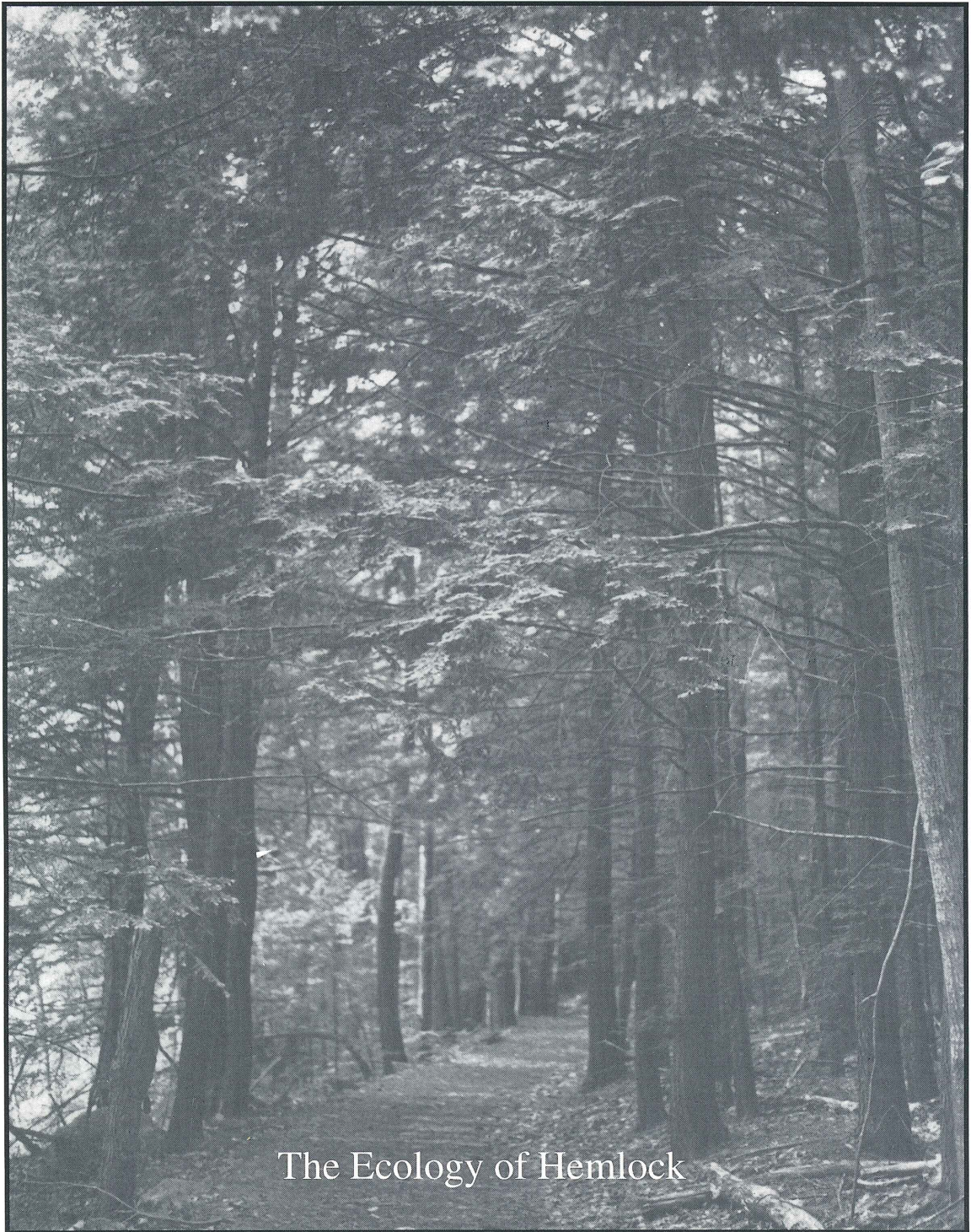


THE HARVARD FOREST 1996 - 97

Harvard University



The Ecology of Hemlock

A SPECIAL FEATURE ON EASTERN HEMLOCK

Over the past ninety years studies at the Harvard Forest have yielded tremendous insights into the history, ecology and biology of eastern hemlock (*Tsuga canadensis*) in the New England region. Our current research on this long-lived, shade-tolerant and economically-important tree species is remarkably broad, ranging from paleoecological and historical studies of hemlock's response to climate change, fire and human land use, to ecosystem analyses of nitrogen cycling, stand structure and composition in hemlock forests to investigations of hemlock's pollination biology. Many of our new regional and intensive studies are motivated by the progressive expansion of the hemlock woolly adelgid (*Adelges tsugae*) across the northeastern U.S. This introduced insect pathogen is currently decimating hemlock forests across our study region in southern Connecticut and threatens to exert a profound impact on hemlock forest ecosystems across its range. Given the great level of scientific and public interest in hemlock and the great need for information on its role in Northeastern forests, we have developed a special section in this year's annual report on the biology and ecology of hemlock beginning on page 26 that outlines our current studies and some of our collective insights into this important temperate tree species.

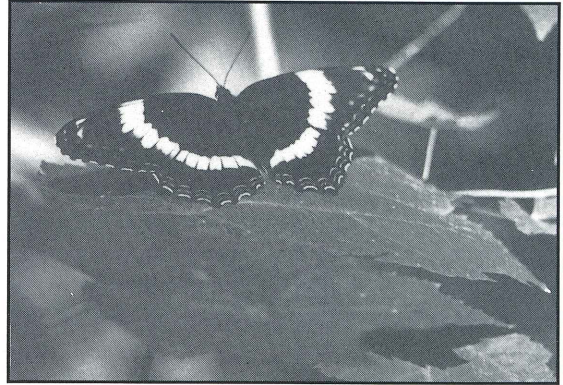


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ANNUAL REPORT OF THE HARVARD FOREST 1996-97

PERSONNEL AT THE HARVARD FOREST 1996-97

John Aber	Bullard Fellow	Joan Kraemer	Clerk Typist, part time
Michael Binford	Associate	Christopher Kruegler	Administrator
Emery Boose	Computer Scientist	Oscar P. Lacwasan	Custodian
Jeannette M. Bowlen	Accountant	Richard A. Lent	Data Manager
John S. Burk	Research Assistant	Anita Locksmith	Summer Cook
Susan L. Clayden	Research Assistant	Harri Lorenzi	Bullard Fellow
Willard Cole	Woods Crew	Lisa Marselle	Summer Cook
Sarah Cooper-Ellis	Research Assistant	Jason McLachlan	Research Assistant
Elaine D. Doughty	Laboratory Assistant	Ellen G. Moriarty	Graphic Artist, part time
Natalie Drake	Palynologist	Glenn Motzkin	Plant Ecologist
John A. Edwards	Forest Manager	Sarah Neelon	Research Assistant
Barbara J. Flye	Librarian/Secretary	John F. O'Keefe	Museum Coordinator
Charles H.W. Foster	Associate	David Orwig	Research Associate
David R. Foster	Director	Dorothy Recos-Smith	Secretary
Donna Francis	Research Associate	Emily Russell	Visiting Scholar
Eldon Franz	Bullard Fellow	Earl Saxon	Bullard Fellow
Janice Fuller	Research Associate	Mayra Serrano	Research Assistant
Jennifer Garrett	Research Assistant	Margaret Silk	Bullard Fellow
Julian Hadley	Research Associate	Benjamin Slater	Research Assistant
Donald E. Hesselton	Woods Crew	Charles C. Spooner	Woods Crew
Guy D'Oyly Hughes	MFS Candidate	P. Barry Tomlinson	E. C. Jeffrey Professor of
Dennis Knight	Bullard Fellow		Biology
Ruth Kern	Research Associate	John Wisnewski	Woods Crew
Keith Kirby	Bullard Fellow	Steven Wofsy	Associate
Matthew L. Kizlinski	Research Assistant	Kerry Woods	Bullard Fellow



INTRODUCTION TO THE HARVARD FOREST

Since its establishment in 1907 the Harvard Forest has served as a center for research and education in forest biology. Through the years researchers at the Forest have focussed on silviculture and forest management, soils and the development of forest site concepts, the biology of temperate and tropical trees, forest ecology, forest economics and ecosystem dynamics. Today, this legacy of research and education continues as faculty, staff, and students seek to understand historical and modern changes in the forests of New England and beyond resulting from human and natural disturbance processes, and to apply this information to the conservation, management, and appreciation of forest ecosystems. This activity is epitomized by the Harvard Forest Long Term Ecological Research (HF LTER) program, which was established in 1988 through funding by the National Science Foundation (NSF).

Physically, the Harvard Forest is comprised of approximately 3000 acres of land in Petersham, Massachusetts that include mixed hardwood and conifer forests, ponds, extensive spruce and maple swamps, and diverse plantations. Additional land holdings include the 25-acre Pisgah Forest in southwestern New Hampshire (located in the 5000-acre Pisgah State Park), a virgin forest of white pine and hemlock that was 300 years old when it blew down in the 1938 Hurricane; the 100-acre Matthews Plantation in Hamilton, Massachusetts, which is largely comprised of plantations and upland forest; and the 90-acre Tall Timbers forest in Royalston, Massachusetts. In Petersham a complex of buildings that includes Shaler Hall, the Fisher Museum, and the John G. Torrey Laboratories provide office and laboratory space, computer and greenhouse facilities, and a lecture room and lodging for seminars and conferences. An additional nine houses provide accommodation for staff, visiting researchers, and students. Extensive records including long-term data sets, historical information, original field notes, maps and photographic collections are maintained in the Harvard Forest Archives.

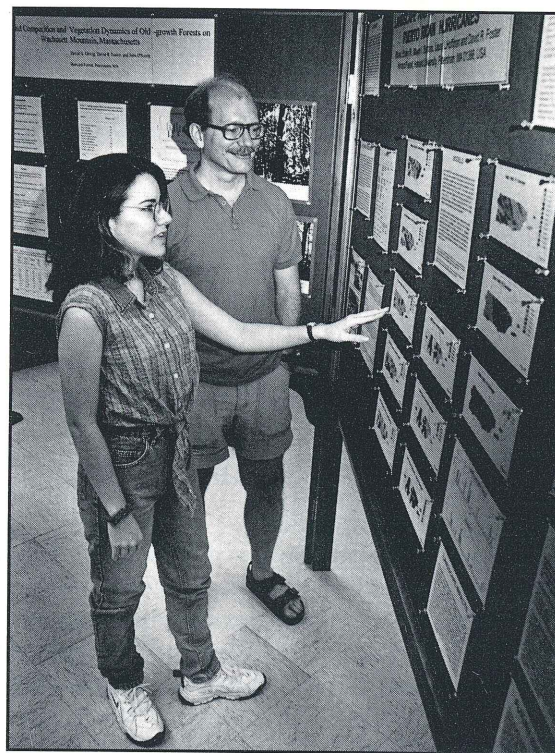
Administratively, the Harvard Forest is a department of the Faculty of Arts and Sciences (FAS) of Harvard University, with the Director reporting to the Dean of FAS. The Harvard Forest administers the Graduate Program in Forestry that awards a Masters degree in Forest Science. Faculty at the Forest offer courses through the Department of Organismic and Evolutionary Biology (OEB), which awards the PhD degree, and through the Freshman Seminar Program. Close association is maintained with the Department of Earth and Planetary Sciences (EPS), the Kennedy School of Government (KSG) and the Graduate School of Design (GSD) at Harvard and with the Department of Forestry and Wildlife Management at the University of Massachusetts, the Ecosystems Center of the Marine Biological Laboratory, Woods Hole, and the Complex Systems Research Center at the University of New Hampshire.

The staff and visiting faculty of approximately 50 work collaboratively to achieve the research, educational and management objectives of the Harvard Forest. A management group comprised of the Director, Administrator, Coordinator of the Fisher Museum and Forest Manager meets monthly to discuss current activities and to plan future programs. Regular meetings with the HF LTER science team provide for an infusion of outside perspectives. Forest management and physical plant activities are undertaken by our four-member Woods Crew and directed by the Forest Manager. The Coordinator of the Fisher Museum oversees many of our educational and outreach programs.

Funding for the operation of the Harvard Forest is derived from endowments and University support, whereas research activities are conducted with grants primarily from the federal government. Major research support comes from the National Science Foundation, Department of Energy (National Institute for Global Environmental Change), the U.S. Department of Agriculture, and the Andrew W. Mellon Foundation. Our summer Program for Student Research is supported by the National Science Foundation, the A. W. Mellon Foundation, and the R. T. Fisher Fund of Harvard Forest.

NEW STAFF

Donna Francis has joined us in the past year from the University of Michigan where she received her PhD in paleolimnology. Donna is working with David Foster and Janice Fuller in our paleoecology group investigating the response of lake ecosystems in central New England to the history and range of land use activities that have occurred in the past 350 years. Ruth Kern received her PhD from the Department of Botany at Duke University in population and community ecology. She is working with David Foster and Glenn Motzkin to link land-use history with vegetation patterns and plant population dynamics. Research assistants joining the Harvard Forest staff include John Burk who replaces outgoing Archivist Sarah Neelon; Jennifer Garrett who is working with Donna Francis and the paleoecology group; Matt Kizlinski who is working in biogeochemistry; and Mayra Serrano, a recent graduate of the University of Puerto Rico who is working with Emery Boose and David Foster on hurricane studies, and replaces Kris Chamberlain who left us earlier this year to join the Peace Corps. Woody Cole joined the Woods Crew as a full-time member.



