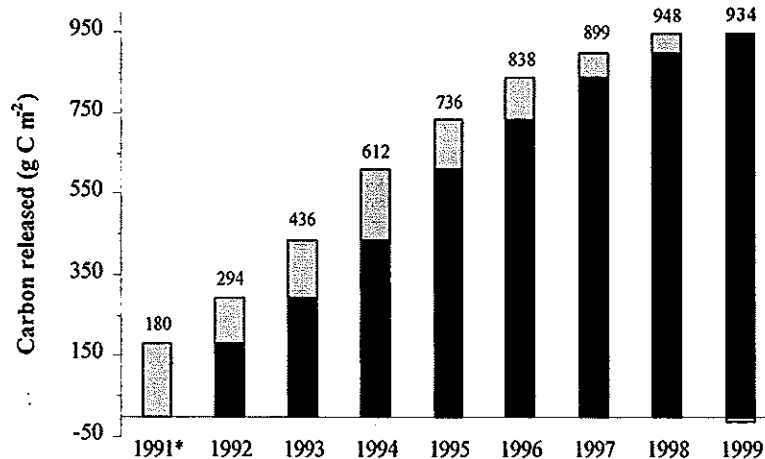
Figure 2. Cumulative difference in carbon released as CO_2: heated plots as compared to disturbance control plots, multiplied by 0.80 to represent the microbial component of respiration. Numbers on bars represent total CO_2 released through the year represented, gray areas indicate ΔC addition for that year .

*1991 value represents a partial year of sampling (June-December).

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Embolism Intolerance of Black Willow (*Salix nigra* Marshall)

P. Melcher, M. Zwieniecki and N. Holbrook

Parameters related to water transport properties of 3 year old potted black willow (*Salix nigra* L.) plants growing in a glasshouse located at Harvard Forest were studied from June to August of 1999 to address current issues surrounding embolism repair. It has been previously demonstrated in other species that the ratio of liquid to gas filled vessels changes diurnally, suggesting that refilling of cavitated vessels can occur during times when neighboring vessels are under tension. However, it is not clear if these "repaired" vessels reestablish complete hydraulic continuity with neighboring vessels (e.g., liquid-liquid contact across pit pores) making them truly "functional" in long distance water transport. We found that experimentally induced xylem sap tensions of 1.5 MPa reduced the hydraulic conductivity (k_h) by 50% for black willows. To investigate the potential of vessel refilling during times of tension driven sap flow we made concurrent measurements of stem specific k_h and leaf water potential (Ψ_L). No diurnal changes in stem specific k_h were observed. This is most likely a result of the fact that Ψ_L never reached values lower than 1.5 MPa throughout the day. The effect of air seeding (the minimum pressure required to force gas across the small diameter pit pores) on whole plant transpiration (measured using a balance) was determined by applying gas pressures across the main stems (base of plant) of intact potted black willows using pressure collars attached to a high pressure gas delivery system. We found that pressures less than 1.5 MPa across the pit-pore gas-water interface (applied pressure plus leaf balance pressure) had no effect on whole plant transpiration rates (Fig. 1); however, when the pressure across the air-water interface of the pit pores were greater than 1.5 MPa, transpiration was dramatically reduced followed shortly by leaf wilting and eventual leaf senescence. This indicates that the critical air seeding pressure is similar to tensions that reduce k_h by 50% and the non-restoration of the transpiration gives supporting evidence that embolism formation is catastrophic for black willow plants. This contrasts with recent observations that many species tolerate and repair cavitation on a diurnal basis. These findings give implications that different strategies for maintenance of the continuity of the hydraulic pipeline from soil to leaf exist and provide insight on issues surrounding evolutionary adaptations, plant distribution, and species sensitivity to drought.

Retrenching at the Harvard Forest DIRT Plots

P. Micks and K. Nadelhoffer

Our main focus on the DIRT experiment in 1999 was the accomplishment of major maintenance work on the two root-exclusion treaments first installed in 1990, along with the other experimental manipulations that comprise the DIRT project. In that year, we began a long-term study of the linkages between forest soil organic matter dynamics and inputs of above- and below-ground litter (DIRT: Detritus Input Removal and Transfer). The goal of the DIRT project is to assess how rates and sources of plant litter inputs control the accumulation and dynamics of organic matter and nutrients in forest soils over decadal time scales. Treatments 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), implemented in 1991, replaced O and A horizon material with B horizon soil, with normal litter inputs allowed to occur thereafter.

The most important finding from the first eight years of the project was the dominant influence of root inputs over above-ground litter inputs on soil respiration. Similar CO_2 efflux patterns were demonstrated in laboratory-incubated soils taken from the plots in the fifth year of treatments. Relative differences in CO_2 flux were proportional to aboveground litter inputs when
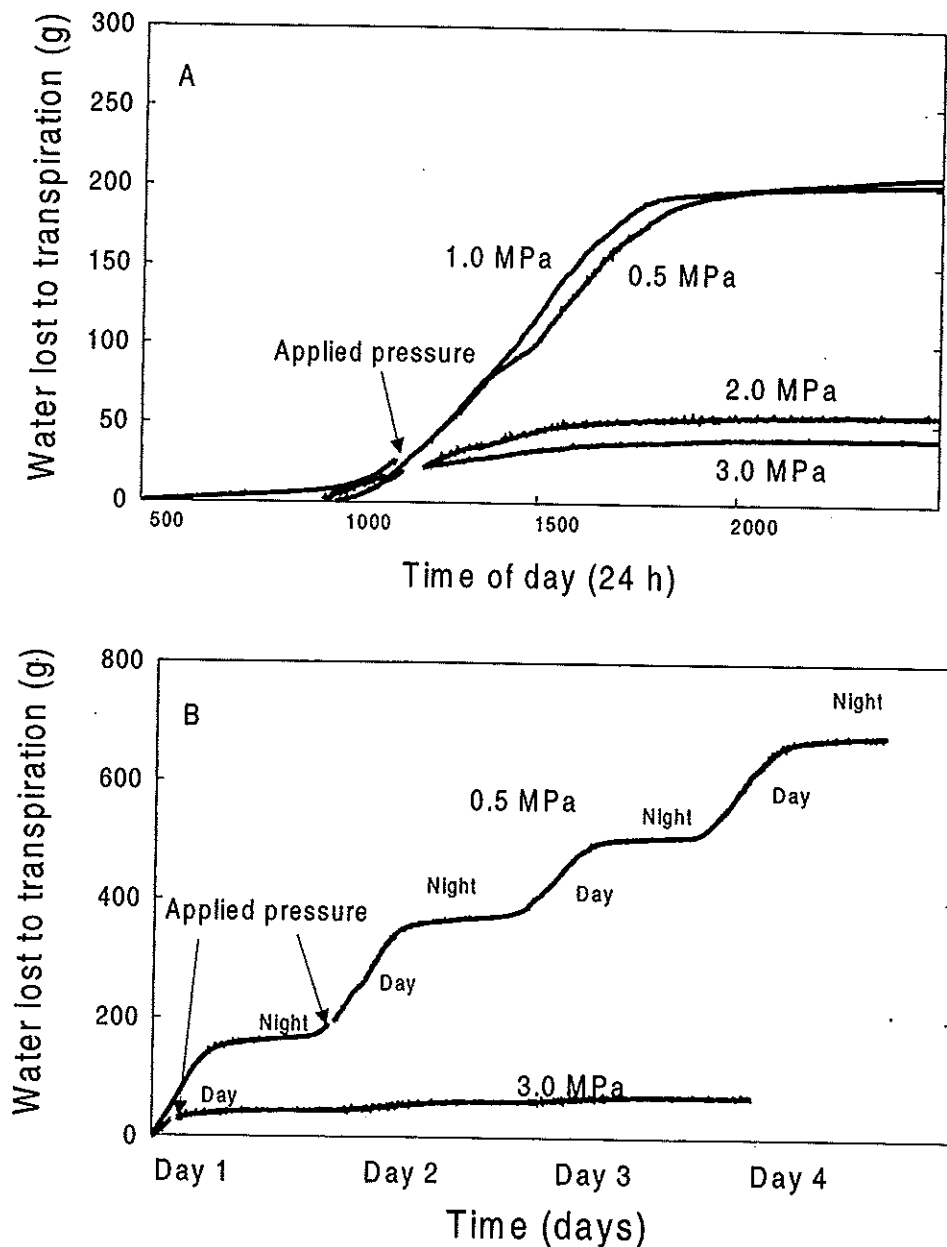
Fig. 1. Whole plant transpiration measured after applying pressures to the main stems of potted intact *Salix nigra* plants. (A) Data collected for a 24 h period, each line represents a different plant and pressure schedule. (B) The transpiration rate monitored for multiple days (for two pressures only). The values near the lines represent the estimated pressure experienced by the plant across the pit-pore gas-liquid interfaces (e.g., applied pressure plus covered leaf balancing pressure). Arrows indicate when pressure was applied.

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roots were intact, although by the eighth year these differences were less clear.

Because of concern that tree roots had reinvaded the root-excluded plots, in August of 1999 we undertook the major task of redigging the trenches around all of these plots and installing new root barriers. Trenches were dug to the original 1 m depth and the original rigid plastic barrier material was removed. We noted that in a few cases roots had penetrated the barrier, but most roots invaded by growing underneath the barrier, despite the fact that root density is very low at those depths in the DIRT study area. Trenches were relined with a combination of heavy-duty nylon-reinforced plastic and polyethylene sheeting, then backfilled with the excavated soil. We expect that retrenching will be necessary every 5-8 years. We anticipate continuing the DIRT experiment for many more years, and this work ensures that we will continue to gain valuable data about the long-term role of plant litter in forest soil organic matter dynamics.

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

Q. Min and K. Moore

Clouds and aerosols affect the forest light environment by enhancing diffuse PAR, or, in the case of optically thick clouds, reflecting most irradiance into the atmosphere. Our efforts are to integrate multiple existing data sets, including surface and satellite measurements (listed in Table 1), to develop a regional climatology of cloud, aerosol and ozone to be applied to forest-atmosphere energy exchange, and to improve satellite-based measurements. Combining various data sets for processing, we currently focus on two sites: Albany, NY the station with the longest record, and Harvard Forest where surface exchange and radiation are measured. Further, we have used one year's worth of satellite data (GOES 10, 1998) to study spatial and temporal effects of cloud and aerosol. Sample recent results are described below.

Optical depth of aerosol and cloud and its spectral dependence are important factors in the total short wave, PAR, and UVB irradiances.

Figure 1 is a six-year time series of aerosol optical depth at 415 nm and Angstrom exponent coefficient from MFRSR at the Albany site. 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. The annual cycle of optical depth for aerosol and thin cloud is evident in Figure 2 (upper); for overcast cloud cases, the mean cloud optical depth in 1995 (a drought year) was smaller than that of 1996.

An operational algorithm developed by Ineichen and Perez (1999) was used to derive a transmittance index (K) from the GOES-10 satellite for all of 1998. Figure 3 shows the comparison of the monthly mean transmittance index (K index) between Harvard Forest and Albany. Both sites show similar characteristic of aerosol seasonal variation, which is consistent with surface observation (shown in Fig. 1). However, under cloudy conditions the K index at the Harvard Forest is smaller before May than that at the Albany site, indicating thicker clouds over Harvard Forest than over Albany.

The spatial statistics of clouds, using the K index images from GOES to identify the cloud cluster areas over both sites, are shown in Figure 4. The left plot shows the statistics for all clouds, illustrating that large cloud systems with cloud cluster areas over $10^{\wedge}6$ km^2 have the same statistics over both sites, due to large-scale circulation. On the other hand, small-scale cloud systems are markedly different due to local circulations. For cloud cluster areas less than 1000 km^2, shown in middle and right plots, the statistics show reversed characteristics for thick and thin cloud cases over two sites.

Figure 5 shows the relationship between the atmospheric transmittance for the Harvard Forest pixel (GOES-10, 1998) and the CO_2 flux; this figure can be compared to Figure 2 of Moore and Fitzjarrald (this volume), which is based on surface measurements of atmospheric transmittance.

45

Reference: Ineichen P. and R. perez, Derivation of cloud index from goestationary satellites and application to the production of solar irradiance and daylight illuminance data, Theo. & Appl. Clim., in press, 1999.

Table 1. Locations of selected sites.