Mayra Serrano and Emery Boose



Janice Fuller

RESEARCH ACTIVITIES

History of Forests, Environment and People in Central New England

In order to understand the impact of human activity and changing environment on regional patterns of forest composition and dynamics, Janice Fuller has analyzed paleoecological data from 11 lake sites arranged across central Massachusetts. Pollen and charcoal records allow reconstruction of vegetation and fire histories for this region for the past 1000 years. These data have been analyzed in conjunction with archeological, historical and ecological data to determine vegetation responses to human disturbance. Prior to European settlement, there were distinct regional patterns of vegetation composition apparently related to climate, disturbance regime (fire) and substrate. A subtle change in forest composition at higher-elevation sites, starting approximately 550 years before present, is recorded in the pollen data and may be related to climatic change associated with the Little Ice Age and/or activity by Native Americans. Further work is in progress to determine whether climate was indeed the driving factor. Donna Francis is examining chironomid (small invertebrates) remains in the same lake sediment, which may provide information about changes in water temperature. Regional differentiation in forest composition became less pronounced as the vegetation in the

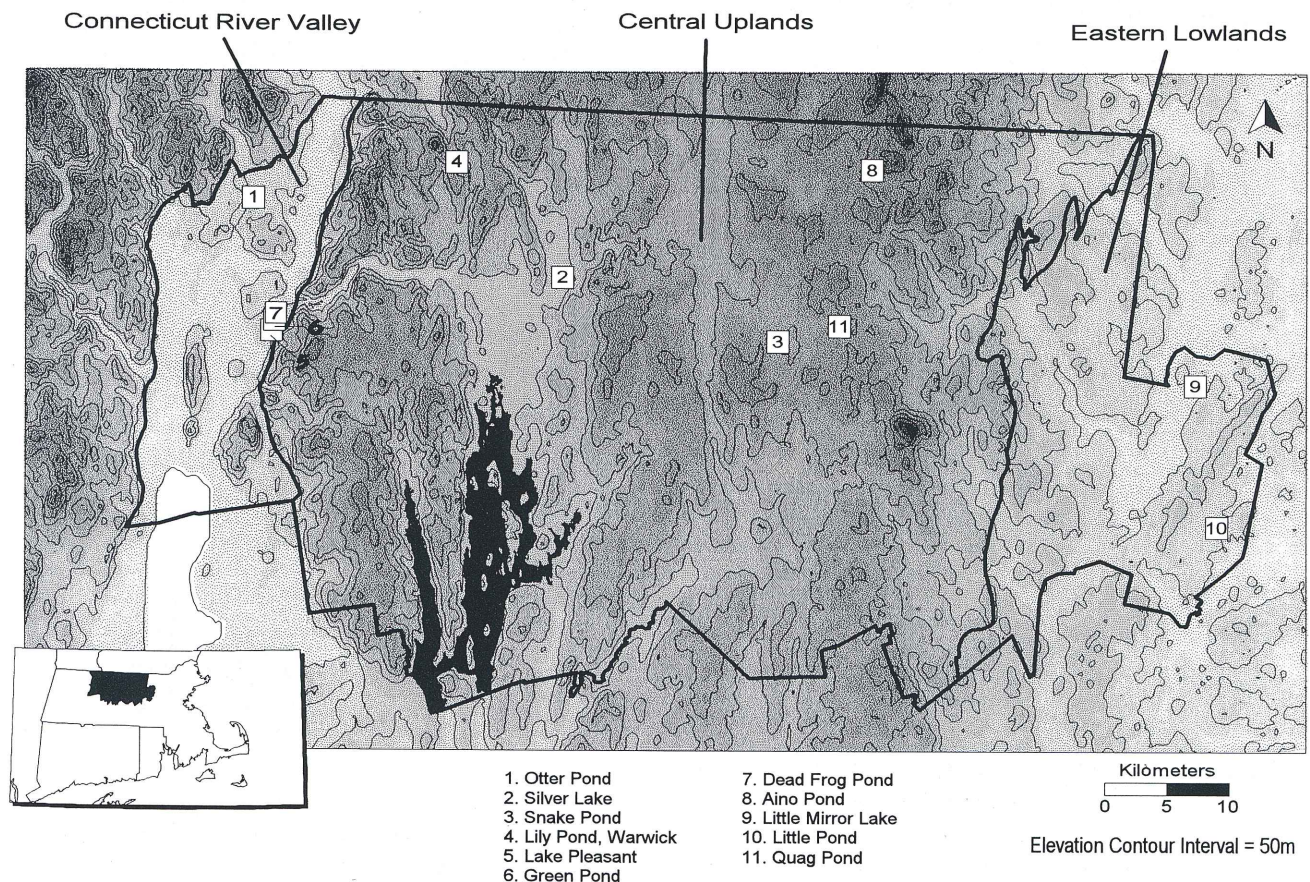
uplands changed, and as hemlock, sugar maple and beech declined in abundance.

Since European settlement, there have been marked changes in forest composition across central Massachusetts. Initially forest cover was reduced dramatically and disturbance-tolerant species, such as chestnut, the birches and red maple, became more abundant. Rates of vegetation change increased sharply soon after settlement at the sites in the Central Uplands of Massachusetts. Forest composition did not change markedly in the lowlands of the Connecticut River Valley and eastern Massachusetts until natural reforestation after agricultural abandonment at the end of the 19th century. Today, forest composition has not returned to that prior to European settlement, despite a reduction in disturbance intensity. Rather, regional patterns of forest composition have become homogenized by widespread disturbance, and are no longer related to the climatic gradient. In association with this project, Mitch Mulholland from the University of Massachusetts has compiled all of the archaeological records for the region and David Foster, Glenn Motzkin and Ben Slater have analyzed historical land-use and forest data. Collectively these studies yield very complementary perspectives on environmental,

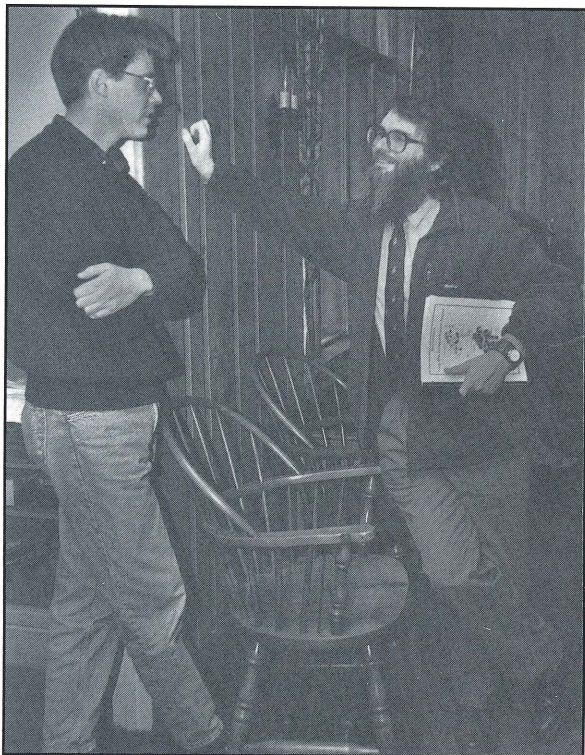
cultural and ecological dynamics and have produced two manuscripts that were accepted for the inaugural issue of the *Journal Ecosystems*.

In related studies, Ben Slater continued his work on the central Massachusetts land-use history and paleoecology project, which has produced two manuscripts in press. He also worked on GIS analysis and produced maps for the Connecticut River Valley pitch pine project, also resulting in a manuscript. Ben and David Foster are working with David Kittredge analyzing data on forest harvesting for the North Quabbin Region.

Site selection, sediment analyses and dating are underway for Donna Francis' project looking at the influence of changing land-use patterns on lake ecosystems of New England. The study investigates the effects of changing land-use patterns on lake ecosystems by examining the sedimentary history of four headwater lakes in southern New England that are similar in physical characteristics but vary in land-use history. Lake characteristics are often influenced by inputs from the surrounding landscape and changing vegetation. Human activity and other disturbances, therefore, can produce changes in the chemistry and biota of a lake. Lake sediments act as a sink for nutrients and other materials



Central Massachusetts study region showing elevational contours, Quabbin Reservoir, the three major physiographic regions and the location of lake sites in our paleoecological study.



Ben Slater and Keith Kirby

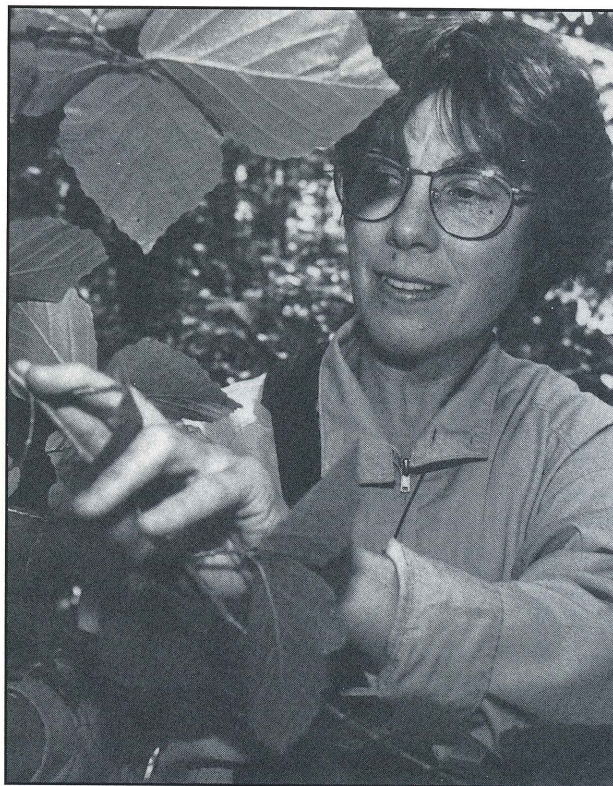
from the landscape, as well as for material produced within the lake itself. Therefore, paleolimnological studies can be used to document changes that have occurred both in the lake and its watershed over time.

Questions being addressed in this study include:

(1) How do broad-scale, long-term disturbances such as deforestation and agriculture in the watershed affect the physical, chemical, and biotic characteristics of lake ecosystems? (2) What are the rates of change in lake ecosystems as compared with terrestrial ecosystems? (3) How do lakes respond when the land-use disturbance ends and natural reforestation and forest maturation occur? Do they return to pre-disturbance conditions, and how long does that take? A set of lakes whose catchments have been influenced by different degrees of human activity are being selected for this study. We are limiting the investigation to effects of agriculture, avoiding urban and industrial influences. Our "least disturbed" site is North Round Pond in Pisgah State Park, New Hampshire, an area that has been studied by Harvard Forest researchers since 1910. The watershed has never been under agriculture of any type, and there is some old growth forest at the south end of the lake. In contrast, the watershed of Pecker Pond in Rindge, New Hampshire was mostly pasture land, and Wickett Pond in Wendell, Massachusetts had a small amount of farming and logging. A fourth pond that has been influenced by more intensive cultivation is being sought.

Long-term Studies of Oak in Central Massachusetts

The role of people, fire and the natural environment in controlling the historical development and dynamics of upland oak forests is a major issue in the management and interpretation of the New England landscape. These factors are being investigated by Susan Clayden, David Foster and David Orwig on the Prescott Peninsula in the Quabbin Reservoir Reserve. This research uses pollen and charcoal analysis of sediments from a small swamp, located in the transition between an oak dominated forest and a hemlock stand, along with other paleoecological approaches, tree-ring analysis (dendrochronology), analysis of historical archives and studies of the modern forests. On the hemlock side, radiocarbon dating indicates that the one meter core of sediments that we obtained represents a full Holocene record that spans the last 10,000 years. Pollen analysis indicates that oak became as abundant as it is today between 3000-2000 B.P. (years before present). Oak was subsequently replaced by a dramatic increase in American chestnut until European settlement when oak, birch, hemlock and red maple increased in abundance. Charcoal analysis of an adjoining lake (Lily Pond, New Salem) indicates high values for



Becky Field, faculty member from the University of Massachusetts, examines the location and condition of bird nests in the forest understory.

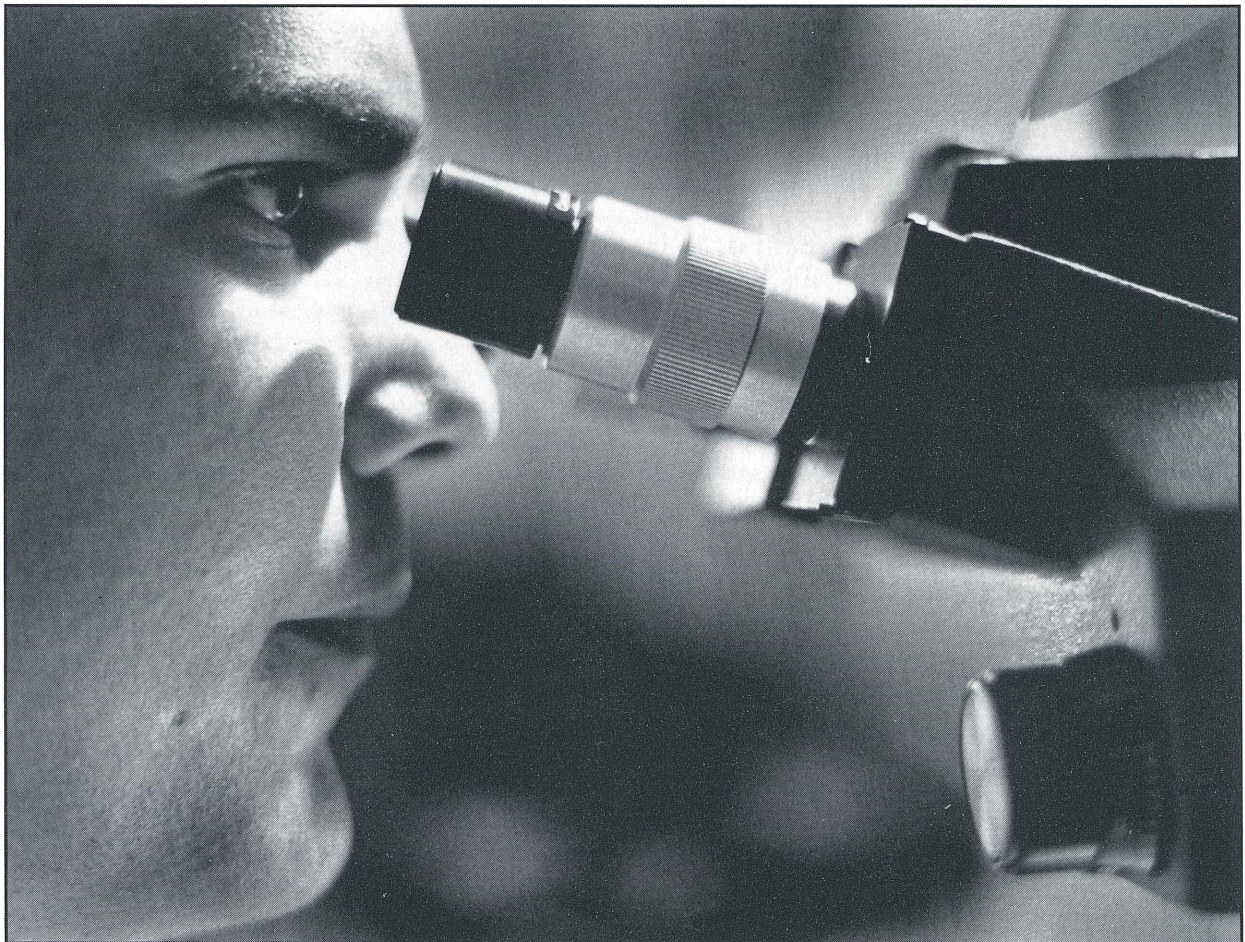
charcoal throughout the pre-settlement period suggesting that both oak and chestnut may have been maintained at high abundance by very occasional fires. Preliminary results of the tree ring study by Dave Orwig indicate that the larger oak and hemlock trees are between ~100-150 years old, while the oldest trees at the site are black gum that exceed 250 years.

Hurricane Impacts to Temperate and Tropical Forests

The impacts of past hurricanes in New England and Puerto Rico, with a focus on the Harvard Forest and Luquillo Experimental Forest LTER sites, are being studied by Emery Boose, Kris Chamberlin, Mayra Serrano, and David Foster with assistance from summer students Laura Hoffman and Will Sloan Anderson. The project employs a combination of historical research and computer modeling. At a regional scale (> 100 km), gradients of wind speed, wind direction, and wind damage are reconstructed for all recorded hurricanes using historical records and a simple meteorological model (HURRECON). At the landscape scale (~10 km), patterns

of damage created by local topography are estimated using a simple topographic exposure model (EXPOS). At specific study sites (~1 km), reconstructions of wind impacts over time may be combined with evidence of other past disturbances (e.g. fire, disease, or human land-use) to build a more complete picture of the site's long-term disturbance regime.

For New England, the 62 hurricanes since 1620 show strong regional gradients from southeast (CT, RI, and southeastern MA coastlines) to northwest (northern VT, NH, and ME) both in maximum intensity and in frequency. These gradients resulted from the consistent direction of the storm tracks, the shape of the coastline, and the tendency for hurricanes to weaken rapidly over land and cold ocean water. Hurricanes were clustered in time, and it was not unusual for New England to be struck by two or even three hurricanes in the same year, while at other times no hurricanes occurred for several decades. Paleocological studies by David Foster and Tom Webb (Brown University) are using these historical data in an attempt to extend the hurricane record back several millennia.



Will Sloan Anderson examines a tree's growth ring to detect past hurricane history.



Dave Orwig coring a tree to determine its age while John O'Keefe looks on.

For Puerto Rico, preliminary studies for 71 hurricanes since 1886 show gradients across the island from southeast to northwest in hurricane frequency and intensity, with all areas subject to repeated damage from hurricane winds. Hurricanes were clustered in time, with peak impacts in the 1890s and around 1930. The steep mountain topography in the Luquillo Experimental Forest creates striking patterns of landscape-level damage in individual storms. Future work will extend the study to major hurricanes from the early 16th C onwards. Hurricanes in Puerto Rico are more frequent and often more severe than in New England, and this difference, plus significant differences in climate, topography, forest vegetation, and land-use history, creates many interesting points of comparison between the two regions.

Forest Response to Experimental Hurricane - Six Years of Change

Working with Elaine Doughty and REU students Kristin McCarthy and Mike Leneway, Sarah Cooper-Ellis has extended the studies of forest composition and structure of the six-year-old experimental hurricane on the Tom Swamp tract and is working with David Foster to synthesize this information in a series of publications. Studies this year focussed on patterns of tree growth and indicated that radial growth rates are highest for chestnut, white pine, red oak, and yellow and black birch, and that all species except white birch have significantly higher

growth rates in the experimental pulldown than in the control. Ingrowth of individual plants from sapling to tree size was heavily dominated by yellow and black birch; as a consequence, birches are increasingly in importance while red oak is decreasing. Sarah Neelon, Kristin McCarthy, and Mike Leneway remeasured saplings and sprouts in the control and experiment and tagged all new stems. The density of saplings and sprouts increased from ~6,000 per hectare before the experiment to ~25,000 per hectare in 1993 but had begun to decline slightly in 1996. Although the density of saplings has increased dramatically, species composition in the regeneration layer has changed relatively little. Red maple has remained important while oak has only a slight presence, and white birch has established and increased as black cherry regeneration declines. By assessing growth rates of trees and saplings as well as relative importance of species in the canopy and regeneration layers, we can begin to interpret and understand the changes in composition and structure of post-disturbance forests.

Wachusett Mountain Old-Growth Forests

In 1995, over 50 ha of old-growth forest were discovered on Wachusett Mountain in eastern Massachusetts. This site contains the highest peak (612 m a.s.l.) and some of the oldest documented forests east of the Connecticut River in Massachusetts. It provides a unique opportunity for research on long-term forest disturbance, vegetation dynamics, and presettlement forest structure.

At the request of the Massachusetts Department of Environmental Management (DEM), which owns the mountain, a northern hardwood stand located on a northwest aspect was extensively sampled in 1996 by Dave Orwig, David Foster and John O'Keefe. This forest contained a mixture of beech, red oak, red maple, sugar maple and yellow birch, and was characterized by widely-spaced, uneven-aged trees with stunted canopies and strongly tapering tree boles. In addition, the forest contained thickets of striped maple, mountain maple, and witch hazel in the sapling layer. An extensive dendroecological analysis of this site revealed red oak ranging in size from 40 cm to over 75 cm dbh and from 170 to 322 years old. Following an initial period of oak establishment from 1670 to 1820, overstory recruitment consisted primarily of yellow birch and beech in the 1800's, and maple species in the 1900's. These gradual changes in species composition over long time periods indicate the protected nature of this stand and suggest that a change in disturbance regime from large-scale to localized disturbances occurred during the last several centuries. A final report to DEM was concluded and verbal reports on the old growth forest and various development schemes were provided at public meetings as outcomes of this study.

During the summer of 1997, David Orwig and summer student Sarah Picard began to establish permanent plots and to sample several additional old-growth stands on Wachusett Mountain. These include steep talus slopes on both eastern and southern aspects, which are dominated by yellow birch, red maple, and red oak, and a hemlock-dominated forest located on a western slope. To-date the oldest tree sampled was a yellow birch that exceeded 360 years in age. Structural and dendroecological information are being obtained from trees in these forests in order to derive a more complete disturbance history of the old-growth landscape on the mountain and to complement land-use history information for the entire mountain. This information is extremely important in helping us understand the historical and current dynamics of these forests and to better direct the protection and management efforts of these stands.

Plant Population Response to Land-use History

Ruth Kern began a life history analysis of plant distribution in relation to land-use history building on landscape and community level studies by Glenn Motzkin and David Foster and extending initial studies by Kathleen Donohue on the population biology of *Gaultheria procumbens* (wintergreen) and other ericaceous plants. Using existing data sets for Prospect Hill at Harvard Forest and the Montague Sand Plain collected by Glenn, Ruth has been investigating patterns of species distribution at each site and examining how the existing patterns are correlated with land-use history. In addition, species' response to land-use history is being compared at the two contrasting



sites. The life-history traits of species behaving in similar and in contrasting ways are being researched in order to understand mechanisms controlling current patterns of vegetation distribution.

Plant Biology

Calamus is the largest genus of palms, with over 350 species and is the major source of rattan canes, which are of commercial importance in Malaysia and Indonesia. Beginning with a student project in Biology S-105, Barry Tomlinson and student Russell Spangler explored the vascular anatomy of *Calamus* in comparison with the well-established model for palm vasculature provided by the small palm *Rhapis excelsa*. It was surprising to find that *Calamus* has unique features not found in the *Rhapis* model and is without direct axial vascular continuity. We interpret this in terms of the hydraulics of the axis, which must be well-protected against xylem cavitation, and suggest that these features may account for the ecological success of the group. There are broader implications of this study in terms of water movement in plants generally. An evidently highly efficient system seems to be dependent on symplastic rather than apoplastic transport in the stem. In the related conifer genera *Cephalotaxus* and *Torreya*, Barry, with student Elizabeth Zacharias, demonstrated an unusual bijugate phyllotaxis, constant in *Cephalotaxus* but alternating with a decussate arrangement in *Torreya* on a regular seasonal basis. The results can be used as evidence that phyllotactic changes are not dependent on the size of

the shoot apical meristem. Material for this study came from the living collections of the Arnold Arboretum.

Barry conducted a study of pollen structure in the distinctive conifer genus *Phyllocladus* in collaboration with Marie Kurmann, showing features of sporoderm morphology that might be interpreted as "vestigial," but are also related to unusual hydrodynamic features of pollen function. Barry also contributed some anatomical expertise to the demonstration by Mike Donoghue and Dave Hibbert that a Cretaceous fossil, interpreted as a basidiomycete, was most likely the bark of a conifer. The chief conclusion of this study was that bark anatomy of conifers is very little known, in part because of technical difficulties in processing material. As a contribution to the series "Families and Genera of Vascular Plants," Barry produced a draft manuscript dealing with the Rhizophoraceae and Anisophylleaceae. This activity showed how little biological information there is for most tropical plant genera, especially relevant in the Rhizophoraceae where the mangrove genera are reasonably well studied because of their ubiquity, abundance and ecological importance.

Mosses of Massachusetts

Sarah Cooper-Ellis has been collaborating with Jeanne Anderson of the Nature Conservancy and Benito Tan from the Farlow Herbarium at Harvard on a compilation of the county distributions of mosses in Massachusetts. They have added 18 species to the state records and 194 additional county records, bringing the known state moss flora to 355 species and 17 varieties. New state and county taxa are based on published records and collections by knowledgeable individuals including present and former Harvard Forest research staff Glenn Motzkin and Paul Wilson. Sarah recently had a manuscript on her related

work on the bryophytes of old-growth forests in western Massachusetts accepted for publication in the *Journal of the Torrey Botanical Society*.

Southern Yucatan Peninsula Region (SYPR)

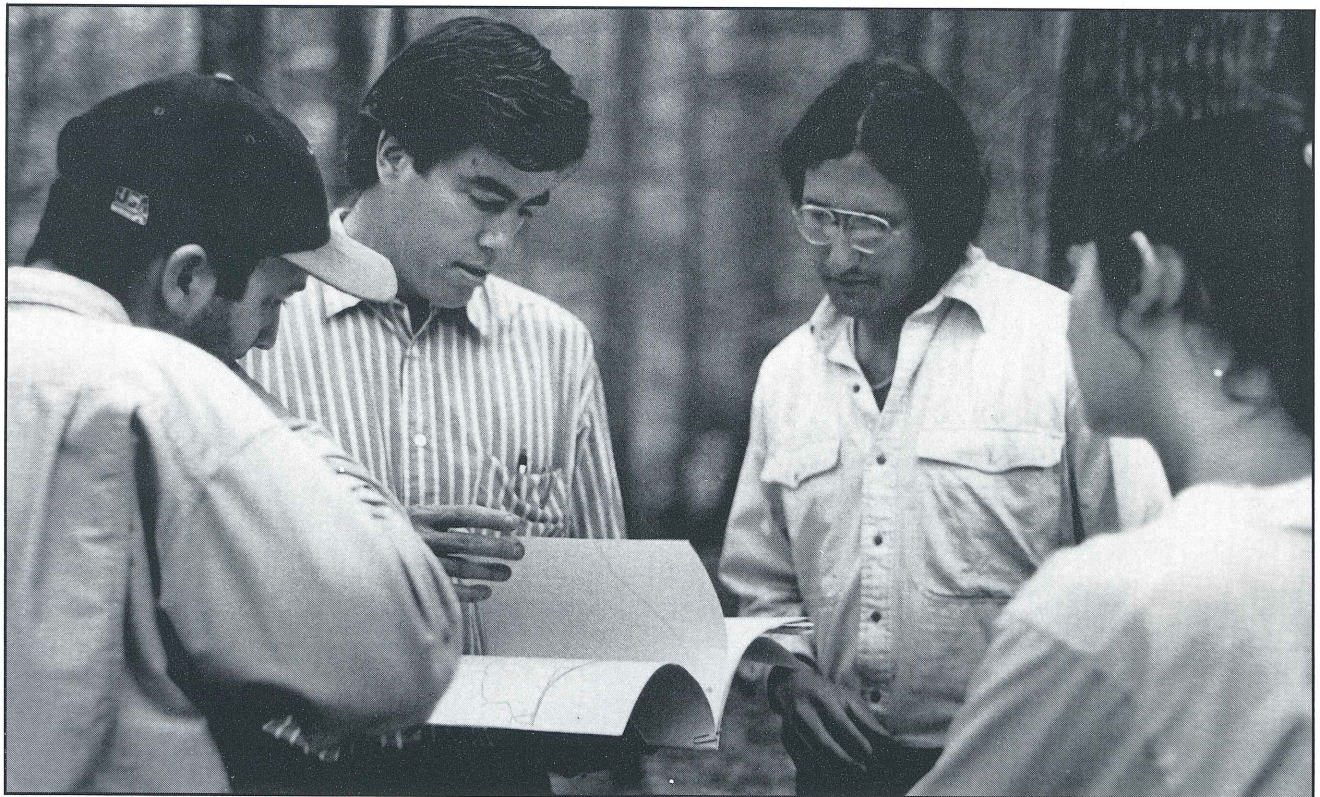
In conjunction with researchers from Clark University (B. Turner, B. Savitsky, J. Geoghegan) and ECOSUR - Chetumal, Mexico, David Foster has received funding from the Land Use Land Cover Change program of NASA to evaluate past and recent changes in vegetation associated with human activity in the SYPR. This project combines social science, economic analysis and Geographic Information Systems/Remote Sensing with ecological studies in an effort to interpret the factors controlling, and the details of, environmental change in this moist tropical region. The area is important today as it has extensive intact forest cover, a low human population, contains several large biosphere reserves, and is becoming the focus of development for ecotourism. From a historical perspective the region is fascinating as it formerly supported a very large Mayan population and a dense array of temples, cities and house sites until approximately 1000 A.D., when the civilization began a major decline and the landscape gradually reforested. Consequently, there are interesting parallels between the history of this tropical region, the Luquillo Experimental Forest in Eastern Puerto Rico and the landscape of New England in terms of historical deforestation/reforestation cycles. These parallels will become the focus of a comparative study of these distinctly different geographic regions. David Foster travelled with the Clark group to the SYPR in July in order to meet their Mexican colleagues and to become more familiar with the region.