Location	Longitude& Latitude	Network	Data Availability
Albany, NY	73.82W 42.69N	QL, SUNYA	10/91 – present
Univ. Park, PA	77.92W 40.71N	QL, SUNYA	11/91 – present
Howland, ME	68.70W 45.20N	QL, SUNYA	10/91 - 04/96
Ithaca, NY	76.64W 42.39N	QL, SUNYA	10/91 - 09/95
Queensbury, NY	73.80W 42.71N	NASA, SUNYA	08/96 – present
Geneva, NY	77.02W 42.88N	UVB,CSU	1994 – present
Burlington, VT	72.86W 44.53N	UVB,CSU	1996 – present
Presque Isle, ME	68.04W 46.68N·	UVB,CSU	1995 – present
Harvard Forest, MA	72.18W 42.54N	NIGEC, SUNYA	Sum. 1991 -present
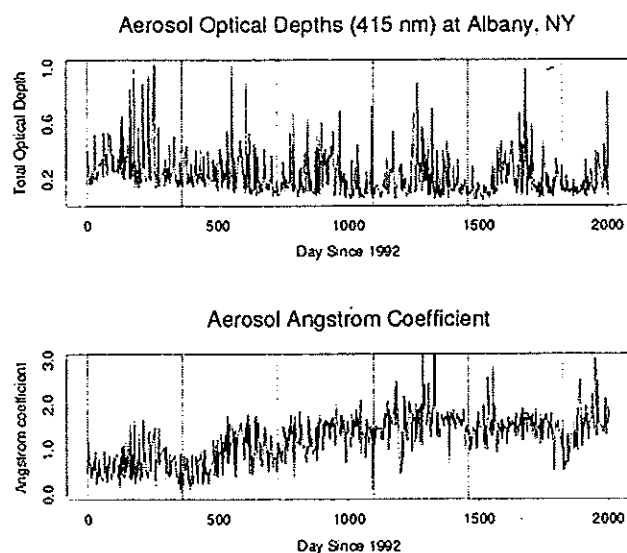
Figure1. Example time series of aerosol optical depth and angstrom coefficient (an indicator of particle size) for the Albany, NY station.
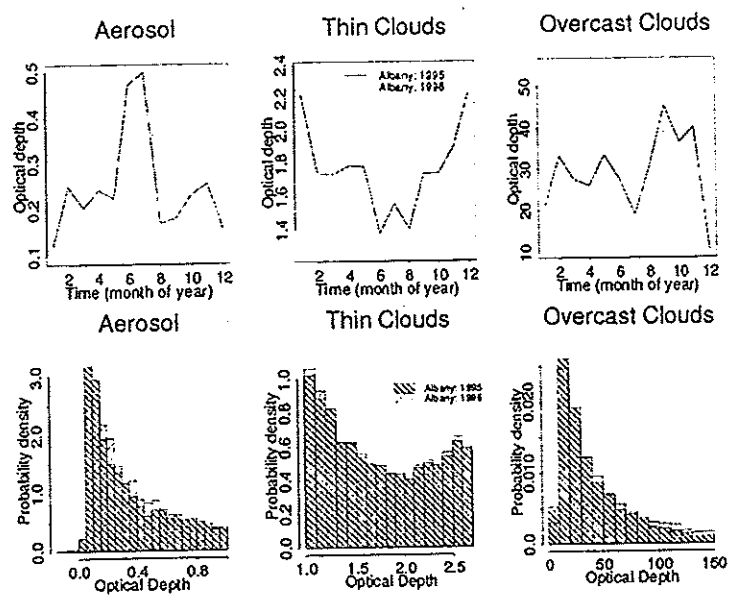
Figure. 2.Aerosol and cloud optical depths at the Albany, NY station for 1995 and 1996.
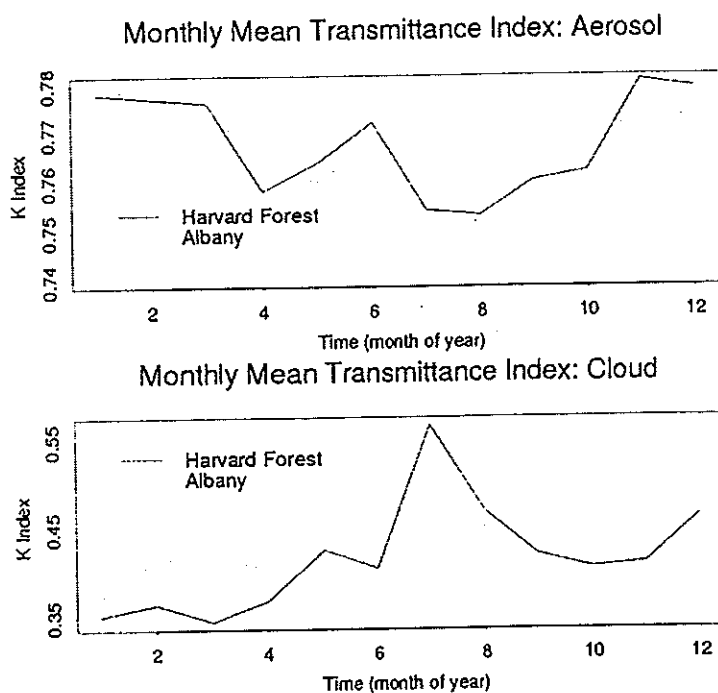
Figure 3. Monthly mean aerosol and cloud transmittances derived from hourly GOES-10 images for Harvard Forest and for Albany.

All Clouds **Thick Clouds** **Thin Clouds**
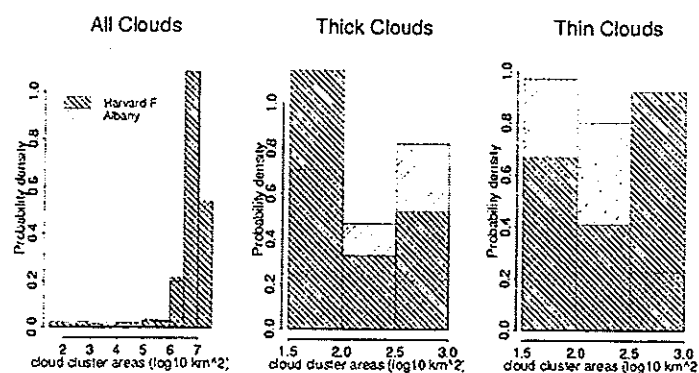
Figure 4. Cloud cluster areas around Harvard Forest and around Albany, NY, derived from GOES-10. Thick clouds have atmospheric transmittances of <0.4; thin clouds have transmittance 0.6-0.7.

Transmittance Index (GOES) vs. CO2 flux: 1998, HF
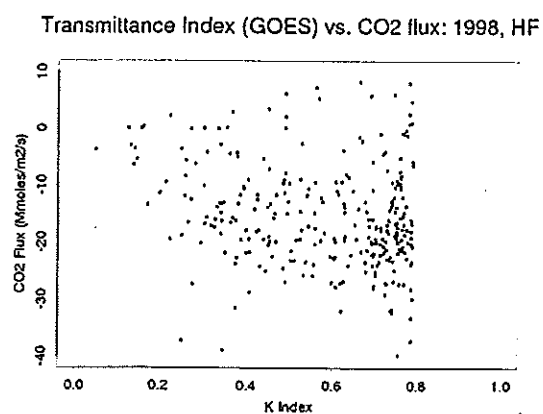
Figure 5. CO2 flux at Harvard Forest (1998 growing season, EMS tower) compared with atmospheric transmittance derived from GOES-10 .

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Ineichen P. and R. Perez. 2000. Derivation of cloud index from goestationary satellites and application to the production of solar irradiance and daylight illuminance data, Theo. & Appl. Clim. (In Press).

Effect of Diffuse Light on Canopy CO_2 Uptake

K. Moore and D. Fitzjarrald

Freedman *et al.* (2000) have recently shown that the presence of boundary layer clouds is associated with enhanced CO_2 uptake at the midlatitude deciduous Harvard Forest. While we noted a similar association in a boreal jack pine forest (Moore *et al.* 2000), in that case decreased C uptake on clear days was accompanied by water stress and stomatal closure, an effect generally not observed at Harvard Forest. This study explores the relationships among clouds, diffuse light, and net photosynthesis at Harvard Forest.

A multifilter rotating shadowband radiometer (MFRSR) was used to obtain time series of direct, diffuse, total and reflected radiation at Harvard Forest in central MA during the growing season of 1998. Diffuse fraction (fraction of total solar radiation represented by the diffuse component) was related to the clearness index or atmospheric transmittance (S/S_0) by an equation similar to those published from other locations (Fig. 1). Midday hourly eddy covariance CO_2 flux is optimal at atmospheric transmittances of 0.5 to 0.6, corresponding to diffuse fractions of 0.6 to 0.7 (Fig. 2). We have found that canopy light use efficiency (mole CO_2 uptake/mole photons) is linearly related to diffuse fraction; light use efficiency under diffuse fraction of 0.6 is twice that under clear skies (Fig. 3). The same relationships were found when the entire period 1992-1998 was studied, using the measured total solar radiation to derive the diffuse fraction, and invoking the solar transmittance-diffuse fraction relation found from the MFRSR.

A lumped-parameter model for C uptake (PnET-Day, Aber *et al.* 1996) was run, adjusting the canopy light penetration for the diffuse fraction. Using a database of regional global solar radiation to derive the regional variation in diffuse fraction, the modeled variation in C uptake was on the order of 20% in the Northeastern US. Ongoing work seeks to develop a regional climatology of diffuse radiation in relation to aerosols as well as clouds.

Aber, J. D., P. B. Reich, and M. L. Goulden. 1996. Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. Oecologia 106: 257-265.

Freedman, J. M., Fitzjarrald, D. R. 2000. Boundary layer clouds and vegetation-atmosphere feedbacks. J. Climate (In Press).

Moore, K. E., D. R. Fitzjarrald, R. K. Sakai, and J. M Freedman. 2000. Growing season water balance at a boreal jack pine forest. Water Resources Research 36: 483-493.

Biogenic Hydrocarbons and Nitrogen Oxides: a Forest Atmosphere Interaction with Implication for Regional Air Pollution

J. Munger, C. Horii and S. Wofsy

Urban centers in the northeastern U.S. are significant sources of nitrogen oxides (emitted as NO from internal combustion engines and industrial boilers, but rapidly converted to NO_2; $NO_x = NO + NO_2$). Nitrogen oxides are catalysts to produce ozone (O_3). Ozone concentrations in the rural atmosphere depend on how much NO_x has been emitted upwind, how efficiently the NO_x reacts to produce O_3, and how long it remains in the atmosphere before it is deposited. Much of northeastern U. S. is covered by oak forests, which emit isoprene, an extremely reactive hydrocarbon that serves as the fuel for NO_x-catalyzed production of O_3 but also contributes to formation of unreactive forms (peroxyacetylnitrate: PAN) that are transported long distances and to removal by formation of hydroxyalkylnitrates that are rapidly deposited (Munger *et al.* 1998). We previously determined that NO_x had a short lifetime against oxidation during summer in the northeastern U.S. region (Munger *et al.*, 1998), but were unable to estimate the relative fractions of NO_x that were stabilized as PAN and transported to remote areas where it could contribute to ozone formation and nitrogen deposition.
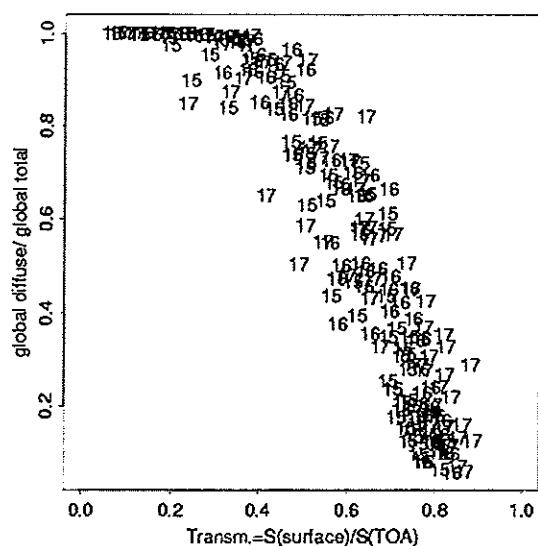
Figure 1. Midday diffuse fraction as a function of atmospheric transmittance, days 150-240, 1998. Numbers represent hour of the day, GMT.

midday 150 - 250 1998
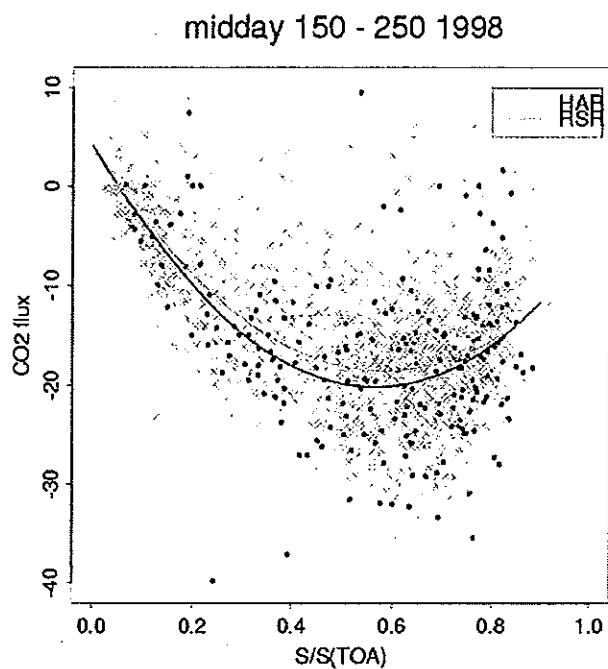
Figure 2. CO_2 flux in 1998 (dots) versus atmospheric transmittance obtained from the MFRSR ("RSR"). Also shown (crosses, HAR) are the CO_2 fluxes for 1992-1997 versus atmospheric transmittance obtained from the SUNY solar radiation instrument.

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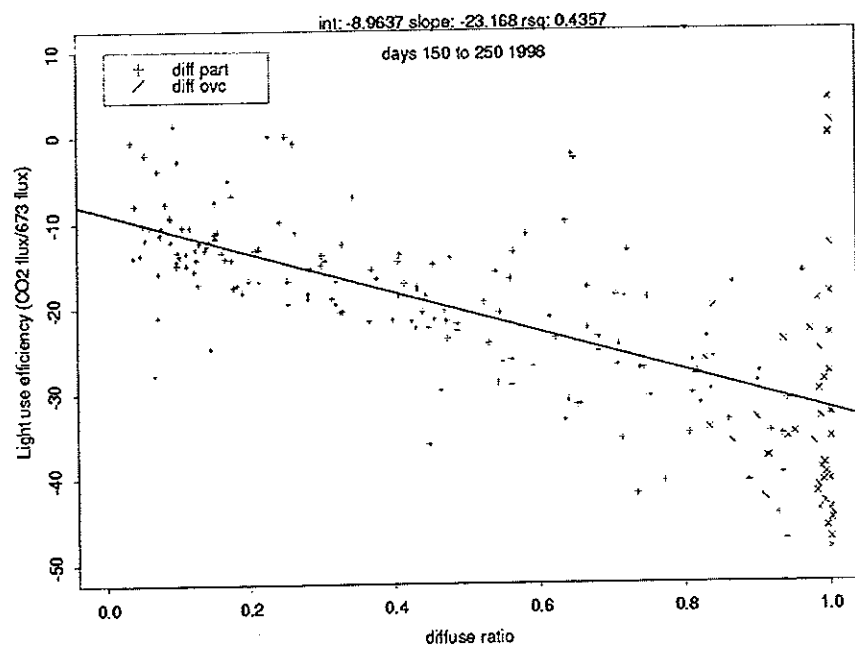
Figure 3. CO2 flux efficiency (mole CO2/mole of photons) versus diffuse fraction.

In August 1999 we installed new instrumentation to allow direct quantification of PAN and HNO_3 and to separately measure the fluxes of NO_2 and HNO_3 as well as continue the flux measurement of total nitrogen oxides (NO_y). Installation of the NO_2 and HNO_3 measurements is presented in a separate abstract by Horii *et al.* (2000). Here we discuss the first set of PAN measurements made at Harvard Forest (Fig. 1) and how NO_y speciation is influenced by isoprene (Fig. 2). Preliminary data for September 1999 show a wide variation in PAN concentrations (Fig. 1). High concentrations in excess of 1 ppb result from PAN production by active photochemistry in polluted air masses, but at the warm temperatures typical of September, the lifetime of PAN is only a few hours and its concentration declines to near zero when production ceases. Figure 2 illustrates the influence of isoprene emissions on NO_y speciation. On day 259 with low isoprene concentrations (and less insolation – not shown) NO_y is dominated by unreacted NO_x at fairly high concentration. Clean conditions with ppb levels of NO_x were observed on the following days. Beginning with day 262 (9/19) NO_y concentrations increase again, but a larger fraction is present as PAN and other forms that have were not measured during this period, which we presume are HNO_3 and organic nitrates. Continued measurements during the coming season will allow us to improve our understanding of the interaction between NO_x pollution and forest emissions that can either enhance rapid removal of NO_x to limit O_3 production or temporarily sequester NO_x for long-range transport and enhanced O_3 production in remote regions.

Munger, J. W., S-M. Fan, P. S. Bakwin, M. L. Goulden, A. H. Goldstein, A. S. Colman and S. C. Wofsy. 1998. Regional budgets for nitrogen oxides from continental sources. Variations of rates for oxidation and deposition with season and distance from source regions. J. Geophys. Res. 103: 8365-8368.

Tree Canopy Asymmetry at Forest Gap Edges

C. Muth and F. Bazzaz

Although plants are sessile organisms, they can forage for resources by growing towards areas with high resource availability and reduced competition. Presumably due to this morphological flexibility, tree canopies are rarely positioned directly above their stem bases and are often asymmetrical. To see if contrasts in light availability lead to the development of canopy asymmetry, we investigated the responses of tree canopies to the heterogeneous light environments at the edges of six experimental gaps. The gaps were created in 1986 and are located in a mixed hardwood forest in the Prospect Hill tract of Harvard Forest. For all gap edge trees greater than 5 cm dbh, canopy extent was determined in eight subcardinal directions around each trunk using a densitometer. Canopies and trunks were then mapped and their spatial distributions analyzed. The magnitude and direction of canopy displacement were calculated based on the direction and distance between each tree's trunk and its canopy center of mass. A clinometer was used to determine canopy depth on both the gap side and the closed forest side of each tree.

We found relatively large displacement values among the study trees. Trees on the north sides of gaps had greater relative canopy displacement than trees on the south sides of gaps. Subcanopy trees had greater relative displacement than canopy trees. There were also species differences in relative canopy displacement, showing a trend of decreasing displacement with increasing shade tolerance. The direction of canopy asymmetry was positively correlated with the direction of gap center (Fig. 1), suggesting some level of foraging precision among tree canopies. This foraging precision was greater for subcanopy trees than for canopy trees. Species also differed in foraging precision: *Betula lutea* was most precise, and *Fagus grandifolia* and *Quercus rubra* were least precise. In addition, canopy depth was significantly greater on the gap side of trees than on the forest side of trees. This asymmetry in canopy depth was greater for subcanopy trees than for canopy trees and greater for shade intolerant species than for shade tolerant species.

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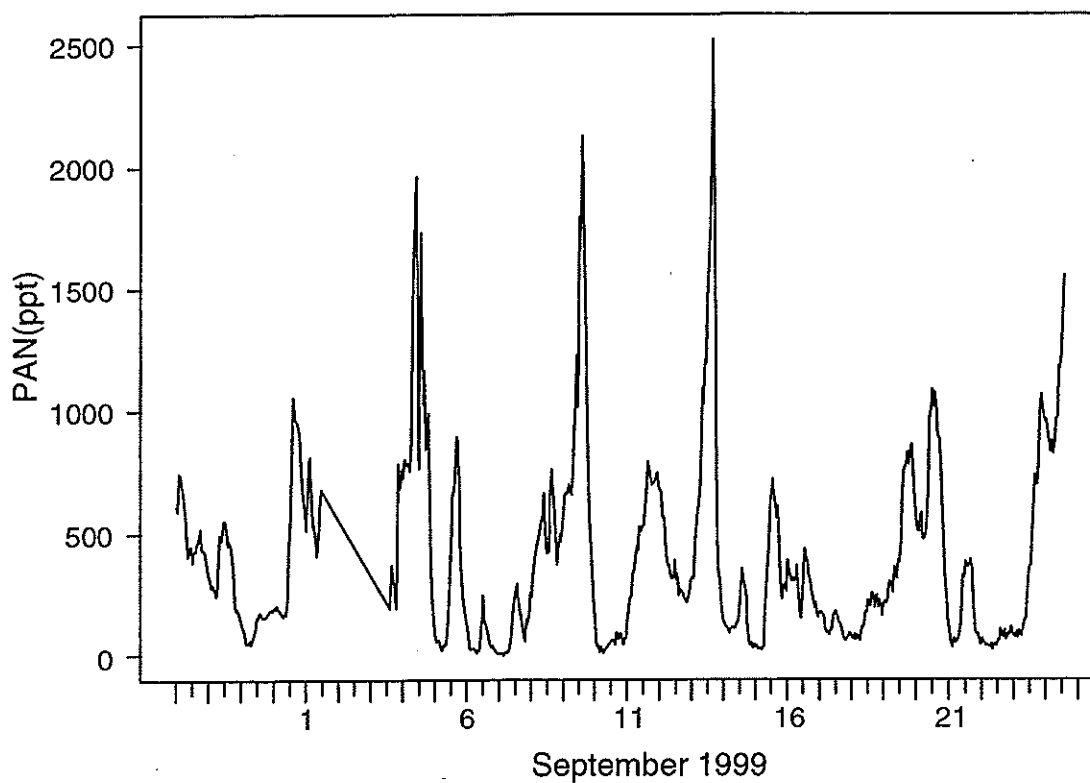
Figure 1. PAN concentrations during the month of September show periods of high concentration driven by active photochemical production in polluted air as well. The lifetime of PAN is very short at typical temperatures in September and the concentrations quickly decrease to near zero when the production of PAN is shut off.
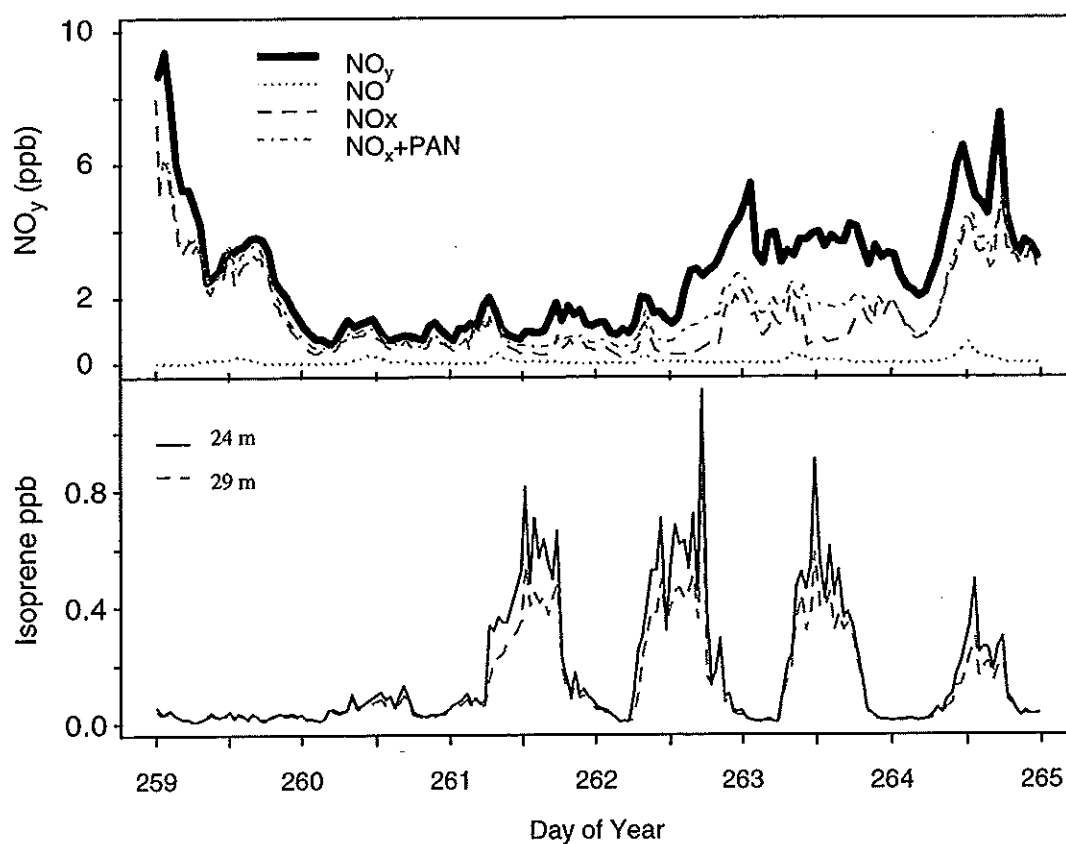
Figure 2. The upper panel shows total NO_y concentrations for the period
September 16-22 along with the contribution from NO, NO_x, and NO_x + PAN. The lower
panel shows isoprene concentrations above the forest canopy at two heights. The
divergence between these lines is proportional to the emission flux. Most of the NO_y is
present as NO_x on days 259-261 when there is little isoprene present and the solar
intensity (not shown) is low. On the sunny days with active isoprene emission the
proportion of NO_y present as PAN increases as does the remainder due to HNO_3 possibly
other organic nitrates, which were not measured at this time.

Munger et al.
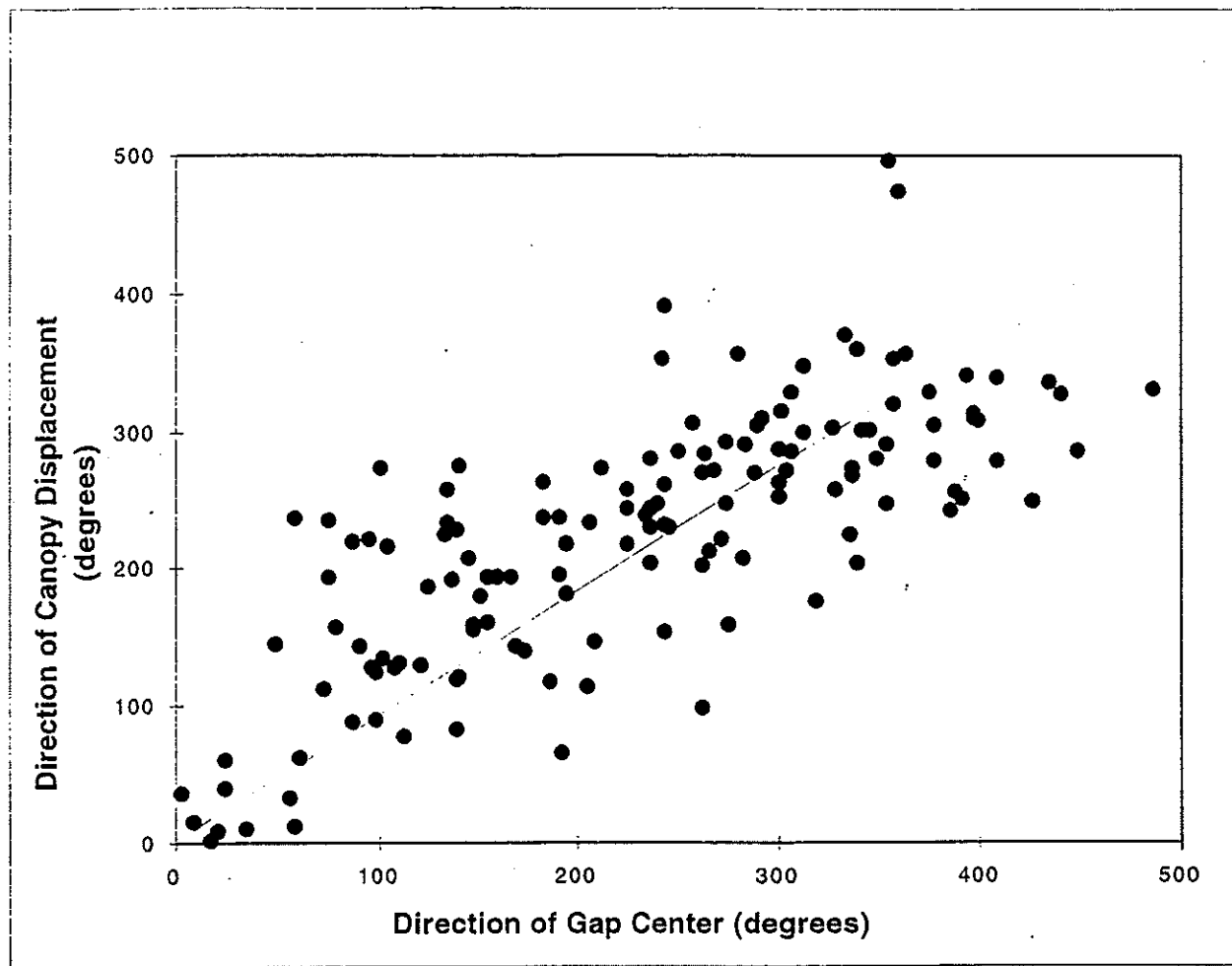
Figure 1. Direction of gap center for each gap edge tree versus direction of canopy displacement for that tree. The direction of gap center was calculated as the direction from the stem base to the gap center. The direction of canopy displacement was calculated as the direction from the stem base to the canopy center of mass. Some points were increased by 360 degrees to make circular data trends easier to view along linear axes. There was a significant circular-circular correlation among the two parameters (n=140, r2=0.1896, p<0.001).

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Thus, trees along gap edges forage for light by occupying both horizontal and vertical gap space. The magnitude and precision of foraging differs among species, size classes, and gap microenvironments. This morphological flexibility in tree canopy shape, therefore, affects species life history strategies, rates of gap closure, and patterns of forest succession.

Tree Canopy Asymmetry and Neighborhood Interactions

C. Muth and F. Bazzaz

A plant's position relative to its neighbors is crucial in establishing competitive interactions. However, plants are morphologically flexible and can place their foraging organs in patches less contested by neighbors in terms of resources and space. The importance of neighbor distance, size, and identity on tree canopy symmetry has not been adequately explored among trees, even though the positioning of tree canopies largely determines their ability to successfully forage for light. These factors were investigated in a 0.6 ha forest plot in central Massachusetts. Basal area, height, and trunk position were measured for all trees greater than 10 cm dbh. Canopy extent was determined in eight directions around each trunk using a densitometer. Canopies and trunks were then mapped and their spatial distributions analyzed. We found that tree canopies were asymmetrical away from near neighbors, large neighbors, and shade tolerant neighbors. Integrated measures of the direction and importance of all neighbors were better correlated with target plant canopy symmetry than were measures based on the direction of the single most important neighbor. Flexibility in canopy shape and position appears to reduce competition between neighbors, thereby influencing forest community dynamics.

Regeneration Following Clearcutting of Red Pine Overstory - Year 10

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 tenth year in 1999. 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 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 1998 remained at very low levels (<1% of stems). White ash was again 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 impact during the regeneration of this stand. Overall stem density of tree species was 19,414 stems/ha, compared with 19,958 stems/ha in 1998, 19,414 stems/ha in1997, and 20,696 stems/ha in 1996. White ash (38.7%) was the most numerous tree species, followed by red maple (26.2%), sugar maple (14.0%) and black cherry (9.7%). These percentages changed little from 1998. Red oak decreased to 6.4% of tree stems, the majority of which were small seedlings. This is the first year in which red oak has shown a decrease. Overall, the percentage of stems that originated as seedlings rather than sprouts decreased slightly to 23.4%, down from 25.4% in 1998, and 23.7% in 1997. The majority of these seedlings (56.5%) were white ash, most less than .5 m tall.