Cape Cod and the Islands

David Foster continued field studies on the outer Cape as background for research that he and Glenn Motzkin are pursuing in the development of an overview on historical dynamics of the New England landscape. The objective is to synthesize existing paleoecological, historical and ecological research and to conduct additional work as necessary to develop an understanding of the vegetation and its history that complements the extensive studies that Harvard Forest researchers have undertaken for central New England. With this objective David and Glenn have been discussing field work and land-use studies on Martha's Vineyard and Block Island. In all of the coastal landscape from the Cape to the smaller islands, there exist conservation concerns and management issues similar to those of the Montague Sand Plain in the Connecticut River Valley where Glenn, Art Allen, David and others have published results of their extensive work on the pitch pine, scrub oak and grassland vegetation. Recognition by Glenn that land-use history (notably the

absence of plowing as indicated by a soil plow layer) strongly controls modern characteristics of the vegetation, has exerted a strong impact on the interpretation and management of sand plain and coastal vegetation.



David Foster and Glenn Motzkin (center) consult with Sebastian Catovsky and Chrissy Frederick on site selection for Sebastian's thesis project.

Harvard Forest LTER Program

The Harvard Forest is one of twenty sites forming the Long Term Ecological Research (LTER) program sponsored by the National Science Foundation. Each site addresses ecological questions of a long-term nature; collectively the sites undertake comparative studies across ecosystems. Representatives from the LTER sites and NSF meet twice annually to develop the collaborative studies. The central theme of the Harvard Forest LTER is a comparison of historically-important, physical disturbances and modern, chemical disturbance in terms of their effects on forest ecosystem structure and function. One fundamental question is whether chronic, low-level additions of pollutants can result in more long-lasting alterations of ecosystem functions than does the natural regime of disturbance. A second major focus of the Harvard Forest LTER program is an evaluation of the long-term legacies of human land-use activities on modern forest structure, composition and function.

The research project involves soil scientists, atmospheric chemists, and ecologists studying physiological, population, community and ecosystem processes.

Principal investigators represent the Department of Biology (F. Bazzaz), Earth and Planetary Sciences (S. Wofsy), Graduate School of Design (M. Binford), and Harvard Forest (D. Foster, E. Boose, R. Lent) at Harvard University as well as the Ecosystems Center-MBL, Woods Hole (J. Melillo, K. Nadelhoffer, P. Steudler), the Complex Systems Research Center at the University of New Hampshire (J. Aber), Mt. Union College (C. McClaugherty), Rutgers University (E. Russell), and the University of Massachusetts (M. Mulholland). The research is organized to maximize the interactions among scientists from different disciplines. Four core experiments include: (1) re-creation of physical disturbances, including catastrophic hurricane blowdown and smaller windthrows; (2) simulation of chronic chemical disturbance by altering inputs of important pollutants; (3) interactions between physical and chemical disturbances; and (4) repetition of treatments to assess the range of variation in response.

The LTER science group meets approximately monthly. The annual Harvard Forest Ecology Symposium is held to present current research. Abstracts from this meeting are published annually. The program for the 1997 symposium is shown on the following page.



Fakhri Bazzaz preparing slides for the Ecology Symposium

Harvard Forest Ecology Symposium 1997

Titles of Abstracts and Presentations

- Aber, J., A. Magill, B. McDowell and B. Currie. Understanding Nitrogen Retention in Carbon Limited Soils.
- Barnes, D. Evaluation of Sources and Sinks for Greenhouse and Ozone-depleting Gases in Rural New England.
- Boose, E., K. Chamberlin and D. Foster. Landscape and Regional Impacts of New England Hurricanes.
- Boose, E., L. Hoffman and D. Foster. Landscape and Regional Impacts of Puerto Rican Hurricanes.
- Bowden, R., R. Clark, C. McClaugherty, and T. Sipe. The Impact of Land-use Legacies on Forest Soil-Plant-Atmosphere Interactions.
- Catovsky, S. and F. Bazzaz. How do Rates of Canopy Carbon Uptake Differ for Eastern Hemlock, Red Oak and Red Maple?
- Catricala, C., K. Newkirk, J. Melillo, P. Steudler and K. Tuovinen. Effects of Soil Warming on Root and Microbial Respiration.
- Cavender-Bares, J. and F. Bazzaz. Changes in Drought Response Strategies with Ontogeny in *Quercus rubra*.
- Clayden, S., D. Foster, D. Orwig and E. Doughty. Holocene Vegetation and Disturbance History From Oak and Hemlock Forests.
- Compton, J., A. Elseroad, E. Cline and R. Boone. The Role of Land-use History and Present Vegetation in Soil Nitrification.
- Compton, J., R. Boone, D. Foster and E. Davidson. Impact of Plowing and Abandonment on Soil C and N Storage.
- Cooper-Ellis, S. and D. Foster. Regeneration Following Experimental Hurricane Disturbance.
- Cooper-Ellis S. and D. Foster. Tree Growth Response to Experimental Hurricane Disturbance.
- Crill, P. and K. Bartlett. Diurnal to Interannual Scales of Variability in Ambient Methane at the Harvard Forest.
- Currie, W. and J. Aber. Using a Spatially-explicit Process Model to Relate Litter Decomposition to Solute Fluxes in Soil Solution.
- Currie, W., K. Nadelhoffer and J. Aber. Redistribution of $^{15}\text{NO}_3$ and $^{15}\text{NH}_4$ in Vegetation and Soil Interpreted with TRACE.
- Donohue, K. Seed and Fruit Characters of Ericaceous Species: Variation Within Natural and Altered Environments.
- Donohue, K. Below Ground Growth Patterns and Vegetative Growth Rates of *Gaultheria procumbens*.
- Donohue, K., L. Williams III and G. Motzkin. The Distribution of Ericaceous Species Along Plow Boundaries in the Montague Sand Plain.
- Donohue, K., E. Zacharias and G. Motzkin. Demographic and Morphological Variation of *Gaultheria procumbens*.
- Fitzjarrald, D., K. Moore, R. Sakai and J. Freedman. Forest-atmosphere Exchange Processes: Report on Activities During 1996.
- Foster, D. and J. Fuller. Detection of Forest Pattern, Dynamics and Response to Disturbance: Historical and Paleoecological Approaches.
- Foster, D., M. Fluet and E. Boose. Human or Natural Disturbance: Landscape-scale Dynamics of the Forests of Puerto Rico.
- Foster, D., G. Motzkin and B. Slater. Land-use History as Long-term Broad-scale Disturbance: Regional Forest Patterns.
- Francis, D. and D. Foster. Influence of Changing Land-use Patterns on Lake Ecosystems in Southern New England.
- Fuller, J., D. Francis and D. Foster. Potential Little Ice Age Climate Signal in Massachusetts Lake Sedimentary Records.
- Fuller, J., D. Foster, J. McLachlan, M. Binford, N. Drake and E. Doughty. Impact of Human Activity on Regional Forests.
- Gardner, A. and J. O'Keefe. Influence of Microhabitat on Tree Seedling Establishment on 1938 Hurricane Sites.
- Goltz, S., D. Hollinger and E. Davidson. Regionalizing Harvard Forest Flux Measurements: Studies from Howland, Maine.
- Hadley, J. Carbon Dioxide Exchange by the Understory of an Old-growth Hemlock Forest.
- Hughes, G. Native and Alien Plant Species Response to Elevation and Land Use on Mt. Kamakou, Molokai, Hawaii.
- Hughes, G. A Landscape Scale Native and Alien Plant Species Response to Elevation and Land Use in Hawaii.
- Jenkins, J. and J. Aber. Effects of Hemlock Woolly Adelgid (*Adelges tsugae* Annand) Infestation on Ecosystem Process.
- Kittredge, D. and D. Foster. Timber Harvesting Patterns in the North Quabbin Region.
- Langtimm, C. and R. Field. Mice and Songbirds: Vertical Distributions and Predator-Prey Interactions in a New England Forest.
- LeBlanc, R., J. Lachance, M. Chesterton and B. Shelley. Effects of Low Flow on Benthic Macroinvertebrates in Small Streams.
- Lefer, B. and R. Talbot. Dry Deposition of Atmospheric Nitrogen in a Forest Setting.
- Magill, A. and J. Aber. Chronic Nitrogen Additions and Litter Decomposition Processes.
- Martin, M. and J. Aber. The Role of Harvard Forest in a NASA/LTER Collaboration to Validate Earth Observation Systems.
- McLachlan, J., D. Foster and F. Menallad. Post-settlement History of Older Growth Hemlock Woodlots.
- Micks, P., K. Nadelhoffer and M. Downs. Effect of Litter Age and N Inputs on Litter Decomposition at the Chronic N Experiment.
- Moody, J., J. Munger and A. Goldstein. Using Transport Probabilities to Characterize Regional-scale Pollution Sources.
- Moore, K. and D. Fitzjarrald. Multifilter Shadowband and Reflectance Measurements at Harvard Forest.
- Motzkin, G., S. Ciccarello and D. Foster. Temperature and Leaf Phenology in Scrub Oak Thickets.
- Motzkin, G., W. Patterson and D. Foster. A Regional-Historical Perspective of Communities in the Connecticut Valley.
- Munger, J., P. Czepl, M. Goulden, A. Goldstein and S. Wofsy. Forest-Atmosphere Interactions: a Large-scale Perspective.
- Nadelhoffer, K., R. Boone and J. Canary. Carbon Turnover in Forest Soils Subjected to Chronically Manipulated Litter Inputs.
- Nadelhoffer, K., M. Downs, P. Micks and K. Kim. Litter Decomposition at the Harvard Forest Chronic N Addition Experiment.
- Neelon, S., S. Cooper-Ellis and D. Foster. Understory Vegetation Response to Experimental Hurricane Disturbance.
- Newkirk, K., C. Catricala, P. Steudler, J. Melillo, J. Aber and D. Pelletier. Soil Warming: 1996 Update.
- O'Keefe, J. Woody Species Phenology, Prospect Hill Tract, Harvard Forest - 1996.
- O'Keefe, J. and A. Gardner. Regeneration Following Clearcutting of Red Pine Overstory - Year 7.
- Orwig, D. and D. Foster. Stand and Landscape Level Impacts of Hemlock Woolly Adelgid Outbreaks in Southern New England.
- Orwig, D., D. Foster and J. O'Keefe. Composition and Vegetation Dynamics of Old-growth Forests on Wachusett Mountain.
- Russell, E. Have the Basic Vegetation Patterns of the Northeastern U.S. Changed Over the Last Few Centuries?
- Shelley, B., K. Byrnes, K. O'Brien and T. Picerno. Spatial Distribution of Aquatic Bryophytes in Three Low-order Streams.
- Shelley, B., M. Chesterton, J. Lachance and R. LeBlanc. Understanding the Effects of Flow Disturbances on the Distribution of Bryophytes.
- Trumbore, S., J. Gaudinski, E. Davidson and E. Belk. Soil Carbon Dynamics at the Harvard Forest.
- Woods, K. Stability, Change and Invasion in Late Successional Forests: Permanent Plot Studies in Northern Michigan.

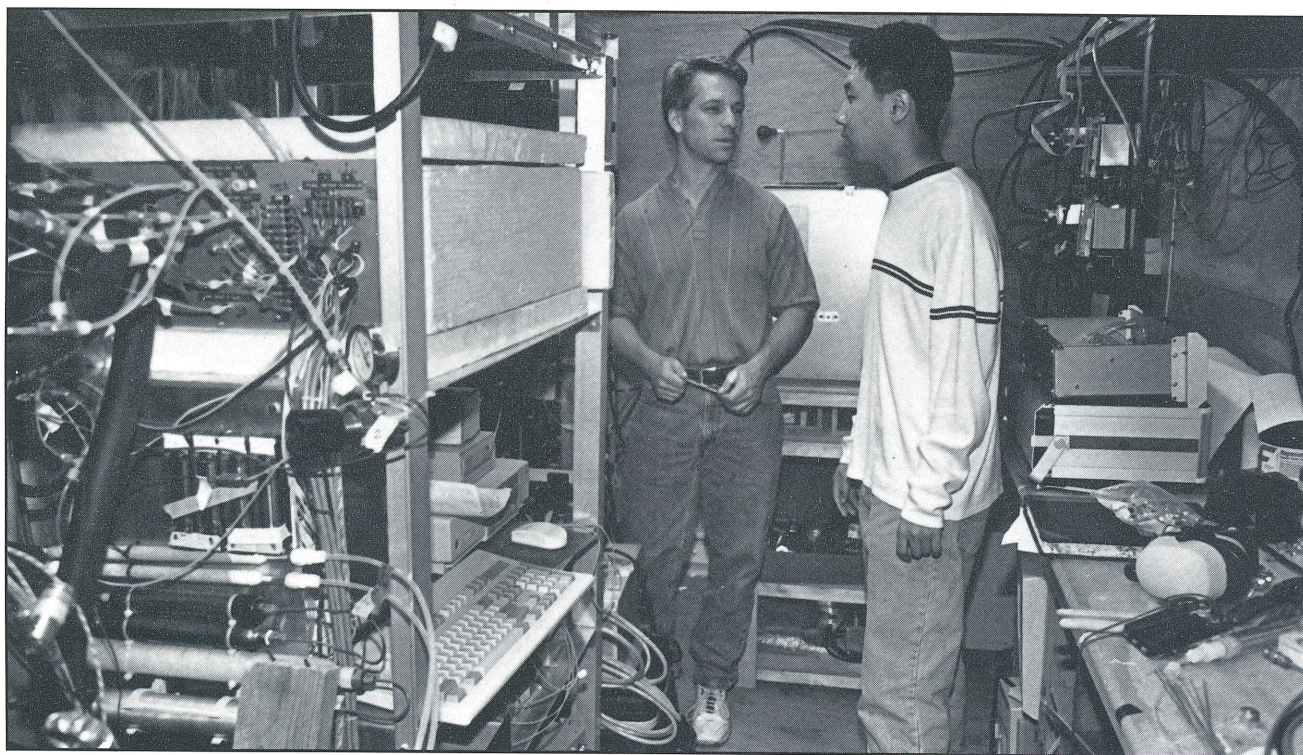
National Institute for Global Environmental Change (NIGEC)

Harvard University serves as the Northeastern Regional Center for the NIGEC program sponsored by the Department of Energy. The purpose of NIGEC research is to improve the understanding of mechanisms of global environmental change, to develop innovative experimental and observational programs that enhance the understanding of ecosystem and regional scale processes contributing to global change, and to provide educational opportunities in global environmental change research. The Center is administered by the Division of Applied Sciences and a large proportion of the field studies are conducted at the Harvard Forest. Researchers include many of the LTER scientists (Bazzaz, Foster, Melillo, Nadelhoffer, Wofsy) in addition to the faculty from the University of New Hampshire (P. Crill, R. Harris, R. Talbot), State University of New York (D. Fitzjarrald, K. Moore) and Woods Hole Research Center (E. Davidson), University of Virginia (J. Moody), University of California (S. Trumbore), U. S. Geological Survey (E. Sundquist) and Harvard Forest (J. Hadley).

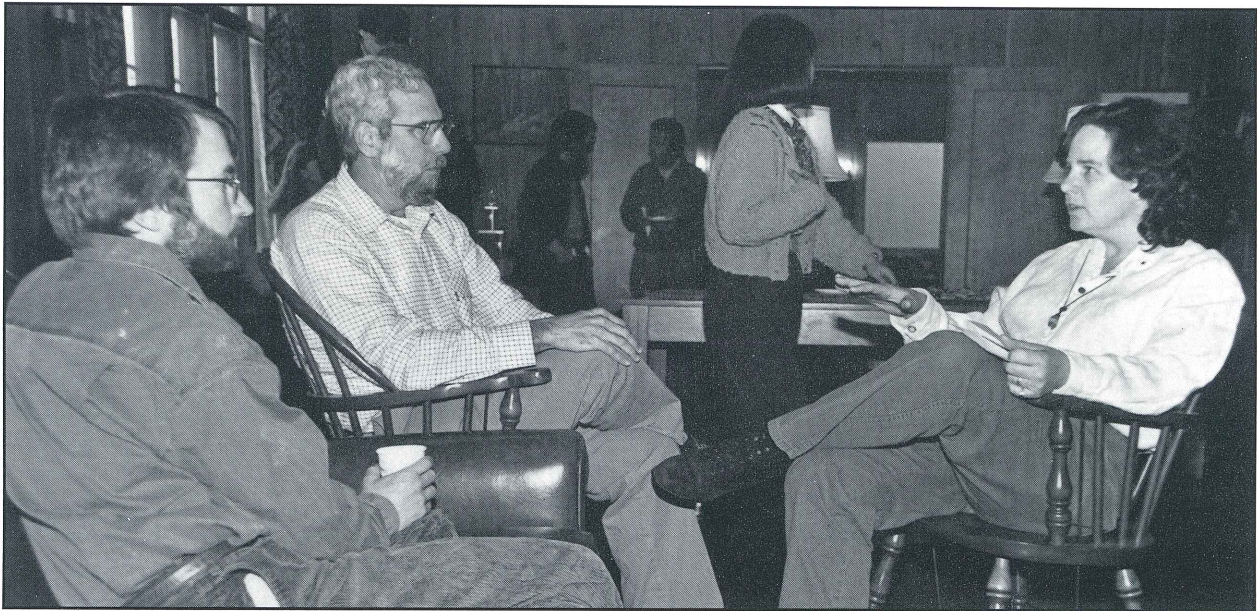
BULLARD FELLOWS

John Aber (University of New Hampshire) spent his fellowship collaborating with David Foster in writing and editing the LTER Synthesis volume. John completed 3 chapters for this volume on: (1) the chronic N experiment; (2) current rates of cycling of carbon and nitrogen across the Harvard Forest in relation to previous land use; and (3) different computer models which have been used to summarize results of extensive field studies. The volume is more than half done and John and David are working with the LTER group to bring it to completion by year's end.

Eldon Franz's (Washington State University) research in the Bazzaz Laboratory in Cambridge focussed on an experiment in the suite of controlled ambient-and doubled- CO_2 chambers designed to define the fitness landscape of plants as a function of insect resistance, herbivory, water stress, and CO_2 . His work also included a proposal for applying the fitness landscape approach in a study of the evolution of the tree/soil feedback in cedar/hemlock forests. He prepared and completed several



Peter Czepiel and Young-Soo Lim from the Department of Earth and Planetary Sciences supervise the array of pumps, sensors and computers at the Environmental Monitoring Station.



Eric Davidson, Paul Steudler and Kathy Newkirk at the Ecology Symposium.

manuscripts, and worked on a review of subsidy/stress research that focuses on a theoretical framework for predicting the vulnerability of ecosystems to change and examined it *vis a vis* certain other approaches.

Keith Kirby (English Nature Conservancy Council) analyzed and interpreted changes in woodland ground flora using data collected previously in Great Britain. He tested the potential of Ellenberg values and plant strategy theory developed by the unit of Comparative Plant Ecology for understanding changes in the ground flora. Keith submitted four papers from work completed or carried out while a Bullard Fellow on: (1) assessments of the amount of fallen dead wood in British woodland; (2) change in composition and structure at Monks Wood (1966-1996); (3) changes in the ground flora at Wytham Woods (1974-1991); and (4) a framework for looking at variations in the ground flora of managed and unmanaged woods.

Harri Lorenzi (Editora Plantarum Ltd., Brazil) studied herbarium specimens of ten large botanical families of the Brazilian flora. The study consisted of the examination of all type specimens available in the Harvard University Herbaria and the New York Botanical Garden of the species found in the Brazilian territory of the families Acanthaceae, Borgainaceae, Labiatae, Rubiaceae, Rutaceae, Verbenaceae, Sapindaceae, Erythroxylaceae, Annonaceae and Bignoniaceae. Field work consisted of photographing and identifying local plants - herbaceous plants, climbers and shrubby garden plants in addition to trees and weeds. This work was concentrated mostly at the Arnold Arboretum. Harri also made progress on the development of an identification key for the Brazilian trees based on leaf image matching.

Earl Saxon's (Wet Tropics Management Authority, Queensland, Australia) research focussed on monitoring tropical forest disturbance and carbon dioxide emissions with nighttime satellite imagery. This study demonstrated a close correlation between nighttime lights and national CO₂ emissions. Earl participated in three research seminars: (1) International Environmental Management; (2) Global Environmental Assessment; and (3) Global Change and Health.

Margaret Silk (University of California) has spent much of her fellowship collaborating with Missy Holbrook (OEB) on glasshouse and experimental studies in Cambridge. Their mutual interests and activities have concentrated on water movement in plants and the physiology of vines and climbing plants.

Kerry Woods (Bennington College) focussed his efforts on a massive data set from long-term studies at two old-growth forest sites in Michigan. Permanent plots date to 1962 at one site (28 plots) and to 1935 at the other (140 plots); all were remeasured in the last few years. These studies were extended to include large mapped stands, increment cores of several hundred trees and deer exclosure studies. These old-growth stands, free of major disturbance for centuries, are nonetheless quite dynamic; species composition continues to change through competitive replacements and invasion of new dominant species. Kerry has also been active on an *ad hoc* committee established by the Ecological Society of America to implement an electronic data archive for the ecological sciences.

EDUCATIONAL ACTIVITIES

Barry Tomlinson taught Biology S-105 (*Biodiversity of Tropical Plants*) at Fairchild Tropical Garden, Miami, Florida under the auspices of the Harvard Summer School. Biology 178 (*Evolution of Plant Development*) was taught with Toby Kellogg and Missy Holbrook, and in the spring term Barry taught the Freshman Seminar with David Foster and members of the Harvard Forest staff. Barry participated in Biology 399 (*Topics in Evolutionary and Organismic Biology*) with a discussion of current research on conifer reproduction. In Biology 309, with student Russell Spangler, work was focussed on rattan anatomy. With undergraduate senior Elizabeth Zacharias, research on conifers at the Arnold Arboretum was completed. During the spring semester readings and discussion were conducted in the area of tree architecture and wood anatomy with graduate students Christine Muth and Renee Richer. Part or all of these activities were conducted at Harvard Forest. With freshman Niki Santos, Barry began a catalogue of the botanical illustrations of Priscilla Fawcett, resident illustrator at Fairchild Tropical Garden until her recent retirement. Ms. Fawcett had illustrated extensively Barry's books and research papers; her published drawings approach one thousand. As an addendum to the course Biology 102 (*Evolution and Biology of the Seed*), an extensive essay on the seed was drafted in collaboration with sculptor Michelle Oka Doner, to be included in an exhibition catalogue.

John O'Keefe served on the thesis committee for Amanda Gardner at Antioch Graduate School, Keene, New Hampshire. He oversaw the field work portion of her project entitled "Influence of Microhabitat on Tree Seedling Establishment in Salvaged and Unsalvaged 1938 Hurricane Blowdown Sites," which was conducted at Harvard Forest. Glenn Motzkin advised Antioch Graduate Student Stephanie Cirrarello on her project investigating effects of temperature on scrub oak leaf phenology in areas of the Montague Sand Plain that are prone to frost pockets.

David Foster served as advisor for MFS student Guy D'Oyly Hughes who successfully completed and defended his thesis "Alien Plant Invasion on Hawaiian Mountains in Relation to Canopy Cover and Feral Ungulate Activity." Guy departed the Harvard Forest after graduation and his marriage for a new position with the Nature Conservancy in Hawaii. David also served on the graduate committee of Sebastian Catovsky (OEB), Kristina Hill (GSD) and Ann Hesperger (GSD) and commenced advising Jeff Parks, ME candidate on a thesis concerning the ecology of Atlantic White Cedar Swamps.

Summer Research Programs

The Harvard Forest Summer Student Research program attracted a diverse group of students to receive

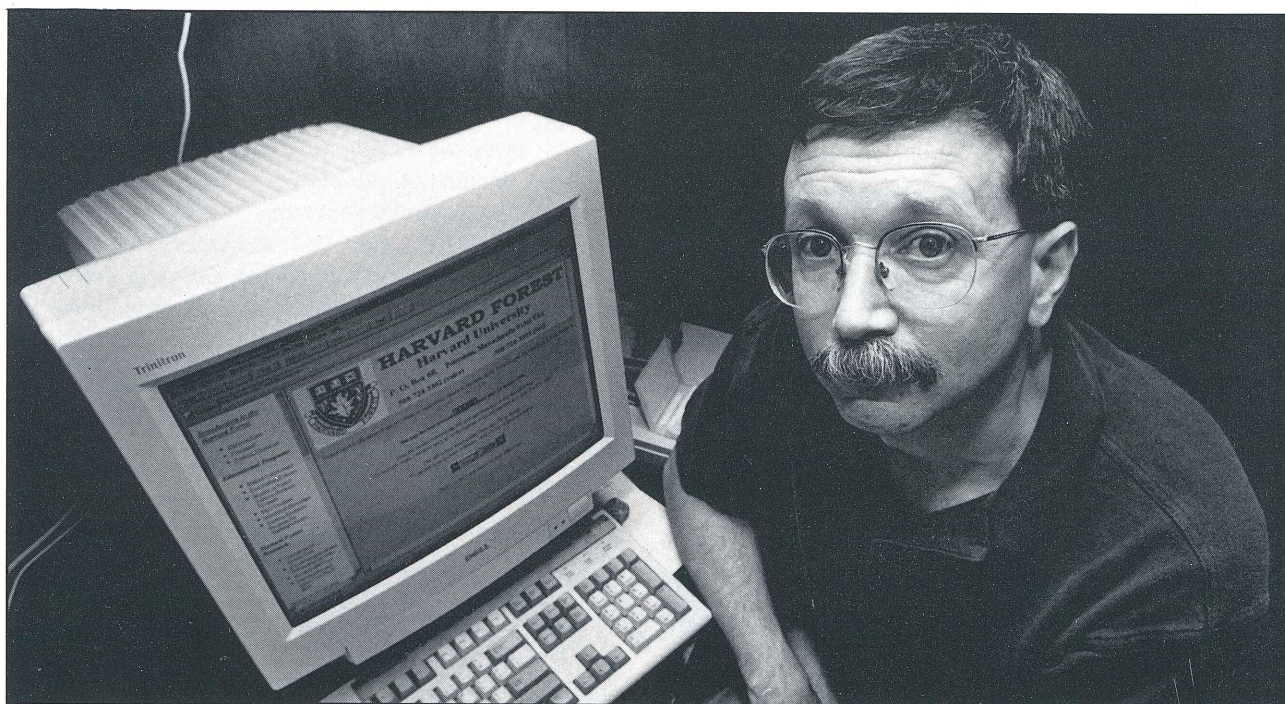
hands-on training in scientific investigations, and to gain experience in working on long-term ecological research. The program, coordinated by Chris Kruegler, Administrator at the Harvard Forest, was supported by NSF Research Experience for Undergraduates, National Institute for Global Environmental Change, Mellon Foundation and the Harvard Forest. Students work closely with faculty and scientists, and many conduct their own independent research studies. The program includes weekly seminars from resident and visiting scientists, discussions on issues pertinent to careers in science (e.g. career decisions, diversity in the scientific community, ethics in science), and field trips on soils, land-use history, plant identification and vegetation. An annual field trip is made to the Institute of Ecosystem Studies (Millbrook, NY) to participate in a Forum on Jobs in Ecology, which includes discussion of environmental occupations with students and professionals employed in the field. The summer program culminates in the Annual Summer Student Research Symposium, in which students present major results of their summer work. The Collaborative Research for Undergraduate Institutions (CRUI) program with nine students and three faculty from Mount Union College, Allegheny College and Gustavus Adolphus College joined the Harvard Forest Summer Research program for the second year.

Summer Students, 1997

William Sloan Anderson	University of Massachusetts
Richard Bakker	Mount Union College
Jesse Bellemare	University of Massachusetts
Dax Bennett	Gustavus Adolphus College
Callie Braun	Gustavus Adolphus College
Cristi Braun	Hampshire College
Kevin Clarke	University of New Hampshire
Brett Danner	Gustavus Adolphus
Christine Frederick	Pennsylvania State University
Heather Frankland	Mount Union College
Samuel Gale	University of Minnesota
Cindee Giffin	Allegheny College
Jessica Graham	Mount Union College
Evan Kane	Michigan Tech. University
Nicole Lavelle	Mount Holyoke College
Delphis Levia, Jr.	Clark University
Young-Soo Lim	Harvard University
Amanda Lodge	Allegheny College
David Mausel	University of Massachusetts
Jack McFarland	University of Virginia
Christy Meredith	Allegheny College
Sarah Picard	Bates College
Trina Roberts	Harvard University
Jonathan Sanderman	Brown University
Nina Wurzbarger	University of California, Davis



Part of the Summer Research Group



Rich Lent and the Harvard Forest Web Page



ACTIVITIES OF THE FISHER MUSEUM

The Fisher Museum plays an important role in the educational mission of the Harvard Forest by providing a public outlet for information related to research in forest biology and management. The Museum also provides a unique setting for conferences sponsored by the Forest and outside organizations. Dr. John O'Keefe has primary responsibility for the development of activities and coordination of the use of the Museum.