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Mean stem height rose to 3.24 m, up from 3.01 m in 1998, 2.92 m in 1997, 2.87 m in 1996 and 2.67 m in 1995. The greater mean height increase over the past year probably reflects reduced ingrowth of seedlings less than .5 m tall, a factor that may also explain the somewhat fewer stems/ha. The tallest stems were 12 white ash, 10 sugar maples, 8 red maples, 3 paper birches, 3 pin cherries and 2 black cherries over 7 m tall, all sprouts. Diameter at breast height (dbh) was recorded for all stems taller than seven meters. Of the five most common species, sugar maple had the tallest mean height (4.38 m), followed by red maple (3.92 m), black cherry (3.22m), and white ash (2.66 m). Because of the preponderance of small seedlings, red oak mean height was only 0.79 m. Until this year's slight decrease, probably due to poor seedling establishment the previous year, the gradual increase in the percentage of stems of seedling origin reflected both the death of smaller sprout stems and the ingrowth of new seedlings. It remains to be seen how many of these seedlings will survive to play a role in the developing stand.

precipitation record largely because of tropical storm Floyd.

For most species initial leaf out in 1999 was neither very early nor late (Table 1). Leaf development progressed a bit faster so that for many species 75% leaf development occurred closer to the dates observed in the early years (1991, 1993, 1998) than those observed in the late years (1992, 1997). The lack of consistency 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.

In spite a drought that lasted into early September, fall coloration and leaf fall in 1999 were generally the latest yet observed, with color peaking near the end of the second week in October. Despite this late season, 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 eight years of observations.

Woody Species Phenology, Prospect Hill Tract, Harvard Forest - 1999

J. O'Keefe and S. Johnson

1999 was the tenth 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 1998-99 was much milder than normal with somewhat below average precipitation and much below average snowfall. Mild conditions continued through the spring. The summer and early fall remained warm and were quite dry except for September, which set a

Tropospheric Ozone and Land Use History Affect Forest Carbon Uptake in Response to CO_2 and N Deposition

S. Ollinger, J. Aber, P. Reich and R. Freuder

To understand mechanisms affecting current forest growth and carbon storage, we analyzed the effects of tropospheric ozone, land use history, nitrogen deposition and elevated CO_2 on northeastern U.S. forests. We included these factors individually and in combination in a forest ecosystem model that was run for period from 1701 to 2000 under different scenarios of land use history.

Physiological ozone response algorithms were derived from a large number of controlled exposure studies and are based on cumulative ozone uptake to internal leaf surfaces. Because ozone uptake is dependent on stomatal conductance, factors that affect conductance (e.g., foliar N concentrations and drought stress) are important regulators of ozone damage. Photosynthetic response to CO_2 was described as a

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)

	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)
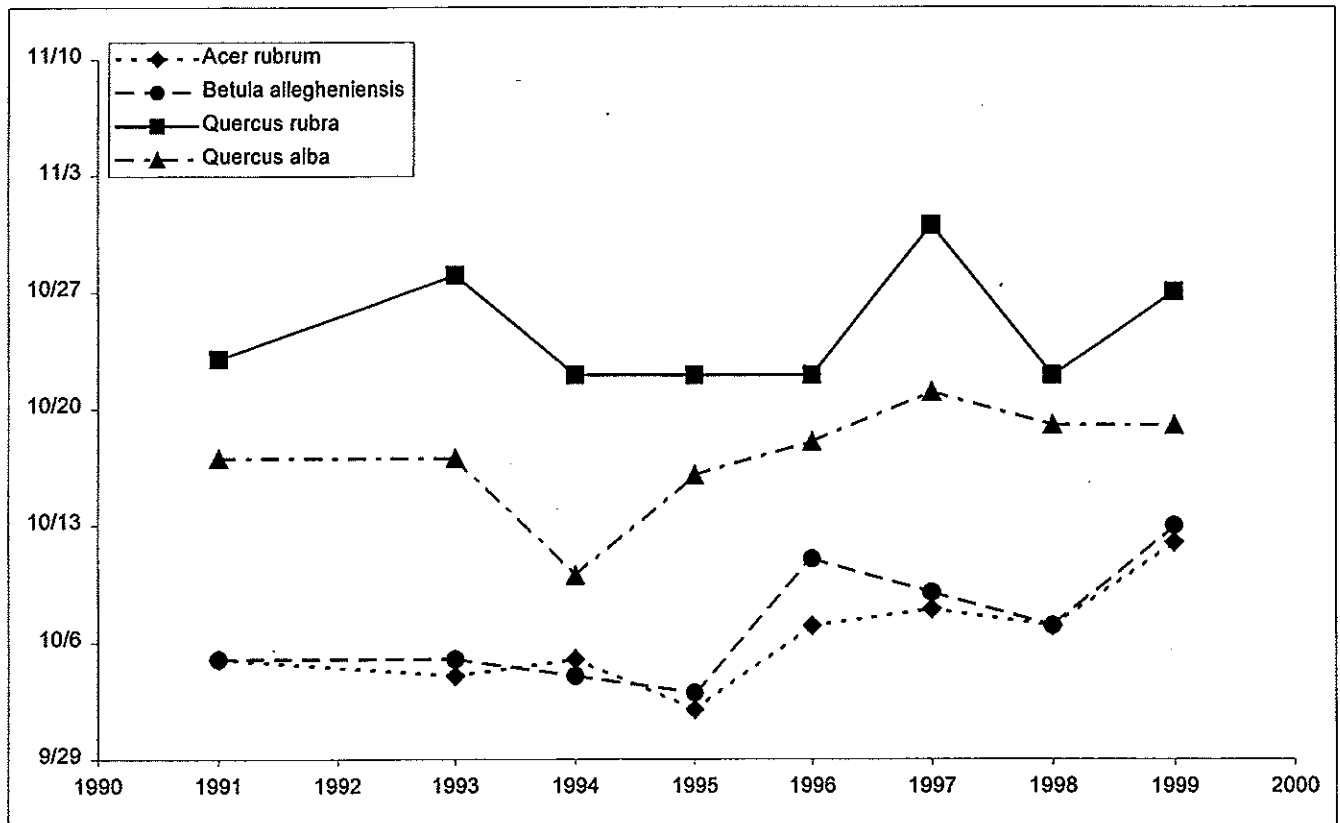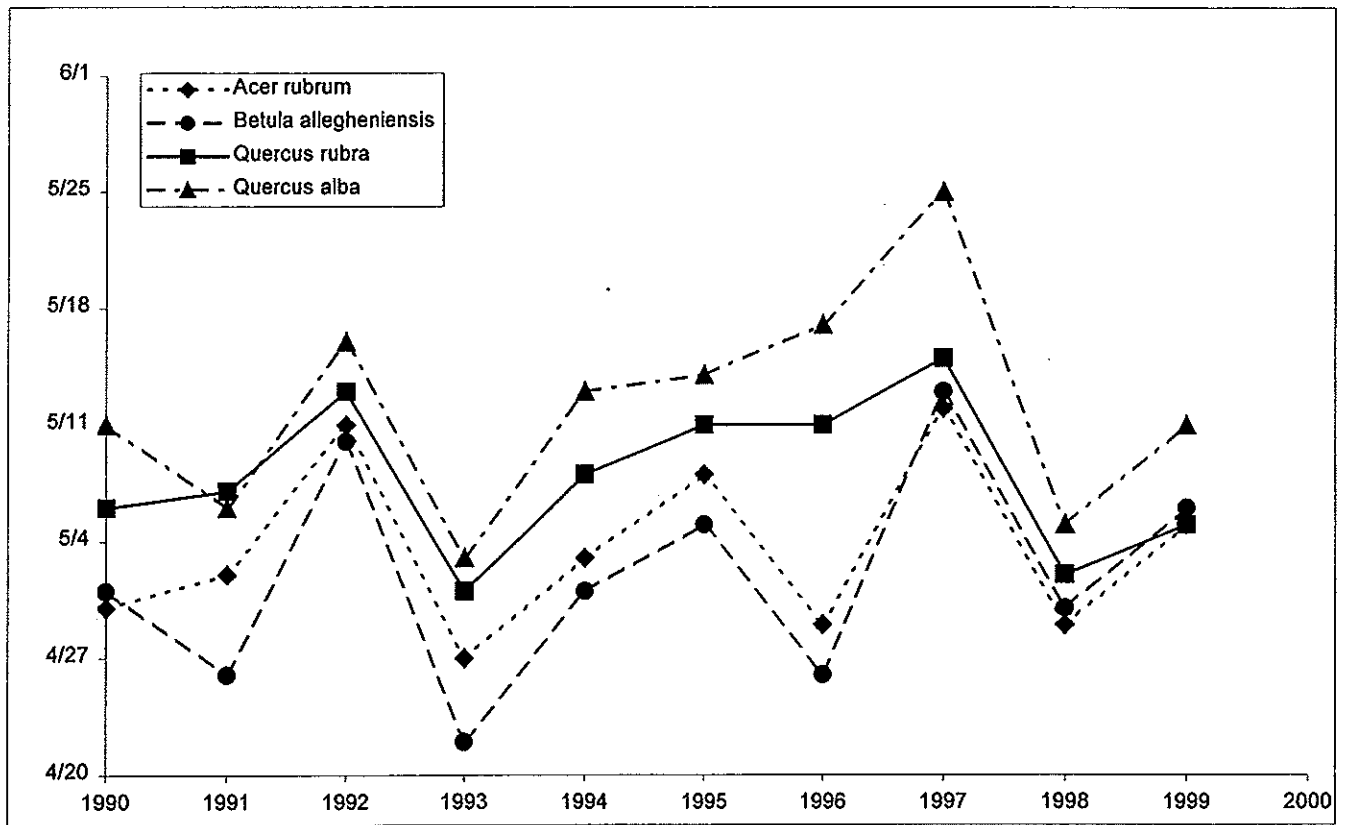
Estimated dates of leafout (50% bud break) (upper) and dates of leaf fall (50%) (lower) for four common tree species: Acer rubrum, Betula allegheniensis, Quercus alba, and Quercus rubra. Fall data was not collected in 1990 and insufficient data was collected in fall 1992 to estimate leaf fall dates.

Figure 1. O'Keefe & Johnson

michaelis-Menten response to internal CO_2 concentrations. N deposition was included as a linear increase from background levels to current levels beginning in the early 1900s. Two land use scenarios were used: A forest harvest scenario which mimicked harvest history at Hubbard Brook, and an agricultural scenario which included a period of agricultural use from 1750-1850.

We applied the model to 64 sites across the northeastern United States where ground-level ozone data were available for the period of 1987-1992 from U.S. EPA monitoring stations. The model was parameterized for northern hardwoods and run for each site under historical scenarios of agriculture and timber harvesting. We ran all sites with both disturbance regimes to allow clear identification of site history effects and because detailed site history data were not available for each location.

Results of the simulations show the interactive effects of N deposition, CO_2 enrichment, ozone and land use. In general, CO_2 and N deposition increased both NPP and NEP. Nitrogen was more effective in the agricultural scenario where N was more limiting. CO_2 was more effective in the harvesting scenario where N was less limiting. For both land use treatments, ozone exposure resulted in a significant (11-29%) reduction in NEP (Fig. 1).

Our simulations suggest that over the past several decades, increases in atmospheric CO_2 and N deposition have caused substantial increases in current rates of growth and carbon accumulation across northeastern forests, but that the magnitude of these gains has been considerably reduced by concurrent increases in ozone. These results have important implications for areas beyond northeastern North America both because many regions experience higher-than-background ozone levels and because the spatial distributions of nitrogen deposition and ozone are not independent (Fig. 2).

Landscape-Level Analyses of Hemlock Woolly Adelgid Outbreaks in Southern New England

D. Orwig, D. Mausel and D. Foster

Hemlock woolly adelgid (HWA) (*Adelges tsugae*), an introduced aphid-like insect from Asia, is expanding across the range of *Tsuga canadensis* (eastern hemlock) in New England and has the potential to severely reduce or eliminate this important late-successional species.

At the landscape level we have mapped the distribution of all *T. canadensis* stands (> 3 ha) prior to HWA infestation in a 5900 km^2 transect through southern New England to characterize the temporal and spatial patterns of damage generated by HWA since the time of its arrival in 1985. Within 114 stands, we obtained information on forest structure and composition, crown vigor, site characteristics, potential replacement species, presence of HWA, and the extent and spatial patterns of canopy damage. Overstory *T. canadensis* importance ranged from 22 - 96% and total stand densities varied from 33 - 1450 ha^{-1}. Adelgid presence and adelgid-induced hemlock mortality was reported in 88% and 74% of the forests, respectively. A distinct trend in decreasing mortality and enhanced crown vigor of overstory and understory hemlock was observed south to north in the transect, coincident with the temporal migration patterns of HWA. Average mortality exceeded 20% on most topographic aspects and was not significantly different among aspects. To date, no site or stand characteristic has been attributed to the intensity of infestation or extent of mortality that occurs. Therefore, additional spatial and multivariate analyses of landscape characteristics are currently being incorporated into our extensive GIS analysis of pre-HWA hemlock distribution and subsequent HWA impacts.

Potential replacement species already present in the canopy and starting to become established in the understory of many deteriorating *T. canadensis* forests include *Betula lenta* (black birch), *Acer rubrum* (red maple), and several *Quercus* (oak) species. It is expected that the pre-existing sapling layer will have little impact on future forest composition as it is primarily composed of *T. canadensis*, which is currently experiencing the same pattern of HWA infestation and mortality as overstory individuals.