Through the continuing efforts of our enthusiastic dedicated volunteers the Museum enjoyed yet another very successful weekend schedule during the summer and fall of 1996, welcoming over eleven hundred visitors. The Sixth Annual Volunteer Recognition Dinner in November provided an opportunity to review the season's highlights while sharing good food and companionship. As now seems customary, Bob Lane shared most active volunteer honors (his fourth time) with several others including Bill and Marianna Berry, Rosalie Fiske, Dick Sherwood and Tom and Laura Webber. Helen Gronich was recognized for her six years of work as volunteer coordinator as she prepared to move to Portland, Maine, and Mary Ann Walker was welcomed as the new volunteer coordinator. On a more solemn note, this past spring the volunteer group was deeply saddened by the death of Carolyn Cameron, who had been a volunteer since the group's inception.

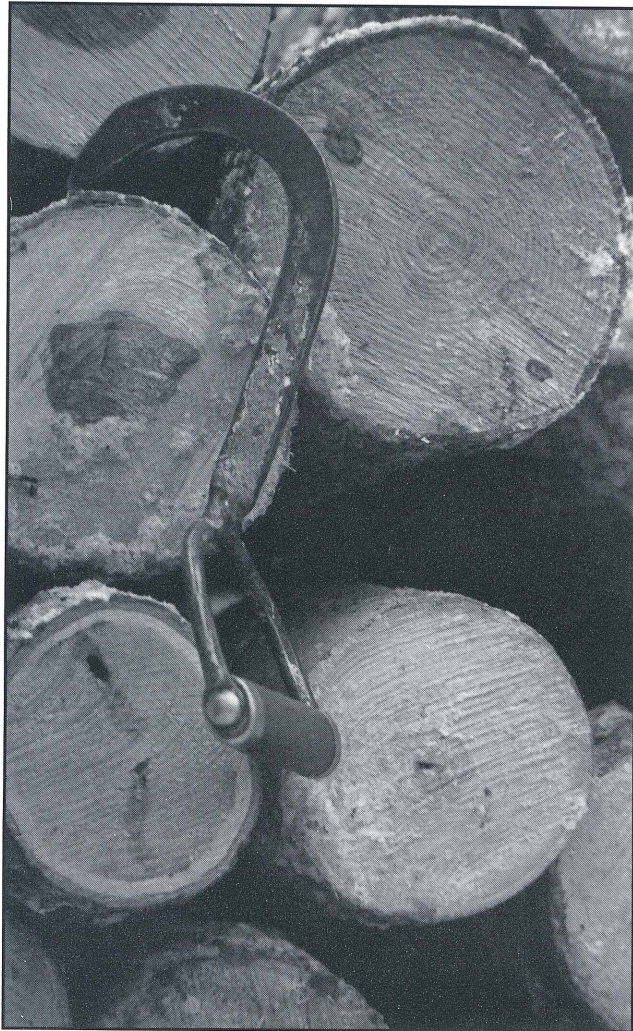
In September the Museum hosted a visit by Professor Ole Olesen and twenty-five Danish university students who were studying the land-use history and development of New England's present landscape. For the seventh year the Rainforest Collaboration visited the Forest in the fall. Students from the first cohort of this joint UMASS-Boston Public Schools program used the visit to

discuss their upcoming applications for college admission. In July, for the third year in a row, many of the students in the Forest's summer program volunteered to spend a Saturday afternoon demonstrating and talking about their summer research projects to fifty minority high school students enrolled in a science enrichment program at UMASS-Amherst. The Harvard Forest visit has proved to be a highlight of the UMASS program. In October, a large group from the Harvard Neighbors program spent a day visiting the Museum and walking through the Forest.

Meetings, Seminars, Conferences

In October, Harvard Forest hosted the National Science Foundation Long-Term Ecological Research Coordinating Committee meeting. Several representatives from each LTER site and the LTER Washington-Albuquerque offices met to review the program's recent accomplishments and discuss future directions. The meeting included a symposium coordinated by David Foster, "Regional Studies in LTER," in which all sites presented overviews of research and keynote speakers (Bruce Hayden, Ingrid Burke, John Aber, and David Foster) presented extended talks on their studies.

Other meetings at Harvard Forest included the Massachusetts Forestry Association, Millers River Watershed Council, New England Rural Water Association, Northeast Loggers Association, New England Chapter of the Wildlife Society, Massachusetts Cooperative Extension Service Coverts Project, North Quabbin Regional Landscape Partnership, Harvard University School of Public Health, Kennedy School of Government and Graduate School of Design, Massachusetts Forest Stewardship Soil Workshop, Mount Wachusett Community College Forest and Wood Products Education and



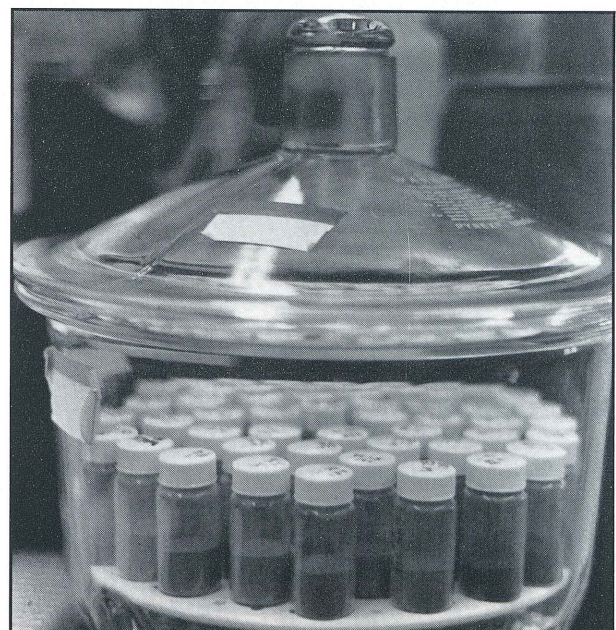
graduate students from the Landscape Architecture Department of the Rhode Island School of Design learned how our landscape has developed while spending three days exploring Harvard Forest under the guidance of John O'Keefe and Glenn Motzkin.

Speakers in the Harvard Forest Seminar series included:

John Aber	University of New Hampshire
Dawn Bazely	York University - Toronto
Herbert Bormann	Yale University
C. John Burk	Smith College
Terry Carlton	Queens University - Toronto
Emily CoBabe	University of Massachusetts
Becky Field	University of Massachusetts
Darrell Herbert	MBL - Woods Hole
Guy Hughes	Harvard Forest
Jerry Jenkins	Ecologist
Keith Kirby	English Nature
Cathy Langtimm	U.S. Geological Survey
Doug Larson	University of Guelph
Lynn Margulis	University of Massachusetts
Tim Martin	University of Washington
Jason McLachlan	Duke University
Brent Michler	U. California, Berkeley
John O'Keefe	Harvard Forest
Pat Peroni	Davidson College
Rob Sanford	University of Southern Maine
Brian Shelly	College of the Holy Cross
Darren Singer	University of Wisconsin
Kerry Woods	Bennington College
Maciej Zwieniecki	Oregon State University

Development Center, as well as meetings of staff from the U.S. Forest Service, Massachusetts Department of Environmental Management and the Massachusetts Forest Stewardship Program.

The monthly meetings of the Athol Bird and Nature Club were held in the Fisher Museum again this year. These meetings included presentations about research on a variety of subjects including the grasshopper sparrow, birds of prey and the bald eagle reintroduction program, local butterflies and rare plants of Massachusetts. In August, we again hosted a group of Spanish environmental scientists attending Real Collegio Computense, a collaborative program between Spanish universities and Harvard University. Later that month new



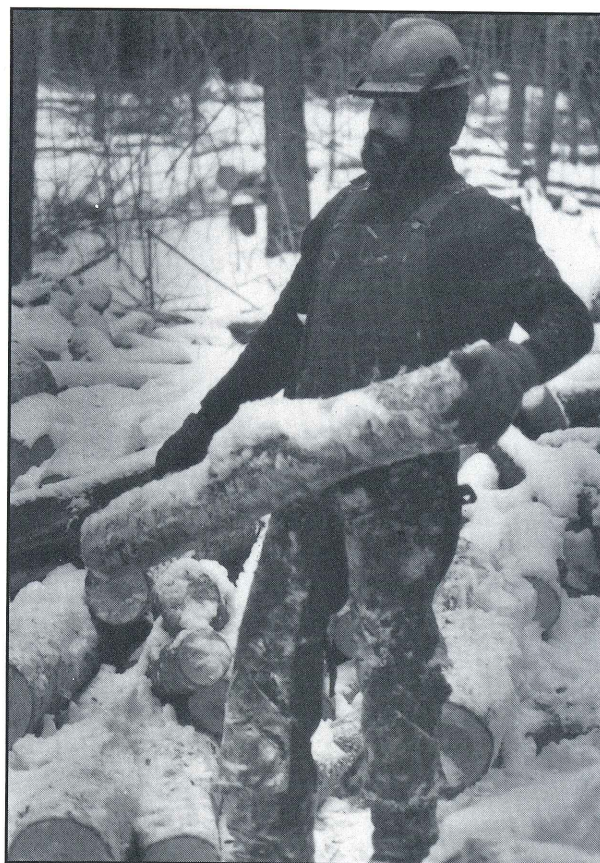
FOREST MANAGEMENT AND MAINTENANCE

Through the generous gift of the R. T. Fisher Family and with funding from the National Science Foundation, Harvard University and Friends of the Harvard Forest, work is well underway to convert the Fisher House to serve as a residential and research center for visiting faculty and students. Special care has been taken to preserve the antique character of the structure while upgrading the house to meet current needs for telecommunications and meeting space. When completed, Fisher House will provide accommodation for as many as twenty overnight guests.

Forest management activities have been focussed on the 11-acre Lewis Property (located on the northern edge of Harvard Forest along Route 32) donated to Harvard Forest in 1996. Sixty cords of firewood and 12,000 board feet of sawlogs have been removed to improve the stand composition and general appearance of the highly visible parcel. This silvicultural activity is part of our continued effort to manage our forest while providing practical demonstrations of woodlot forestry for landowners in the region.

Harvard Forest Archives

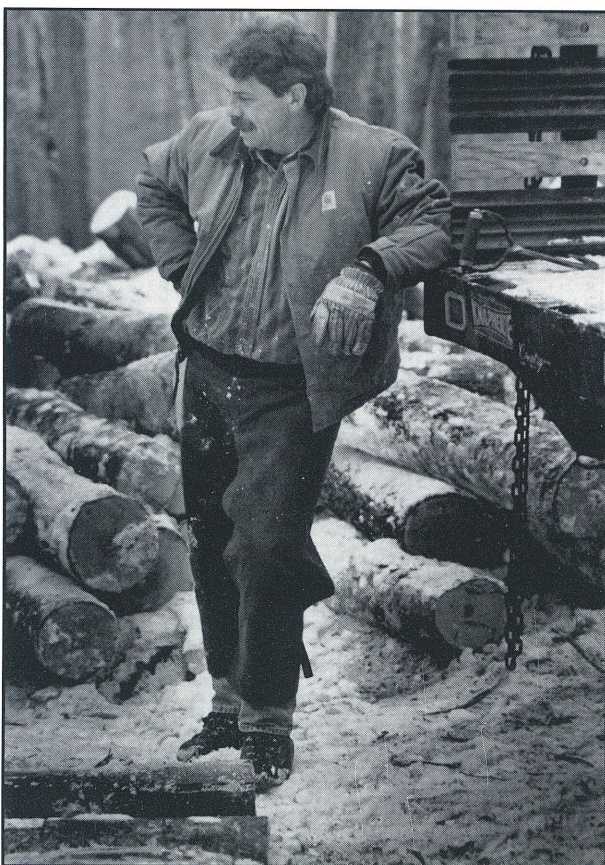
The development of the new archive facility proceeded rapidly this year. The new space consisting of three large rooms provides a comfortable and inviting work



John Wisnewski working the woodlot



Fisher House renovations - exterior



Woody Cole contemplating the next cord

area in which to use archival materials along with computer and associated equipment for air photo analysis, Geographic Information Systems and Remote Sensing. Researchers from many institutions including the Trustees of Reservations, Antioch Graduate School, U.S.G.S., Mount Grace Land Trust, University of Massachusetts and the Marine Biological Laboratory as well as Harvard Forest researchers used the Archives regularly throughout the year. Sarah Neelon, Research Assistant, catalogued and stored Harvard Forest's extensive map collection in the new facility. Research files, photographs, slides and correspondence from the papers of two former directors, Dr. Hugh Raup and Dr. John Torrey, were incorporated into the collection. To assist researchers further in using the archives, Rich Lent is in the process of creating a searchable database of all materials. John Burk, newly hired archivist, is expanding the effort towards consolidating all of our holdings in this new facility.

Computers

Five new computers and eight ZIP drives (100 mb) were purchased and installed and existing computers are being augmented with additional memory and Windows 95, which permits high speed peer-to-peer networking among computers in all Harvard Forest buildings. A total of 40 staff and general use computers are currently connected to the Internet via the Faculty of Arts and Sciences (FAS) computer network based in Cambridge.



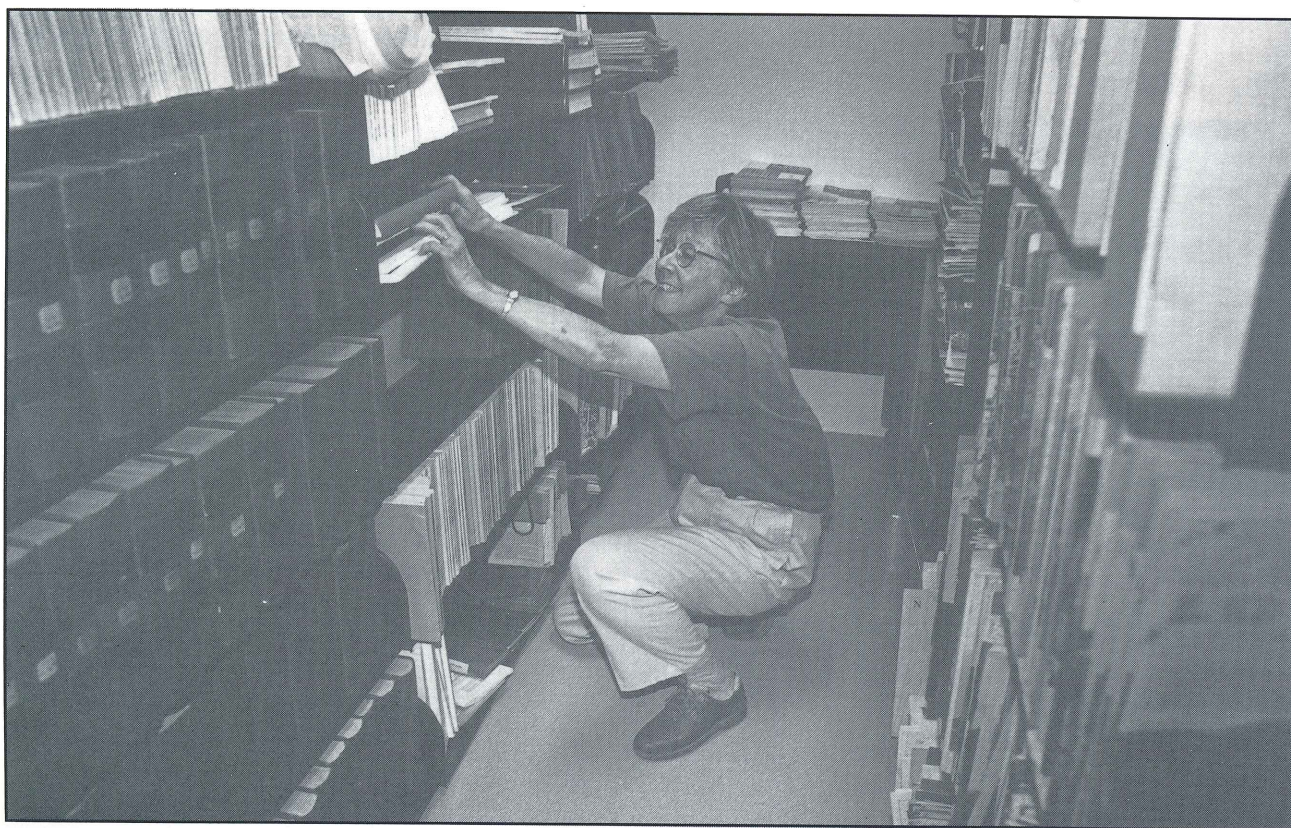
Fisher House renovations - interior

STAFF ACTIVITIES

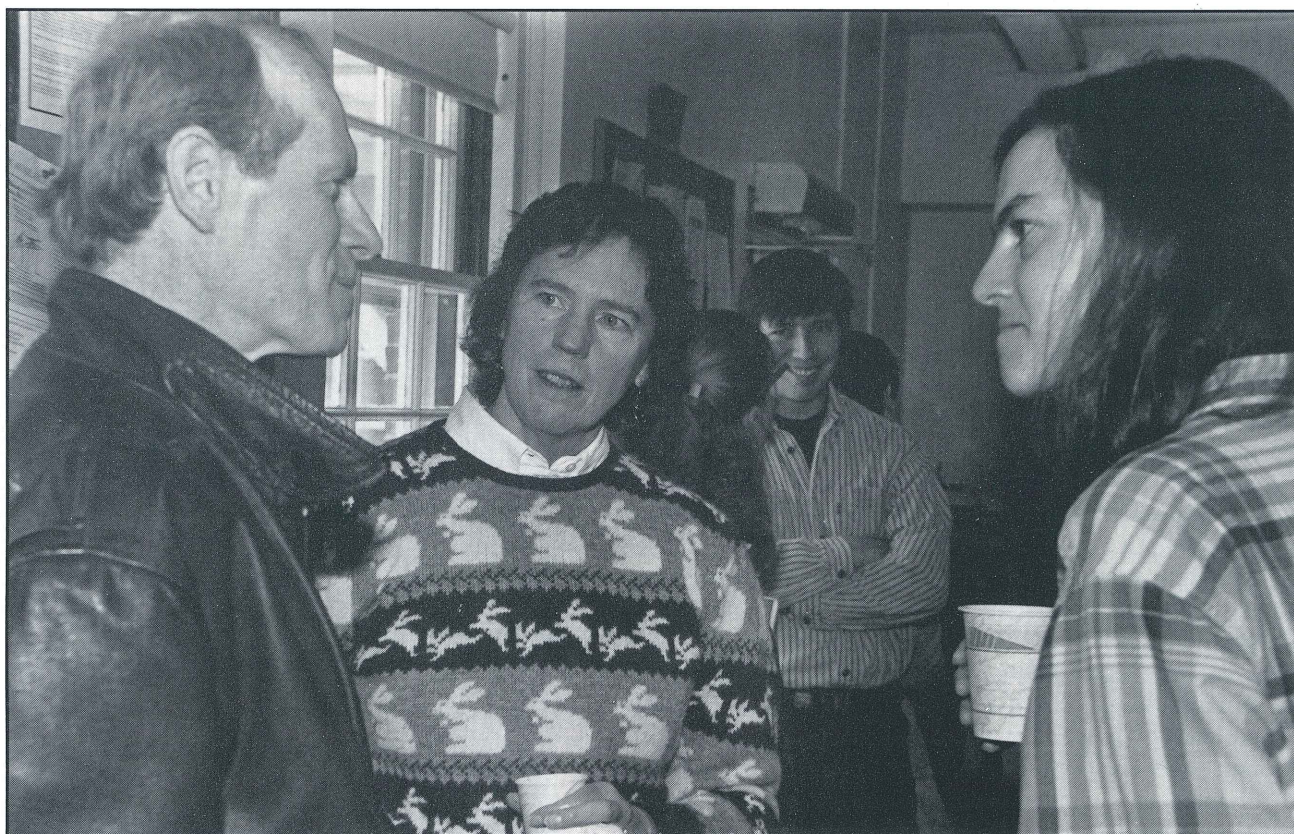
Emery Boose, Kris Chamberlin, and David Foster presented their work on hurricane research at the Ecological Society of America (ESA) meeting in Providence, RI, and Emery gave a talk at the 22nd Conference on Hurricanes and Tropical Meteorology, sponsored by the American Meteorological Society, in Fort Collins, Colorado. Emery continued to serve on the LTER Climate Committee and as the Forest's IT (Information Technology) contact for FAS. Sarah Cooper-Ellis, Sarah Neelon and David Foster presented a poster on understory vegetation response to the experimental hurricane at the ESA meetings and Sarah Cooper-Ellis presented her work on bryophyte indicators of old-growth forest in western Massachusetts at the 4th Eastern Old-growth Forest Conference in Clarion, Pennsylvania. Janice Fuller presented a paper entitled "Vegetation responses to human disturbance in central New England" at ESA, and gave a seminar at Johns Hopkins University "Climate versus people driving vegetation changes in central New England." Ruth Kern presented a poster at the International Association of Landscape Ecology conference "The Pace and Pattern of Landscape Change", at Duke University in March.

Rich Lent represented Harvard Forest at the 1996 LTER Information Managers meeting at the Archbold Biological Field Station, Florida and served on the working committee to develop a network-wide information system. He served on the research committee of the Massachusetts Division of Fisheries and Wildlife Partners in Flight Working Group, concerned with conservation of neotropical migrant birds. Rich collaborated with Nick Brokaw of the Manomet Center for Conservation Science on a book chapter on vertical structure and biodiversity in forests, presented a seminar at Amherst College and edited the Proceedings of the 8th Annual Harvard Forest Ecology Symposium with Dottie Recos-Smith.

Glenn Motzkin gave a talk at the LTER workshop "The relationship of biodiversity and productivity" held at the Center for Ecological Analysis and Synthesis in Santa Barbara. He presented a poster on the history of pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts at the ESA meetings and led educational programs for students from the Rhode Island School of Design and Clark University. John O'Keefe attended the ESA meetings, the New England Society of American Foresters meeting in Portland in March and the eastern Old-Growth Forest Conference in Clarion, Pennsylvania in June. In October, John presented a paper titled: "Ecological History of Massachusetts' Forests," at a



Barbara Flye and the Harvard Forest Library



Eldon Franz, Emily Russell and Susan Clayden

conference on Massachusetts Forest History at the University of Massachusetts and has completed the manuscript for publication with David Foster. He accompanied the Rainforest Coalition group on a trip to the UMass Nantucket field station in April. In collaboration with David Foster and David Orwig, he examined the old-growth forest discovered at Wachusett Mountain. John serves on the boards of the Massachusetts Forestry Association, Millers River Watershed Council and Mount Grace Land Conservation Trust and on the Massachusetts Project Learning Tree Steering Committee, the Quabbin Science and Technical Advisory Committee, and Secretary Trudy Coxe's Advisory Board on Environmental Education.

Dave Orwig attended the ESA meeting and presented a poster with David Foster entitled, "Forest ecosystem response to hemlock woolly adelgid outbreaks in southern New England" and two posters: (1) Stand composition and vegetation dynamics of an old-growth forest on Wachusett Mountain; and (2) Recruitment dynamics in an old-growth remnant hemlock-hardwood forest in northwest Pennsylvania (Cook Forest) at the Eastern U.S. Old-growth Forest Conference in Clarion, PA, in June. Ben Slater attended the first annual Idrisi User's Conference in Worcester, MA. He took two courses

at the University of Massachusetts, "Introduction to North American Archaeology" and "Introduction to Environmental Biology."

David Foster presented talks at the ESA, the National Center for Ecological Analysis and Synthesis in Santa Barbara, at the plenary session of the International Association of Landscape Ecology at Duke University, a symposium on the Fate and Future of Northeastern Forests at Connecticut College, and the Luquillo Experimental Forest, Puerto Rico. He attended LTER Coordinating and Executive Committee meetings in Washington, D.C., Corvallis, Oregon, Minneapolis and Harvard University. David, Marianne and Christian joined the Harvard Alumni Association on two trips - "Costa Rica and the Panama Canal" and "In the Wake of Lewis and Clark" up the Columbia and Snake Rivers. David participated in NSF reviews of the LTER projects in Puerto Rico and the Harvard Forest. Having completed a three-year term as an editor at *Ecology/Ecological Monographs* David joined the editorial boards of two new journals: *Ecosystems* and *Northeastern Naturalist*. He continues to serve on boards of the Conservation Research Foundation and Highstead Arboretum and on the Executive Committee of the LTER program, NIGEC program and Man and the Biosphere Temperate Ecosystem Directorate.

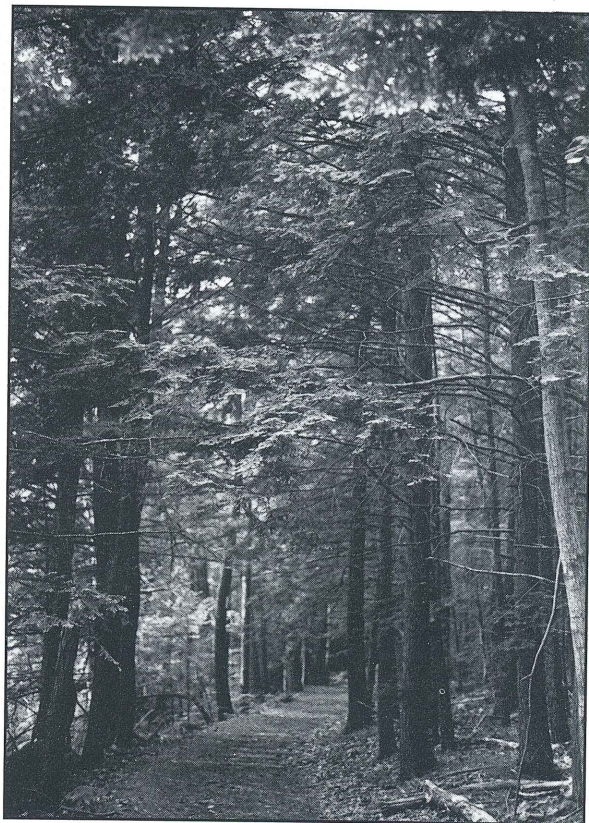
THE HISTORY AND ROLE OF EASTERN HEMLOCK IN NEW ENGLAND

Introduction - D. R. Foster

One of the interesting and provocative issues that has emerged in the field of ecology over the past few decades has revolved around the question of whether individual plants or animals may serve as keystone species that play a critical role in controlling or defining ecosystem processes and determining major community characteristics. In an era in which species are being locally eradicated or driven globally extinct, the possibility that individual taxa may be crucial for the maintenance of specific structures, processes or organisms in natural ecosystems has become a major impetus to studies of biodiversity. The broader issue of the role of individual species in controlling forest organization and function and the selective decline or elimination of species through time has been the focus of considerable research in the northeastern U.S., in large part because the history of the region has involved a series of such reductions or eliminations as a consequence primarily of human activities. The decline and very gradual recovery of hemlock across its range 4800 years ago due to a new insect pathogen, the decline of chestnut from the fungal blight introduced from eastern Asia, the outbreak of gypsy moth on oak, aspen and birch forests and the selective elimination or alteration of animal populations -- wolves, passenger pigeons, deer and beaver among many -- have all exerted major impacts on forest, aquatic and wetland ecosystems across the northeastern U.S. Studies of these species dynamics and their consequences have also provided great insights into the factors structuring natural ecosystems.

Among all of the plant species that may be important in controlling both terrestrial and aquatic ecosystems across New England, few emerge as prominently as eastern hemlock. Widespread, abundant, long-lived and extraordinarily shade tolerant, hemlock has always been classified as a pre-eminent part of the "climax" and pre-settlement forest of the region. By nature of the extremely dense shade that it casts and the deep, acidic litter that may accumulate below it, hemlock has the potential for controlling forest composition and dynamics, for creating distinctive wildlife habitats, and for defining a range of very distinctive ecosystem structures and processes. Although hemlock currently has a somewhat bimodal distribution, with greatest abundance on rocky ridges or talus slopes and in moist cool ravines, it grows on a range of sites including wetlands. It also was undoubtedly much more abundant and more widespread in pre-settlement times. Thus, from the rocky highlands through the mesic woodlands and riparian areas and into the wetlands of New England, hemlock plays an important role in our landscape.