A
NPP: Agriculture

C
NPP: Timber Harvest

B
NEP: Agriculture

D
NEP: Timber Harvest

Legend:
- ■ background
- □ CO_2
- ▨ $CO_2 + O_3$
- ▨ $CO_2 + N$ dep.
- ▨ $CO_2 + O_3 + N$ dep.
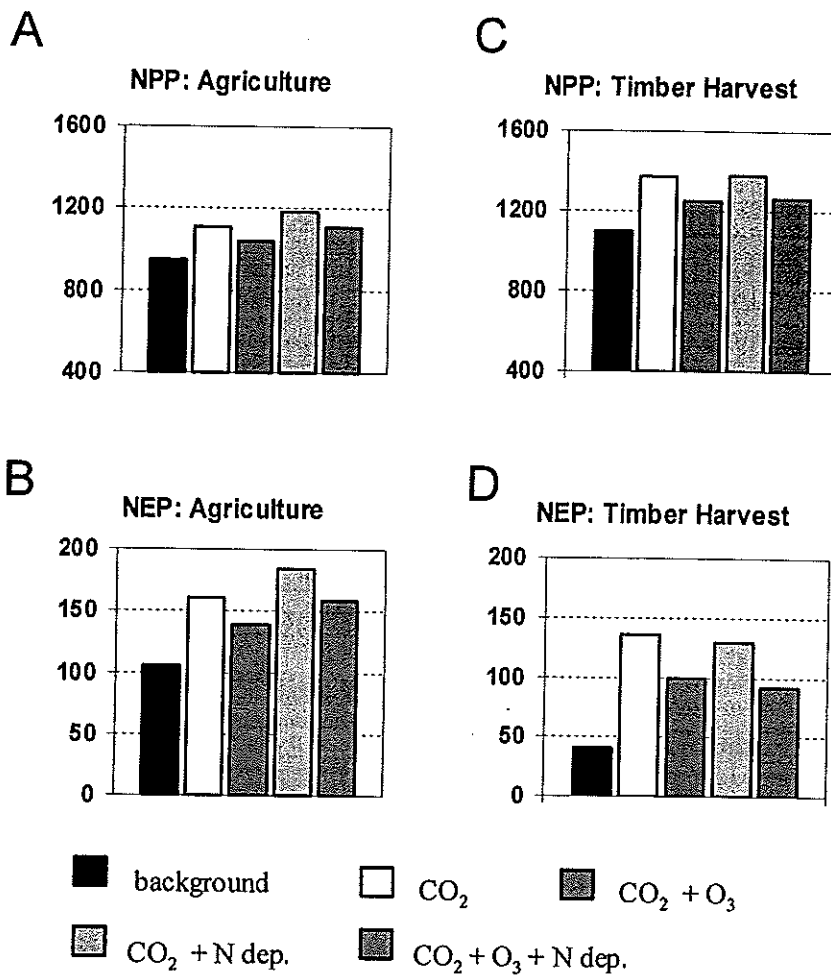
Fig 1. Predicted mean net primary production (NPP) and net ecosystem production (NEP) under different combinations of CO_2, O_3 and N deposition and two land use history scenarios. Values shown are means (n = 64) of predictions for the year 2000, at the end of 300-year simulations (1701-2000).

$R^2 = 0.42$
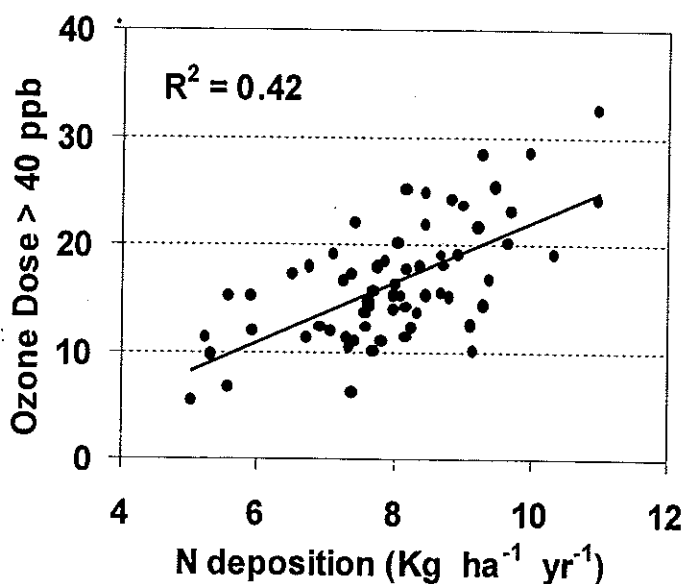
Fig 2. Mean ozone Dose > 40 ppb in relation to annual wet + dry nitrogen deposition for the 64 study sites across the northeastern U.S. region.

Ollinger et al.

Ecosystem Analyses of Hemlock Woolly Adelgid Outbreaks in Southern New England

D. Orwig, R. Cobb, M. Kizlinski, S. Currie 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 two 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. 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.

Stand and Community Reorganization Dynamics Associated with Hemlock Woolly Adelgid Outbreaks in Southern New England

D. Orwig, S. Van de Gevel and D. Foster

To examine the patterns of overstory mortality and the subsequent understory response and community reorganization associated with HWA infestation, we examined the dynamics of eight hemlock stands varying in infestation level in south-central Connecticut. Over the last five years, mortality of overstory and understory hemlock has risen to over 60% in half of the stands and continues to increase 5 to 15% per year. The health and vigor of remaining trees has deteriorated in all stands, with the majority of trees containing less than 25% of their foliage. We have observed no sign of tree recovery on these sites and predict that all sampled trees will die within the next few years. A rapid recolonization of these forests with seedlings of black birch (*Betula lenta*), red maple (*Acer rubrum*), and oak (*Quercus*) has continued to occur following additional hemlock mortality. Seedling densities have increased in moderately damaged sites and have thinned but increased in cover and height in heavily damaged areas. Several stands now have birch saplings 3-5 meters tall. Hemlock continues to be absent from the seedling layer and the few remaining saplings are heavily infested with HWA. With the exception of slight increases in fern (*Dennstaedtia*) and raspberry (*Rubus*) species, herb and shrub percentages have remained stable across sites, despite thinning canopies. We will continue to examine the ongoing dynamics in these forests to gain detailed information on the mechanisms and rate of vegetation recovery.

Reconstructing Changes in Vegetation Composition and Fire Occurrence on Cape Cod, Massachusetts

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

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 approaches are particularly relevant along the coast of New England where 1) human impact on the vegetation (especially sandplain communities) has been great, and the rate of human development is currently increasing; 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 will provide a coherent understanding of regional changes in fire and vegetation over the past 1500-2000 years along the coast of New England from changes in the abundance of fossil pollen and charcoal preserved in lake sediments. At the same time it will provide essential baseline data for other studies currently underway at the Harvard Forest describing modern and historical vegetation.

Existing paleoecological studies along the New England coast have demonstrated large changes in vegetation composition since the last glacial period, but few have focused on the past 2000 years with great enough detail to make specific conclusions about the relationship between human impacts and changes in vegetation composition and fire occurrence. Our approach is to reconstruct landscape-scale vegetation change for sites across the region with fine enough temporal resolution so that changes before, during and after European settlement can be evaluated. We are considering two main landscape attributes when selecting lakes to study. The first attribute is landform type, because soils and landforms likely influence both vegetation composition and fire occurrence. The second landscape attribute is proximity to human settlement, since we know that human impacts on vegetation have had a large effect on the distribution and composition of vegetation. Using this scheme, we will address the following questions: 1) What were the pre-dominant plant communities before European settlement and how were they distributed with respect to landform? 2) How dynamic were plant communities along the coast over the past 2000 years? 3) How has the occurrence of fire and the composition of vegetation changed over the period of European settlement?

Our results to this point have demonstrated that European settlement is distinctly represented in each of our sediment cores by increases in pollen from open landscapes and a reduction in sediment organic content, indicating upland land clearance. Before European settlement, the variation in pollen and charcoal is related to substrate and landscape position; oak and hardwood pollen are more abundant and charcoal less abundant on moraine sites, and pine pollen and charcoal abundance are higher on outwash sites. The magnitude of changes following European settlement are large, but the direction differs among sites; charcoal and pine pollen increase dramatically at some sites and decrease at others, whereas oak and hardwood pollen decline at most sites. Although landforms and landscape position have largely driven fire and vegetation patterns over the past 1500 years, land use over the past 350 years has been a significant factor influencing modern vegetation composition and the occurrence of fire.

Forest Types and Forest Regeneration in Southern Yucatan, Mexico

D. Pérez-Salicrup and D. Foster

The Southern Yucatan Peninsula (SYP) contains the largest and most rapidly disappearing track of continuous tropical vegetation in Mexico. The region is covered by a mosaic of two major old growth forest types, which can be readily distinguished in terms of their structural features (i.e, canopy height, tree density, epiphyte abundance, etc.). Additionally, shifting agriculture begun in the 1960s has left large tracks of forest of different successional ages following agricultural abandonment. We evaluated: a) whether the two naturally occurring forest types could be recognized based on their tree species composition on a large geographical scale, and b) whether the

succession process in terms of tree species reestablishment following agricultural abandonment was affected by differences in precipitation across the study region. We established a network of 150 permanent 500 m^2 circular plots, concentrated in six regions within a 22,005 km^2 area in SYP (Fig. 1). The six regions where plots were concentrated captured local gradients of environmental conditions (i.e., precipitation, elevation, topography, etc.), and land use history (i.e., intensity of timber extraction, shifting cultivation, etc.). The naturally occurring forest types were readily identified with DCA, NMS, and Discriminant Function Analysis (Fig. 2). Both forest types were present in all but one of the six study regions. This result supports the notion that these two major forest types are associated with local micro-topographic features, rather than with regional gradients of natural conditions or land use history. Within clusters of each of the forest types, the six geographical regions were distinguished, which indicates that there are slight tree composition differences in both forest types across the six regions where plots were established. These differences could be the result of natural conditions and human land use. A Mantel's test between matrices of Sorensen's index of similarity and geographic distance between all plots showed a significant positive correlation, which indicates that geographically closer plots share more tree species than distant plots. However, plots within a forest type consistently shared more tree species than plots on different forest types irrespective of geographic distance. Hence, a forest plot is more likely to share tree species with a distant plot of the same forest type, than with a closer plot of the other forest type. These results suggest that the difference in tree species assemblage between the two major forest types in SYP is not related to regional gradients of natural conditions and land use history, but differences within a forest type across the six regions are. The regeneration of tree species did not differ between the six regions, which suggests that the local precipitation gradient is of no consequence for the rate of species accumulation following agricultural abandonment.

The Effects of Spring Climate on Interannual Variation in Soil Respiration

K. Savage and E. Davidson

The response of forest soils to inter annual climatic variability provides information about how soil processes, such as soil respiration, might respond to long-term changes in temperature and precipitation. In general, soil respiration rates respond positively to increasing temperature and are reduced under very wet and very dry soil moisture conditions.

We have been measuring soil respiration rates at the Harvard Forest since 1995, and at the Howland Forest, ME. since 1996. This long-term data set at two mesic temperate forests has given us the opportunity to analyze annual variations in soil respiration under naturally varying climatic conditions. Respiration was measured at weekly intervals during the summer, and biweekly to monthly during the fall, winter and spring. Measurements were made using dynamic chambers at 6 sites in Harvard Forest and 5 sites at the Howland Forest. Sites ranged from well to very poorly drained soils. Soil temperature and moisture were measured concurrent with respiration measurements.

Figure 1 shows the spring through fall mean respiration rates for 1996 through 1999 at the Harvard Forest. During the springs of 1996 and 1998, respiration rates began to increase sharply in late May, whereas rates did not begin to increase until mid June in 1997, and respiration rates were unusually low throughout the spring and summer of 1999. Temperatures were warmer during the springs of 1996, 1998 and 1999 compared to 1997. There was also a noticeable difference in spring precipitation. The precipitation totals for May and June 1996 (236 mm) and 1998 (250mm) were greater than those for 1997 (112 mm), and 1999 (113 mm). Hence, springtime soil respiration was most strongly affected by precipitation, with low rates in both dry springs and high rates in both wet springs.
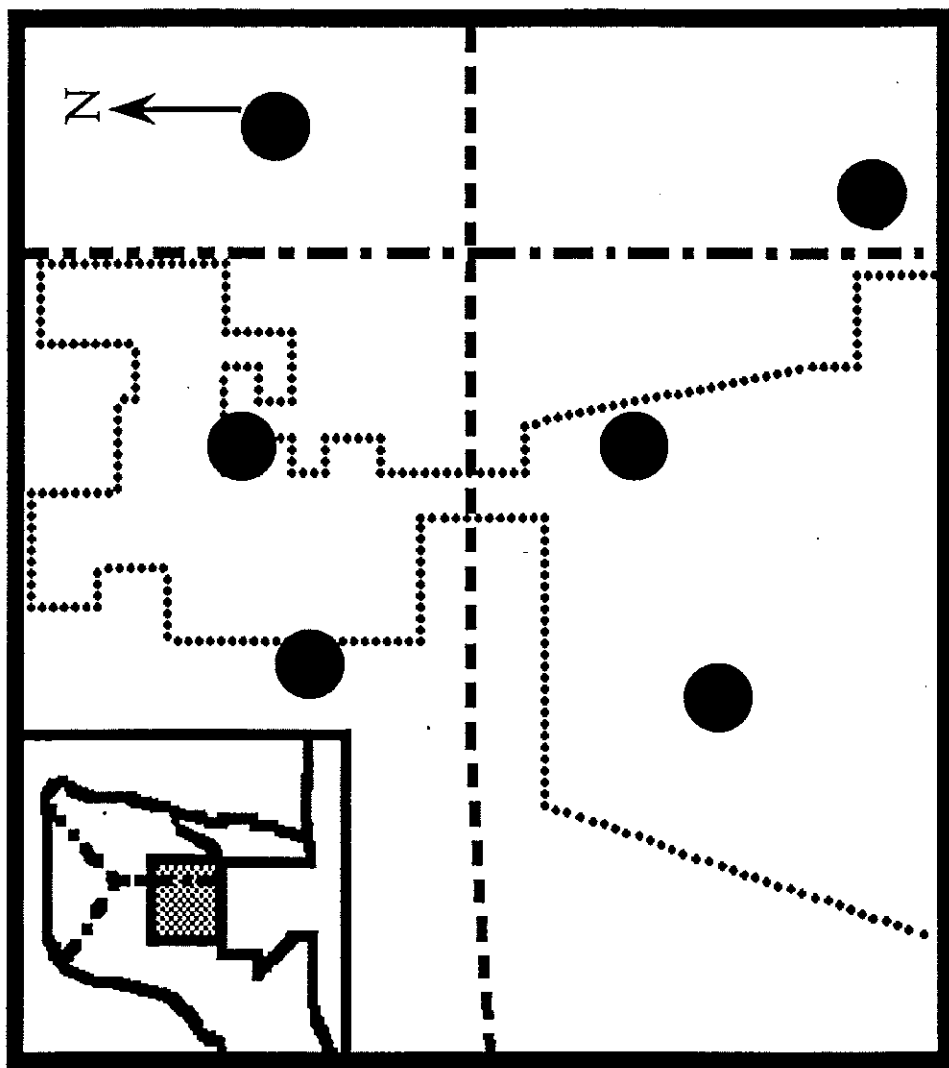
Figure 1. Study sites in the Southern Yucatan, Mexico. Black circles indicate the six regions where permanent 500 m^2 circular plots were established. The six regions capture local gradients of rainfall, soil depth, and 20th century land use. Dashed line represents Mexican highway 186, dot and dashed line represents the border of the Mexican states of Campeche and Quintana Roo. Dotted line represents the polygon of the Calakmul Biosphere reserve, the largest in Mexico with tropical vegetation.
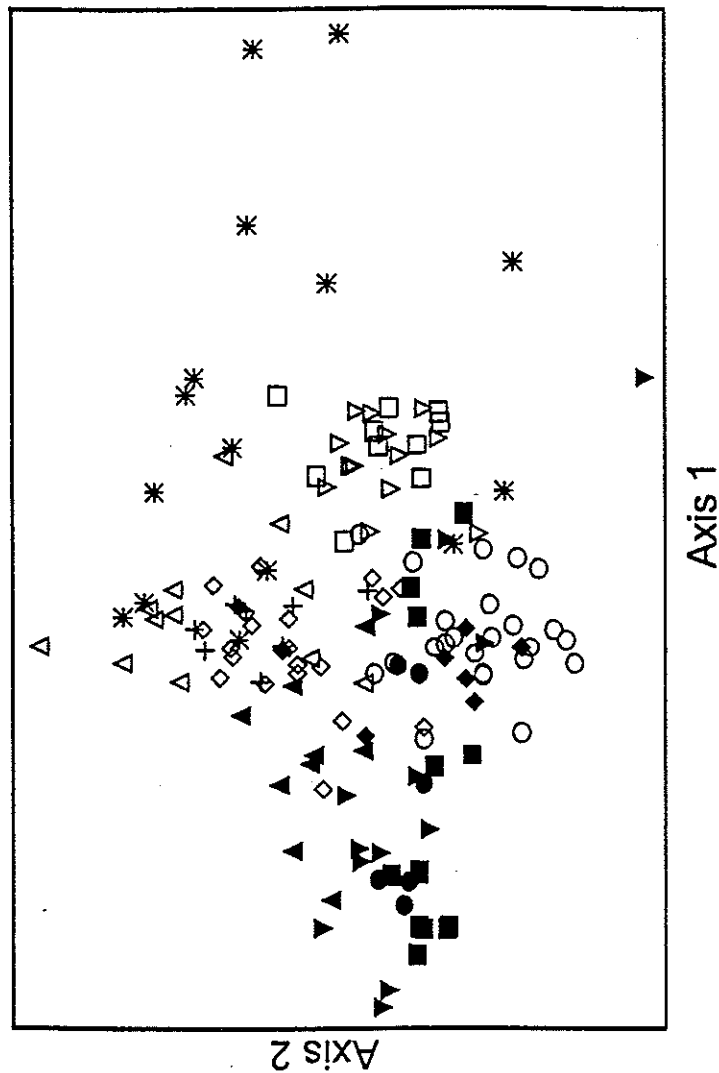
Figure 2. Principal Components of a Detrended Correspondance Analysis of tree species abundance in 500 m^2 circular plots in the Southern Yucatan, Mexico. Black symbols represent "bajo" forests, open symbols "mediano" forest, and stars represent plots of different succession ages following shifting agriculture. While the two natural forest types clearly represent a continuum, the extremes can be clearly distinguished along the first axis. Plots with longer succession periods are non distinguishable from mature "mediano" forest.

Figure 1

Harvard Forest

Mean Daily Soil Respiration Rate (mg C m^{-2} hr^{-1})

····o··· 1996
—△— 1997
—□— 1998
—◇— 1999

400
300
200
100
0

100   125   150   175   200   225   250

Figure 2

Howland Forest

Mean Daily Soil Respiration Rate (mg C m^{-2} hr^{-1})

—△— 1997
—□ - 1998
—◇— 1999

400
300
200
100
0

100   125   150   175   200   225   250

JD
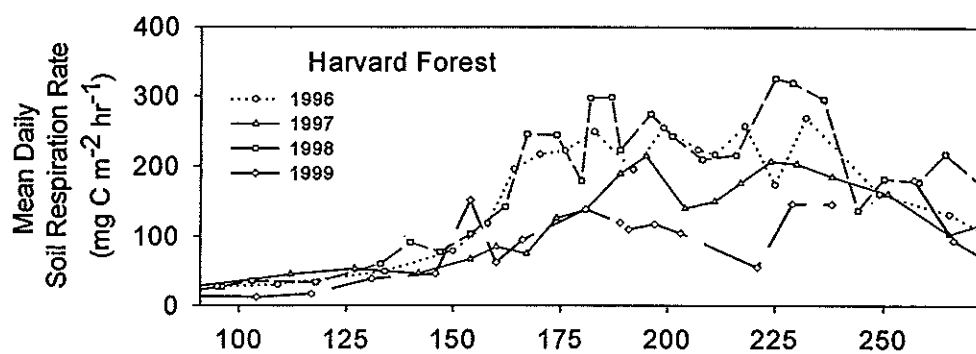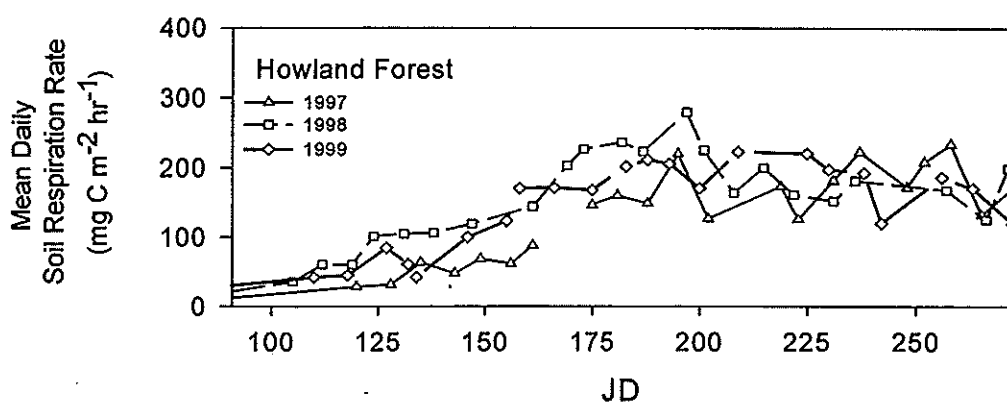
Table 1

	Yearly Soil Respiration kg C m^{-2} yr^{-1}			Difference Between Years kg C m^{-2} yr^{-1}		Spring Total Soil Respiration*			Differences Between Springs		Spring Difference as a Percentage of the Annual Difference	
	96	97	98	97-96	98-97	96	97	98	96-97	97-98	96-97	97-98
Harvard Forest	0.76	0.64	0.86	-0.12	0.23	0.18	0.11	0.18	-0.07	0.08	60%	33%
Howland Forest		0.66	0.80		0.15		0.11	0.21	_	0.10	_	69%

* Spring totals are from May 1st to June 30th and are in kg C per 61 days

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Figure 2 shows the mean respiration rates for 1997 through 1999 at the Howland Forest. The spring of 1997 had a lower precipitation total (130 mm) than 1998 (211 mm) and respiration rates began to increase in mid June in 1997 whereas respiration began to increase in early May in 1998. The 1999 season experienced low precipitation, however the dry conditions did not impact respiration rates during the spring as was observed in 1999 at the Harvard Forest.

Spring played an important role in the total annual variation in carbon respired in both forests. At the Harvard Forest, the early increase in respiration rates during the springs of 1996 and 1998 compared to the dry spring of 1997, accounted for 60% and 33% of the inter-annual variability in annual soil respiration (Table 1). At the Howland Forest, 69% of the difference in annual respiration rates between 1997 and 1998 was attributed to springtime differences (Table 1). In both forests, warm wet springs caused respiration to increase earlier in the season and subsequently peak earlier in the year, whereas dry springs delayed peak respiration, and these differences played a significant role in the inter-annual variation in carbon release from upland soils.

Advances in Understanding Microbial Regulation of Soil Methane Consumption

P. Steudler, G. Nowicki, Y. Hrywna, J. Gulledge and C. Cavanaugh

Consumption of CH_4 by soil microbes is believed to be an important process regulating atmospheric CH_4 concentrations. Soil bacteria, such as methanotrophs (CH_4 consuming organisms) and ammonium oxidizers (organisms that transform ammonium to nitrate) are thought to be the microbes that consume atmospheric CH_4. Many ecological studies in native and intensely managed systems have examined the physical controls and the consequences of human activities on consumption rates but few have characterized the microbes that are involved in the process of consuming CH_4 at atmospheric concentrations. These specialized microbes appear to have unique physiological properties that enable them to grow on the very low concentrations of CH_4 found in the atmosphere. What is not well known is the identity of the microbes actually carrying out the consumption in the soil.

This paper reports results from an approach that combines both process and molecular studies to characterize these microbes. We are using the long-term Harvard Forest nitrogen addition experiment as a case study to examine the physiological and molecular diversity of the microbes consuming atmospheric CH_4 in greater detail. These forest stands have been fertilized with NH_4NO_3 for 10 years so microbes and their activities can be compared in the natural soils and in the N amended plots.

We have been measuring various parameters at these sites including the rates of soil CH_4 consumption and environmental factors controlling the rates over the past decade. In the field, we measured rates of CH_4 consumption in the whole system using small chambers placed over the soil surface for short periods. In the laboratory, we used soils from the field experiments to find the locations in the soil profile where the organisms are consuming CH_4. We are also investigation the biochemical pathways using inhibitors of reactions and the enzymes of CH_4 consumers. Using molecular methods, we are attempting to identify these organisms.

Methane consumption rates in the high N amended plots compared to the controls have declined over the past decade. In the first year after N additions were begun, the high N plots showed an immediate reduction in consumption rates (relative to the controls) of about 25%; this reduction reached 35 - 45% over the next 3 years. The pine plot showed a further reduction to about 65% by 1993. We made a set of growing season measurements in 1998, a decade after the additions were begun, and surprisingly found that the reductions had reached about 65% and 90% in the hardwood and pine plots, respectively.

We are using a variety of process level measures including, methane consumption kinetic parameters, inhibitors specific for either methanotrophs or ammonium oxidizers, and phospholipid fatty acids (PLFA) markers to compare changes in CH_4 consuming organisms between the control and N treated plots. Kinetic parameters of atmospheric methane oxidation from control stands exhibited high-affinity CH_4 uptake

($K_{m(app)}$) of 12 to 58ppm, with high maximal uptake rates ($V_{max(app)}$) up to 26 nmol h^{-1} g dry $soil^{-1}$. The N amended soils had significantly lower kinetic parameters with $K_{m(app)}$ values of 7-25ppm and substantially reduced $V_{max(app)}$ values of 0.6-3.8 nmol h^{-1} g dry $soil^{-1}$. These data suggest N addition selects for organisms that have even higher affinities for CH_4.

We also used specific chemicals to inhibit CH_4 consumption reactions to differentiate the groups of organisms consuming CH_4. Laboratory studies using inhibitors specific for either methanotrophs (picolinic acid) or ammonium oxidizers (allylsulfide) showed that the activity of methanotrophs was about twice as large as the ammonium oxidizers in the upper mineral soil layer in the pine control plot. While the CH_4 consumption rate in the low N addition plot was reduced by 60% compared to the control, the results from the inhibitor tests showed that the CH_4 consumption rates for both microbial groups were nearly equal. This suggests that the reduction in over all consumption rate in the low N plot was mostly due to a decrease in methanotrophic activity. In other laboratory studies investigating the mechanism for this reduction in CH_4 consumption by N addition suggest that, in these stands, it is simple competition for enzyme by added ammonium. That is, reaction sites on the enzyme were taken up by the abundant ammonium molecules which, in a sense, out-competed the CH_4 molecules for the enzyme site (Gulledge and Schimel 1998).

There are phospholipid fatty acids that are specific for ammonium oxidizers and either type I or II methanotrophs. We collected soils from the organic and upper mineral soils in all treatments of both stands and analyzed for the PLFA markers. Preliminary analyses of the PLFA data from the mineral soils of the hardwood and pine control plots indicated that type II methanotrophs were the dominant CH_4 consuming organisms present. We found very low concentrations of the PLFA markers specific for type I methanotrophs in these soils indicating they may play a minor role in CH_4 consumption. Further data analysis is continuing on the PLFA signatures from the N amended plots.

Additional information about the identity of the organisms consuming CH_4 will come through the application of molecular techniques. We have extracted the DNA from samples of soils at the different depths and used molecular probes for the genes that control the formation of the enzymes oxidizing methane or ammonium. Further research that separates the mixtures of genes, sequences the genes and identifies candidate organisms in progress. We are also trying to identify the presence or absence of methanotrophic and ammonium oxidizing bacteria using 16S rRNA probes. These probes are constructed from a sequence of molecules in the DNA that allows identification of a particular species of CH_4 consuming organisms. We currently have a set of probes designed for type I and II methanotrophs and are testing them using pure cultures of specific methanotrophs and environmental samples.

Gulledge, J. and J. P. Schimel 1998. Low-Concentration Kinetics of Atmospheric CH_4 oxidation in Soil and Mechanism of NH_4^+ Inhibition. Appl. Env. Micro. 61(2):592-601.

Rapid and Spatially Coherent Variations in Soil Surface CO_2 Fluxes

E. Sundquist, G. Winston, L. Bergen and N. Finnegan

Using an automated chamber technique, we have documented diel and other rapid variations in CO_2 fluxes at the soil surface in a well-drained area of Harvard Forest. Our method deploys six chambers over an area of a few hundred square meters. The chambers operate in cyclic sequence so that a flux measurement is performed once every 12 minutes and each chamber is redeployed every 72 minutes. Fluxes are calculated from the rate of CO_2 increase observed in air circulated between each chamber and an infrared gas analyzer. We also monitor soil temperature, soil moisture, and soil gas CO_2 and CH_4 concentrations using probes that provide two depth profiles within the area sampled by our chambers. We perform these measurements approximately once a month over a period of approximately 24 to 48 hours. During each measurement period we are able to assess both temporal detail and spatial coherence in CO_2 fluxes, and to relate these fluxes to depth-dependent soil properties.

The observed CO_2 flux variations are spatially coherent over the scale of our measurements. Diel flux variations typically follow diel patterns of soil temperatures (Fig. 1), but we have also observed that CO_2 fluxes increase after rainfall (Fig. 2). These rapid variations are significant in comparison to long-term means. The mean range of the fluxes shown in Figure 1 was 72% of the flux averaged over the entire measurement period. The post-rainfall increase in fluxes shown in Figure 2 was an average of 53% of the mean flux prior to rainfall.

The temporal resolution of our records enables us to see that the CO_2 flux response to both temperature and rainfall is very rapid. Diel temperature patterns at depth lagged behind the observed trends in CO_2 fluxes. The rainfall flux response occurred even when the event was so ephemeral that it did not affect soil moisture a few centimeters below the soil surface (Fig. 2). Following this event, an increase in shallow soil gas CO_2 concentrations was propagated downward through time. These observations lead us to the conclusion that much, if not all, of the temperature and rainfall sensitivity on these time scales resides in the uppermost few centimeters of the soil.

Because the uppermost soil layers are probably rich in relatively labile organic matter, the observed short-term sensitivities may not be representative of long-term soil response involving more refractory organic material. Rapid CO_2 flux variations are comparable in magnitude to those observed over longer timescales, and great care must be taken to discriminate short-term from long-term influences.

Radiocarbon Measurements in Soil Organic Matter and Soil Respiration at the Harvard and Howland Forests

S. Trumbore, J. Gaudinski, E. Davidson and K. Savage

We have measured radiocarbon in organic matter, soil CO_2 and soil respiration at Harvard and Howland Forest sites to determine the turnover time of detrital, humified, and mineral-associated organic material, and to assess the contribution of each of these pools to total soil respiration (Gaudinski *et al.* in press). Figure 1a shows the

radiocarbon signature of CO_2 respired from well-drained soils at the Harvard (1996-1999) and Howland (1998-1999) sites. At both sites, the ^{14}C content of soil respiration exceeds that of atmospheric CO_2 and thus reflects the importance of decomposition of organic matter that has resided in the soil for several years to decades. Howland and Harvard forest well-drained sites show very similar ^{14}C values for soil respiration. There are clear differences in the amount of spatial variation in ^{14}C between years. The clearest contrast is between 1998, a wet year with large differences in ^{14}C among chambers at one site, and 1999, a dry year with low variation in ^{14}C emissions. Seasonal trends in ^{14}C are also apparent, with decreasing ^{14}C during the course of the summer in most years at both sites.

Changes in the $\Delta^{14}C$ of respired CO_2 reflect differences in partitioning of sources: recently fixed photosynthate has $\Delta^{14}C$ close to atmospheric CO_2 of the same year, while decomposition of leaf and root detritus and humified organic material in O horizons (where 80% of the soil organic matter resides) has $\Delta^{14}C$ values greater than atmospheric CO_2. We hypothesize that the decreased variability in 1999 results from a reduction in the fraction of soil respiration derived from the organic horizon layers, and that increased heterogeneity in wet years results from enhanced CO_2 emissions from the O horizon that are highly variable due to spatial variations in the thickness and makeup of organic horizons. Detailed analysis of the 1999 data will enable us to determine what shifts in sources explain differences in CO_2 emission and $\Delta^{14}C$ in 1998 and 1999.

In addition to measurements of soil respiration and isotopes in well-drained soils that make up the majority of the flux tower footprints at Harvard and Howland sites, we are also studying wetlands, which are important components of the landscape in both forests. While drought decreases CO_2 emissions from uplands, it has less inhibitory effect and can even increase emissions from wetlands, as oxygen diffuses into the drying peats. During the droughts of 1995 and 1999, emissions from the wetlands were nearly as large as emissions from the uplands. Figure 1b shows the ^{14}C data for soil respiration from the swamp sites in Harvard and Howland Forests. Note the change

Figure 1. Normalized soil CO_2 effluxes (open symbols), 4 cm soil temperatures (pit 1) (solid line), averaged 5cm soil moisture (pit 4) (solid symbols) for August, 1998 at the North Pierce Farm site in Harvard Forest.
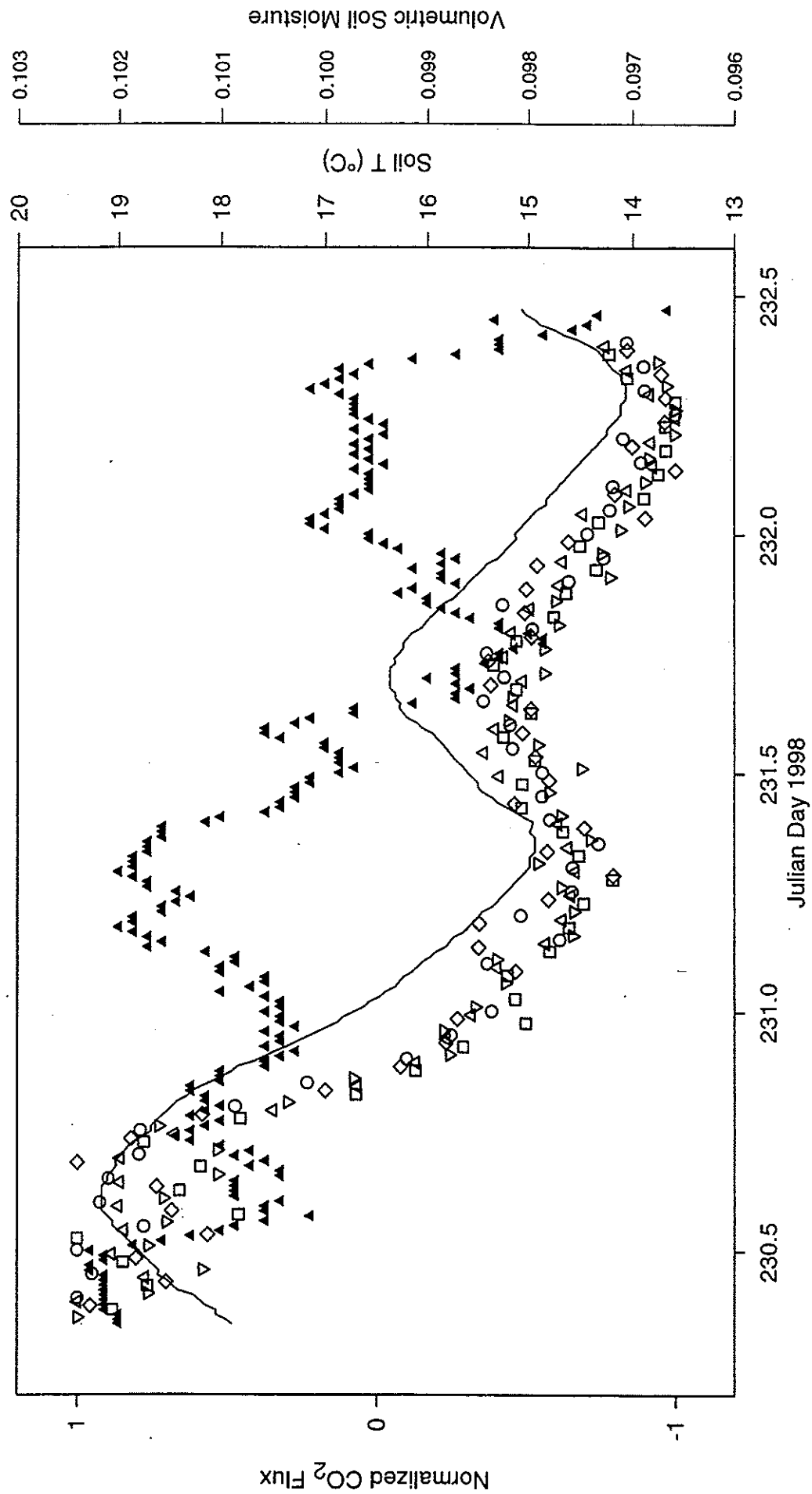
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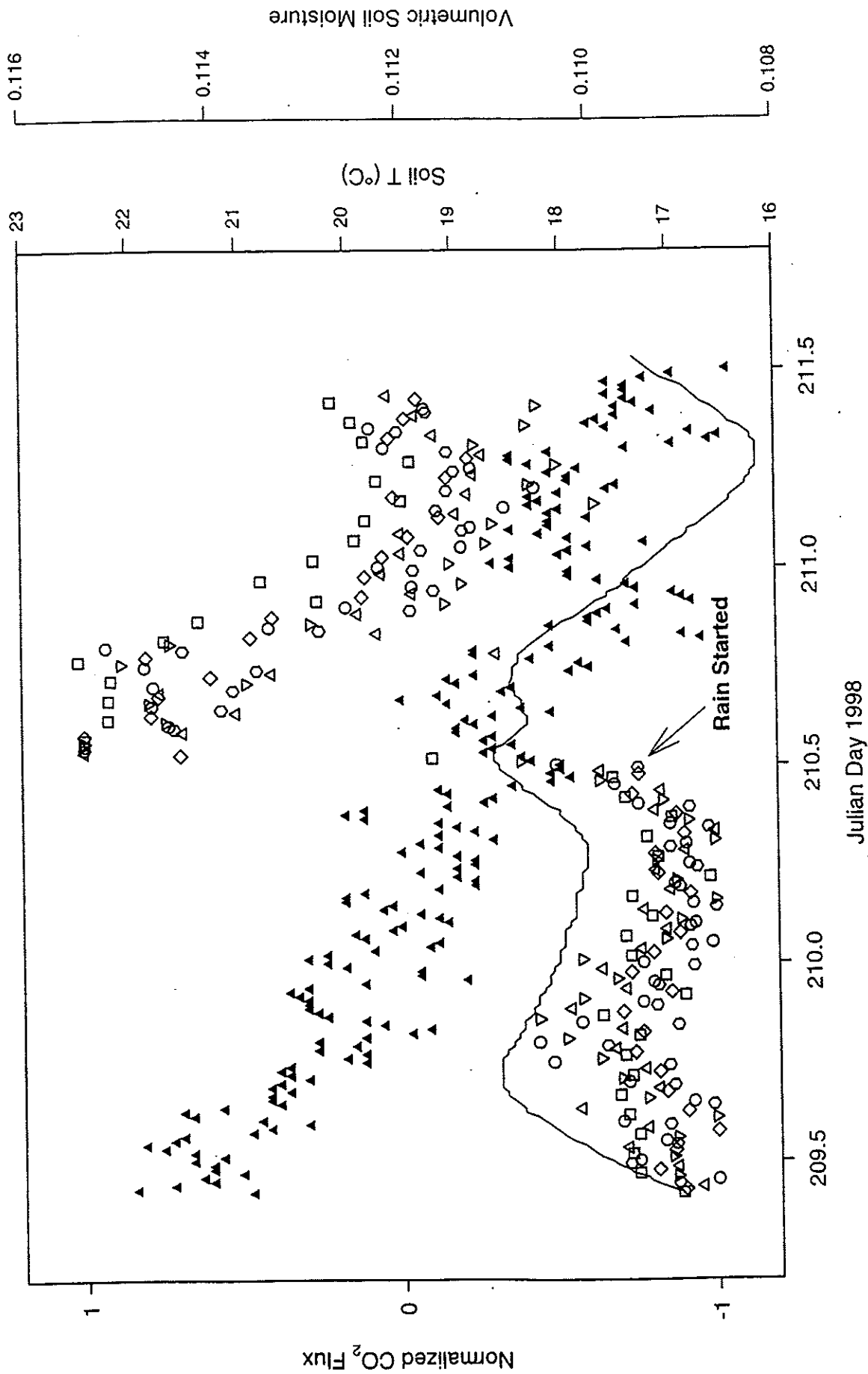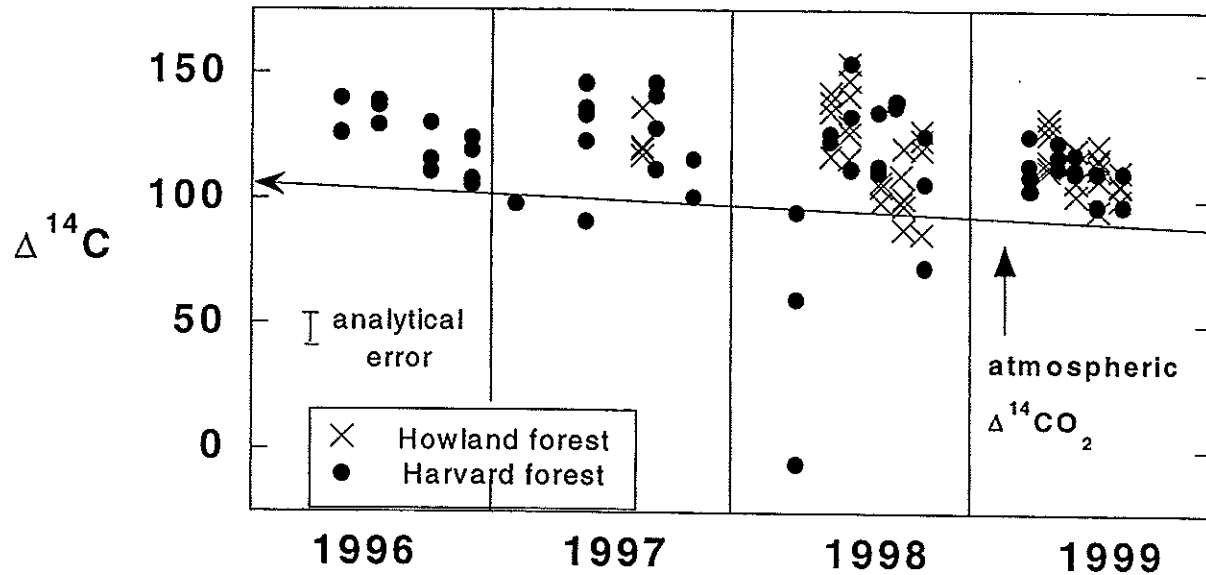
Figure 2. Normalized soil CO_2 effluxes (open symbols), 5 cm soil temperature (pit 4) (solid symbols) and averaged 5 cm soil moisture (pit 4) (solid symbols) for July, 1998 at the North Pierce Farm site in Harvard Forest.

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Radiocarbon in soil respiration from well-drained soils in Harvard and Howland forests

$\Delta^{14}C$

150

100

50

0

analytical error

X   Howland forest
●   Harvard forest

atmospheric $\Delta^{14}CO_2$

1996   1997   1998   1999

Radiocarbon in soil respiration from swamps

$\Delta^{14}C$

600
500
400
300
200
100
0
-100

X   Howland forest swamp
●   Harvard forest swamp

1996   1997   1998   1999
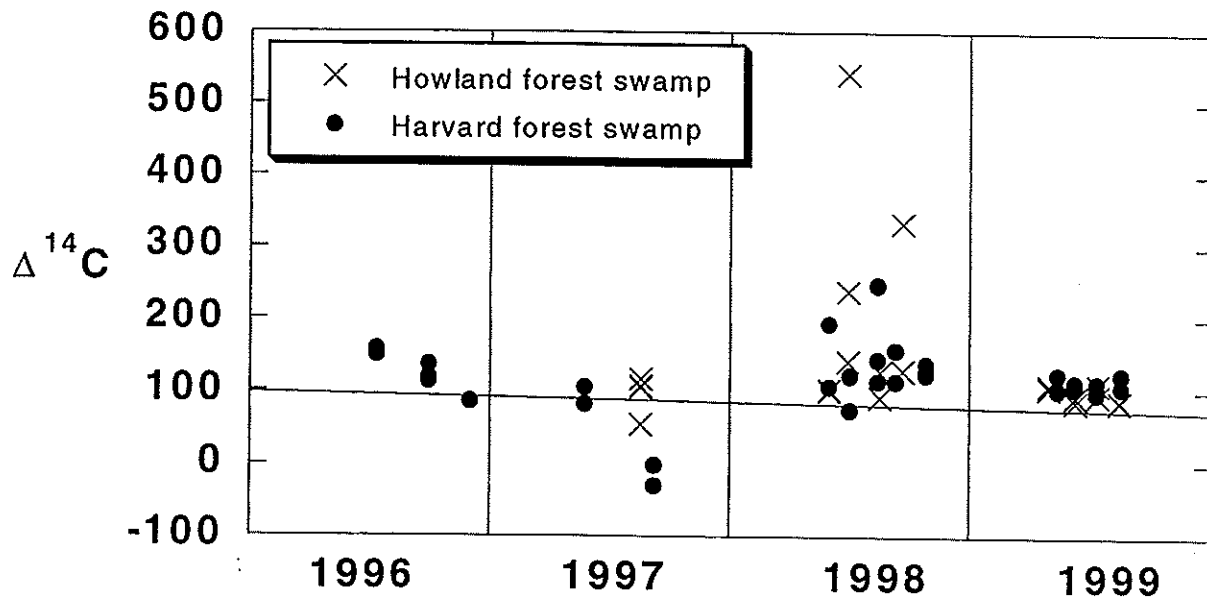
Figure 1. Radiocarbon data are given in Δ notation, the per mil deviation in $^{14}C/^{12}C$ ratio from a standard (1895 wood). Positive $\Delta^{14}C$ values indicate the predominance of C derived from the atmosphere since the period of weapons testing which peaked in the mid-1960's. Negative values indicate that C has resided long enough for significant radioactive decay of ^{14}C (which has a half-life of 5730 years). Analytical error on all samples is ± 6 per mil.

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in scale from Figure 1a; spatial and temporal variability at the swamp sites are larger than at the upland sites. We attribute this to the interaction of water table depth with the vertical distribution of radiocarbon in organic horizons in these swamp soils. We hypothesize that decomposition-derived components of the soil CO_2 flux are predominantly from the area near the water table. As the water table depth crosses the bomb ^{14}C peak values (at about 15-20 cm depth below the moss surface), the $\Delta^{14}C$ values of respired CO_2 reflect the changing substrate age. For example, we attribute low $\Delta^{14}C$ values in late summer 1997 to enhanced decomposition of prebomb carbon below the bomb ^{14}C peak. In 1999, we similarly expected to see depleted ^{14}C values as the drought progressed, but did not observe them. Again variability in the $\Delta^{14}C$ of CO_2 respired in 1999 is low compared to 1998.

Gaudinski, J.B., S. E. Trumbore, E. A. Davidson, and Shuhui Zheng. 2000. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates, and partitioning of fluxes. Biogeochemistry (In Press).

Ancient Forest Plant Species: a European and North American Perspective

K. Verheyen and M. Hermy

In both Europe and North America, it has been proven that some of the species in the original forest flora - the so-called 'ancient forest plant species' - are reluctant to colonize secondary forests. Recently, it has been suggested that these species can be considered as a guild. The latter implies that the ancient woodland plant species share some traits which inhibit dispersal, establishment or persistence in secondary woodlands However, no systematic comparison between traits of ancient and other forest plant species has been made yet. Furthermore, the existence of ancient forest species in northeast America offers a unique chance to compare these species - with respect to traits and taxonomic or

phylogenetic aspects - with their European counterparts.

Therefore, the aims of this research are: (1) to compile of a list of Northeastern American ancient forest plant species from the available literature; (2) to make an ecological comparison between ancient and other forest plant species of northwestern Europe and northeastern America based on a core list of plant traits; (3) to determine taxonomic, phylogenetic and ecological similarities between northwestern European and northeastern American ancient forest plant species.

Does Canopy Status Affect Wood Specific Gravity (and Carbon Sequestration) in Forest Trees?

D. Woodcock and A. Shier

The radial increases in wood specific gravity (density relative to water) known in many tree species have been interpreted as providing mechanical support in response to the stresses associated with wind loading. If this interpretation is correct, canopy trees should: 1) be more likely to have radial increases in specific gravity and 2) exhibit greater increases than subcanopy trees. We tested this hypothesis by determining wood specific gravity for three species of forest trees (*Acer rubrum*, *Fagus grandifolia*, and *Tsuga canadensis*) growing in central Massachusetts. Differences between canopy categories were most evident for maximum specific gravity, which was higher in canopy trees (Fig. 1). Radial trends were significant in all three species, and there was a high degree of variation from tree to tree. Tree height and diameter are related to the degree of radial increase or decrease. In contrast, no significant predictors were identified for average specific gravity. If specific gravity of the outside wood is included as an explanatory variable, it is possible to derive regression equations to represent average specific gravity of individual trees. Of the dominant tree species for which we have data, *Acer rubrum*, *Betula papyrifera*, and *Pinus strobus* show radial increases in specific gravity and *Fagus grandifolia*, Tsuga canadensis, and *Quercus rubra* show decreases (Fig. 2). We associate the increases with early successional status or characteristics and
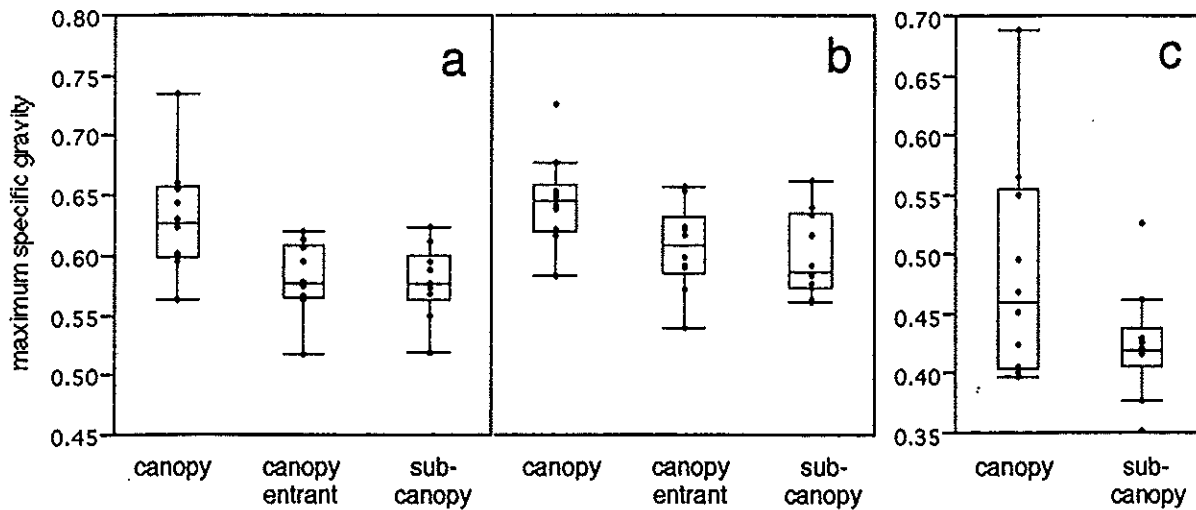
Fig 1. Maximum specific gravity as a function of canopy category for a) *A. rubrum*, b) *F. grandifolia*, and c) *T. canadensis*. The box plots show the median (central bar), middle 50% of the distribution (box), the outermost data points within the main portion of the distribution (bars), and outliers.

Fig 2. Radial trends in specific gravity for 6 northern hardwood forest species showing a) increases and b) decreases. n = 30 for *A. rubrum* and *F. grandifolia*; n = 20 for *T. canadensis*; and n = 5 for *P. strobus, B. papyrifera,* and *Q. rubra*. The middle values are the average of all middle segments.

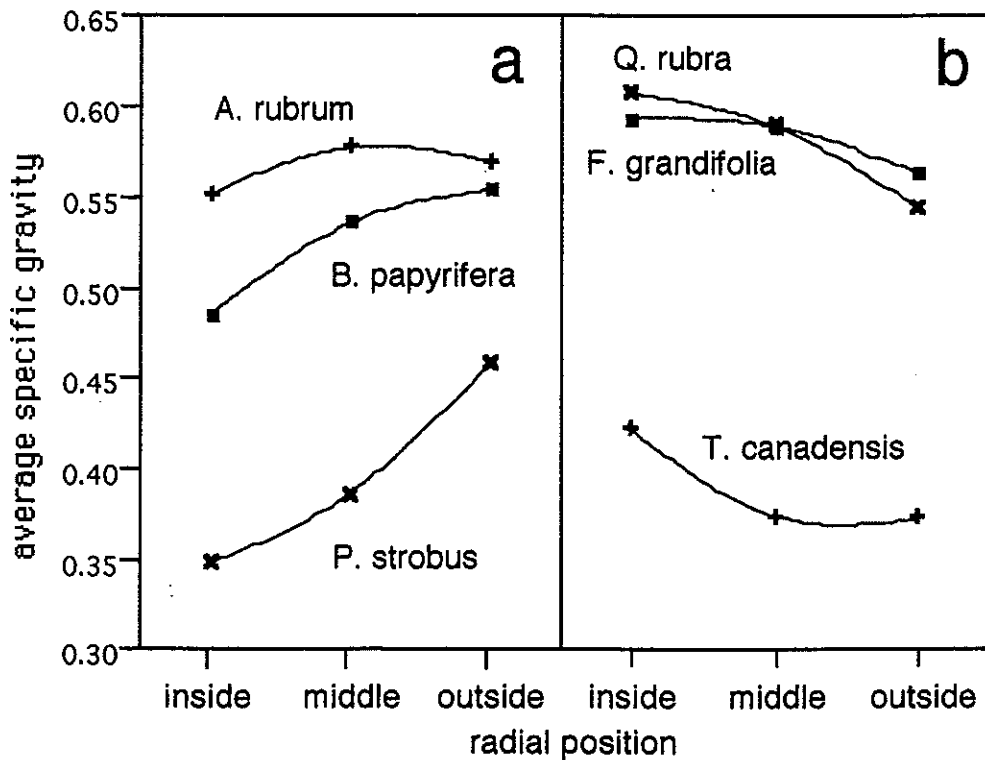the decreases with late successional status or persistence in mature forest. Variations in specific gravity include directional trends that may be important in evaluating forest carbon stores. Successional trends at this site involve a shift from species showing radial increases to those showing radial decreases. In addition, trees with low-specific-gravity wood are prevalent early in succession and then appear again as important late-successional taxa (*T. canadensis*).

gravities is largest in young trees/early wood and the convergence in values seen later in growth is most likely due to constraints relating to support in mature trees.

Radial Trends in Wood Specific Gravity in Forest Trees: a Developmental and Ecological Interpretation

D. Woodcock and A. Shier

Analysis of ~100 individuals representing six species of mixed-northern-hardwood-forest trees shows three species (*Acer rubrum, Pinus strobus and Betula papyrifera*) with radial increases in specific gravity and three species (*Q. rubrum, Tsuga canadensis and F. grandifolia*) with decreases. We interpret the occurrence of increases or decreases as reflecting successional status. In canopy trees of *A. rubrum, F. grandifolia* and *T. canadensis*, the range of specific gravity is greatest in the inner wood and lowest in the outer wood. A larger data set including tree species from wet, dry, and montane tropical forests, in addition to temperate-latitude species, also shows a greater range of specific gravity in the inner wood when considered by species. The species we studied show a negative relationship, encompassing both radial increases and decreases, between specific gravity of the inner wood and degree of radial trend. This relationship is also evident in trees from a variety of forest types. The greatest rates of radial change occur in smaller-diameter trees, but small trees also show a great deal of variation compared to larger trees. Based on the above points, we propose a model for radial trends (Fig. 1) in which a) degree of increase/decrease varies with specific gravity of the inner wood; b) radial increases are considered an early successional and radial decreases a later-successional characteristic, with the difference between these two categories reflecting growth strategy and considerations relating to support; and c) the range of specific
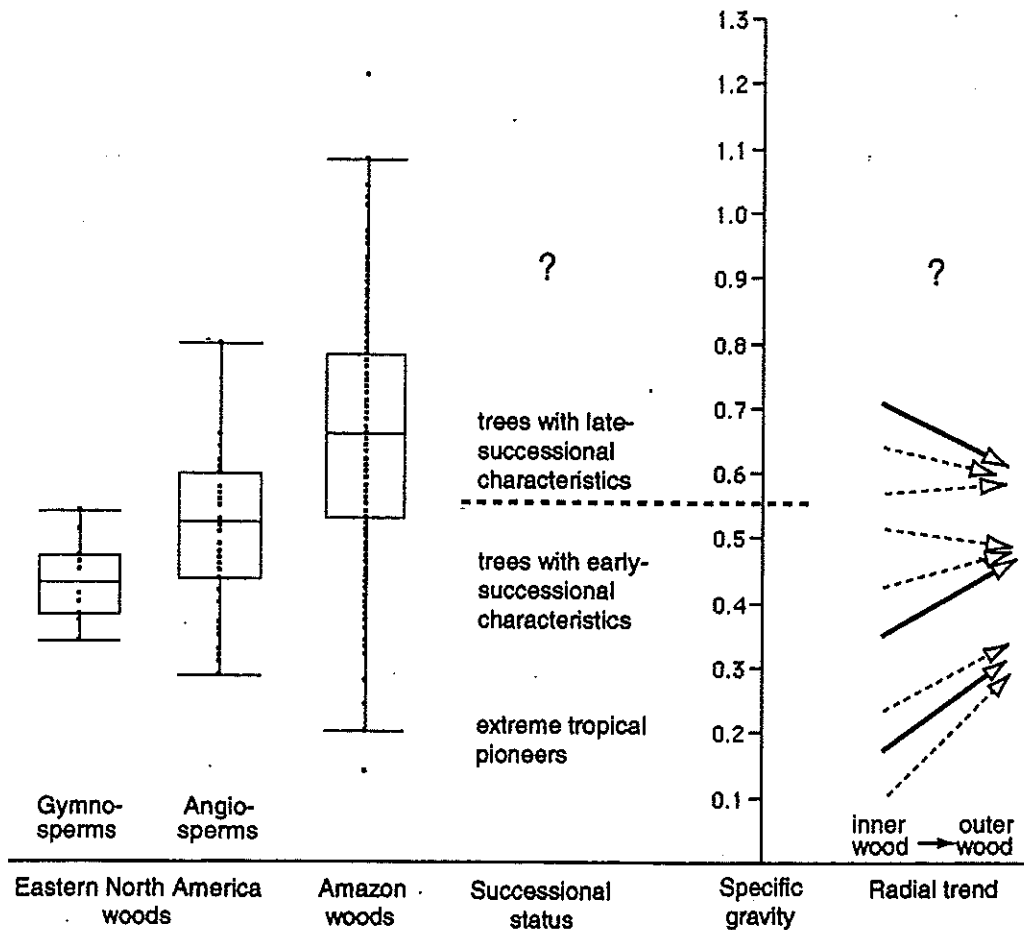
Fig 1. Model of radial trends for different values of specific gravity and successional position. This interpretation is for Angiosperms only. Plotted on the right is wood specific gravity for eastern North America (n = 82) and Amazon forest (n = 266) tree species (data from Forest Products Laboratory 1999 and Fearnside 1997). The eastern North America data do not include tropical/south Florida species, some of which have high-specific-gravity wood.

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