Unfortunately, nearly 5000 years after a natural pathogen decimated hemlock populations across its range, an introduced insect pathogen (hemlock woolly



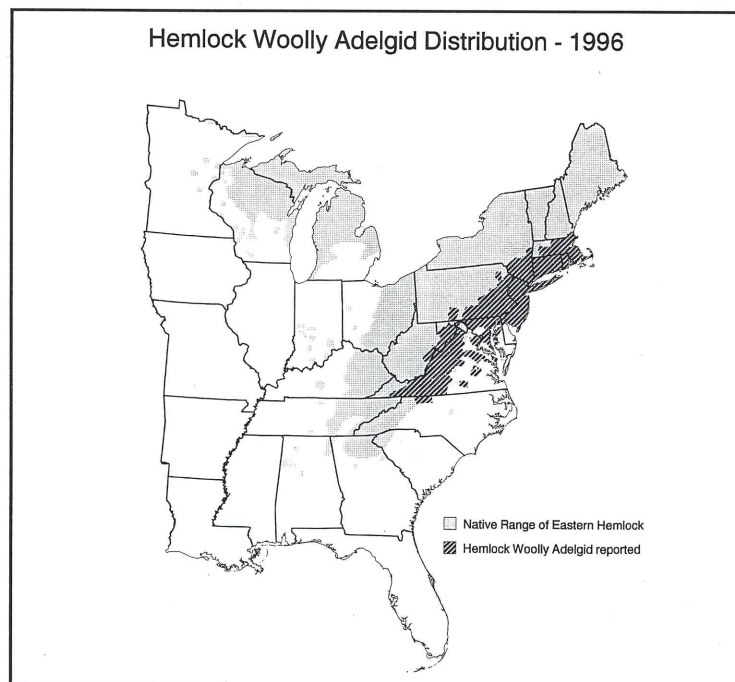
adelgid) threatens to exert a parallel impact on hemlock and the ecosystems that it occupies. The emergence of such an important ecological, economic and aesthetic impact on northeastern forests spurred the Harvard Forest into a major research effort to document and understand this process on a regional, local and plant scale. As suggested by paleoecologists, historical research and modelling studies, the decimation or loss of hemlock could exert a profound effect on forest ecosystems over the next centuries. Therefore, in contrast to the case of the chestnut blight for which we have only a partial understanding, we would like to be in a position to understand and interpret the consequences of the introduction of hemlock woolly adelgid and the potential loss of a dominant conifer species.

Studies of hemlock in New England forests actually have a very long history at the Harvard Forest and thus this new research activity can take advantage of a legacy of information. Bob Marshall, founder of the Wilderness Society and a student of R. T. Fisher at Harvard Forest, conducted an exhaustive examination of stand development and age structure of hemlock forests for his Masters in Forest Science, published in 1927. Earl Smith,

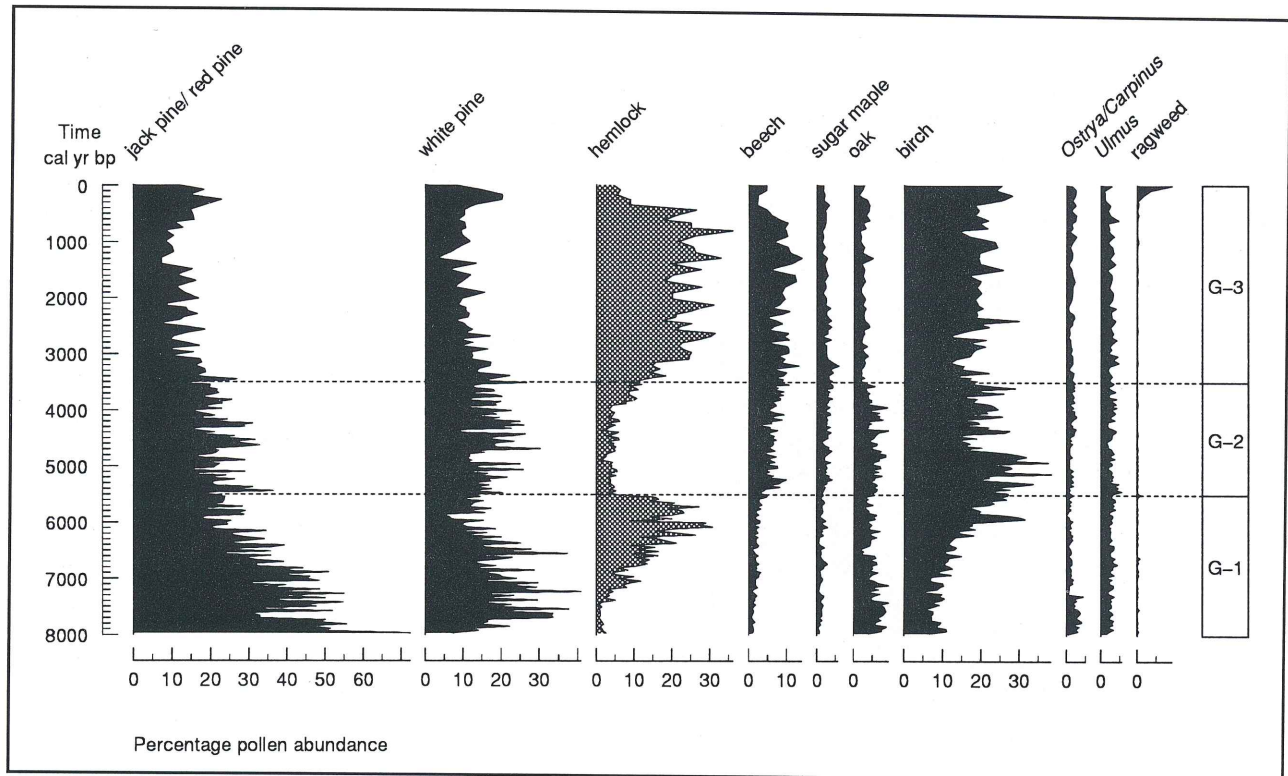
a MFS student in the 1940s, followed this work with an insightful study of land-use history and stand dynamics in hemlock forests. Smith's thesis was one of the first studies to note the slow rate of hemlock dispersal and spread across a landscape from which it had been cleared and thereby to identify areas that had never been cleared or burned by the presence of large hemlocks or an abundance of the species. A series of subsequent studies added much to our knowledge of the changing role of hemlock in New England forests: Al Cline and Steve Spurr's (1942) and David Henry and Mark Swan's (1974) analyses of the old-growth forest at Pisgah in southwestern New Hampshire; Spurr's thesis and study on forest associations at the Harvard Forest (1956b) and his early study of hemlock's role in forest succession after the hurricane of 1938, a study followed up some 40 years later by Dave Hibbs (1983); Margaret Davis' (1958) analysis of the post-glacial history of New England, which outlined the 8000-year history of hemlock in the region; Earl Stephens' painstaking reconstruction of the natural and human history of an older growth hemlock forest and the subsequent paper by Chad Oliver and Stephens (1977) on

the role of exogenous versus endogenous disturbance in controlling forest dynamics; the architectural analyses of hemlock by Dave Hibbs (1981) and the application of diverse approaches to interpreting forest history and developing silvicultural information on hemlock by Matt Kely (1984, 1986). Subsequently, there has followed a range of paleoecological, historical and modern studies (Foster 1988a, b; Foster and Zebryk 1993; Foster *et al.* 1992, 1996, 1998; Fuller *et al.* 1998; Whitney and Foster 1988).

The remarkable depth of past and current studies on one very important species and the extremely precarious nature of hemlock's place in modern New England forests provided the motivation to develop the following summary of our current research on eastern hemlock. Although this detailed and coordinated format strays somewhat from the historical structure of Harvard Forest Annual Reports, we felt that our Friends and a wider readership might enjoy and benefit from the broad perspective that we are developing on this important species. Most certainly, ours is a perspective and understanding that is growing in a landscape that is changing rapidly.



The distribution of eastern hemlock and the status of the hemlock woolly adelgid in the eastern U.S. in 1996



The post-glacial history of hemlock is clearly depicted in this pollen diagram from Graham Lake in Southern Ontario, Canada. Approximately 5000 years before present hemlock declined precipitously due to an apparent insect pathogen and was replaced by birch, beech, oak, sugar maple and white pine. After more than 1000 years the species recovered to become a dominant tree in the region. With intensive harvesting and land use in the last 200 years hemlock has again decreased across the landscape.

The Post-glacial History of Hemlock

Janice Fuller and Glenn Motzkin

Following deglaciation at the end of the Wisconsin glacial period, hemlock extended its range northwards from its full-glacial refugia to reach southern New England between 10,000 and 9,000 years before present. Hemlock became abundant in many parts of this region, forming mixed woodland with beech, sugar maple, birch and white pine. There was a dramatic decline in the abundance of hemlock, as recorded in pollen data, approximately 5000 years before present. As this decline appears to have been rapid, more-or-less synchronous across eastern North America, and unique to hemlock, it has been suggested that it was the result of a pathogenic outbreak. Recent evidence from Quebec supports this hypothesis and indicates that the decline may have been caused by an insect pest.

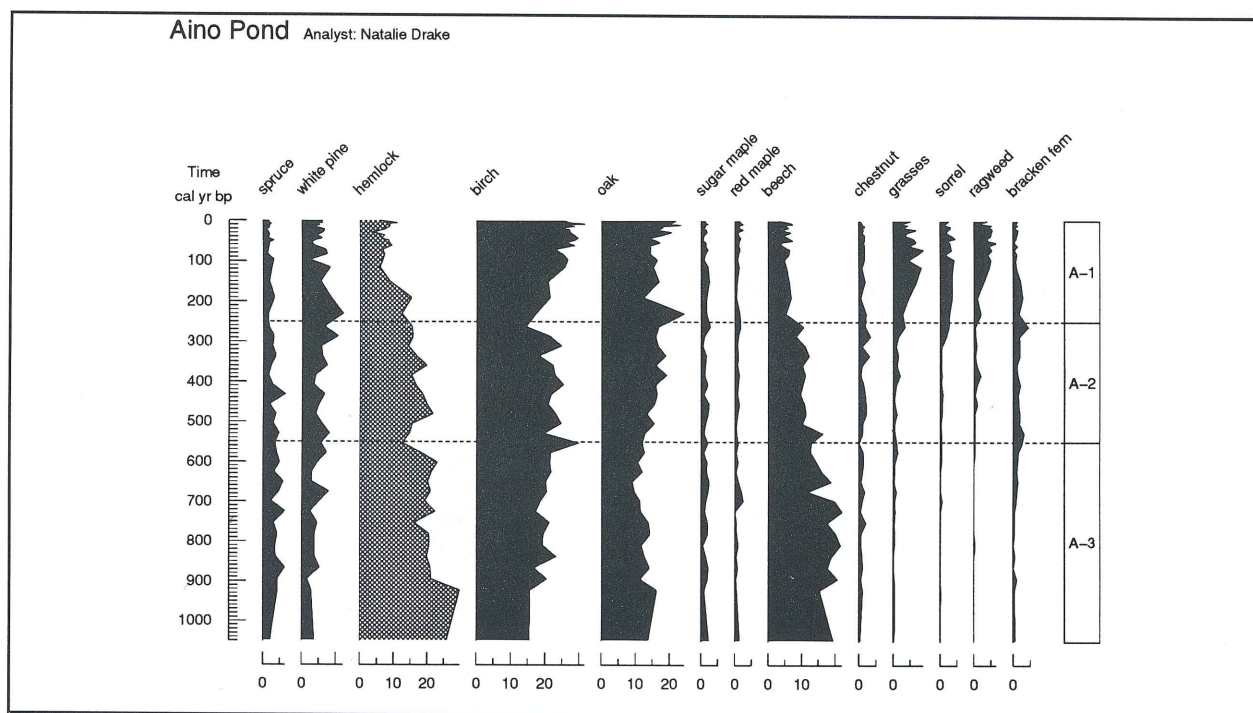
Hemlock is a long-lived, slow-growing and shade-tolerant coniferous tree species and its decline ap-

proximately 5,000 years ago exerted a pronounced impact on forest dynamics and ecosystem properties. Other species increased in abundance as hemlock declined, including oak, elm, birch, pine, beech and sugar maple. In central Massachusetts, pine, oak and red maple appear to have replaced hemlock (Foster and Zebryk 1993). At some sites in the Northeast, hemlock populations fully recovered after 1000-2000 years, whereas at others, it never regained its former abundance. Changes in climate and/or the shift in forest composition may have prevented hemlock from re-invading some habitats and reaching pre-decline abundances. Presumably the gradual recovery of hemlock after its decline may have resulted from the slow evolution of resistance to the pathogen. Although this Holocene history thereby contains the optimistic note that such species' recovery is possible, it also underscores the geological timescale required for such evolutionary and ecological processes.

The Regional Response of Hemlock to European Settlement and Land Use

Janice Fuller and Glenn Motzkin

Prior to European settlement pollen data from our central Massachusetts study region, which extends from the Connecticut River Valley to eastern Massachusetts, suggest that hemlock dominated the upland vegetation along with beech, sugar maple and birch (probably yellow birch) (Fuller *et al.* 1998). Oak, chestnut and hickory were more abundant at lower elevations, which are warmer, supported larger Indian populations and had higher fire frequency. Hemlock declined sharply soon after European settlement as other taxa, more tolerant of disturbance, such as birch, red maple and oak, increased (Foster *et al.* 1998). Through much of the 19th century the landscape was extensively cleared for agriculture, and hemlock and other tree species were largely restricted to small, isolated woodlots that were frequently cut for a variety of forest products. After widespread agricultural abandonment in the second half of the 19th century, hemlock spread slowly onto old agricultural lands, where it is frequently found today in the understory. However, because of its slow rate of spread and growth, mature stands of old hemlock are largely restricted today to sites that were not cleared for agriculture during the past 300 years.



Pollen from a lake in North Central, Massachusetts shows that the last 1000 years of history embraced a long decline in hemlock and beech and increase in oak, pine and other species. Before European settlement, change to a cooler and more variable climate (the Little Ice Age) may be the cause of the decline whereas the forest clearing in recent centuries yields a clear signal of increase weeds, grass and removal of hemlock and beech.

Post-settlement Dynamics of Hemlock Forests

Jason McLachlan

In order to take this regional perspective on the history of hemlock down to the scale of individual forests, we have been using paleoecological and tree-ring studies to reconstruct the history of mature forests from the time of European settlement to the present. Results from four old and mature hemlock stands at Harvard Forest indicate that the appearance of great age and stability in these forests is often misleading. Although the forests studied on the Slab City and Prospect Hill tracts are among the best examples of older growth forests in the town of Petersham, analysis of pollen from the soils shows that these forests have changed remarkably over the past 300 to 500 years due to historical impacts by humans. Along with changes in the growth rings, the pollen indicates that a wide array of pre-settlement forest types on these sites were transformed into forests dominated by sprout hardwoods (chestnut, birch, oak) following intensive cutting in the 18th and 19th centuries. The current hemlock-dominated forests did not develop until the last 100-125 years when human impacts have been minimal.

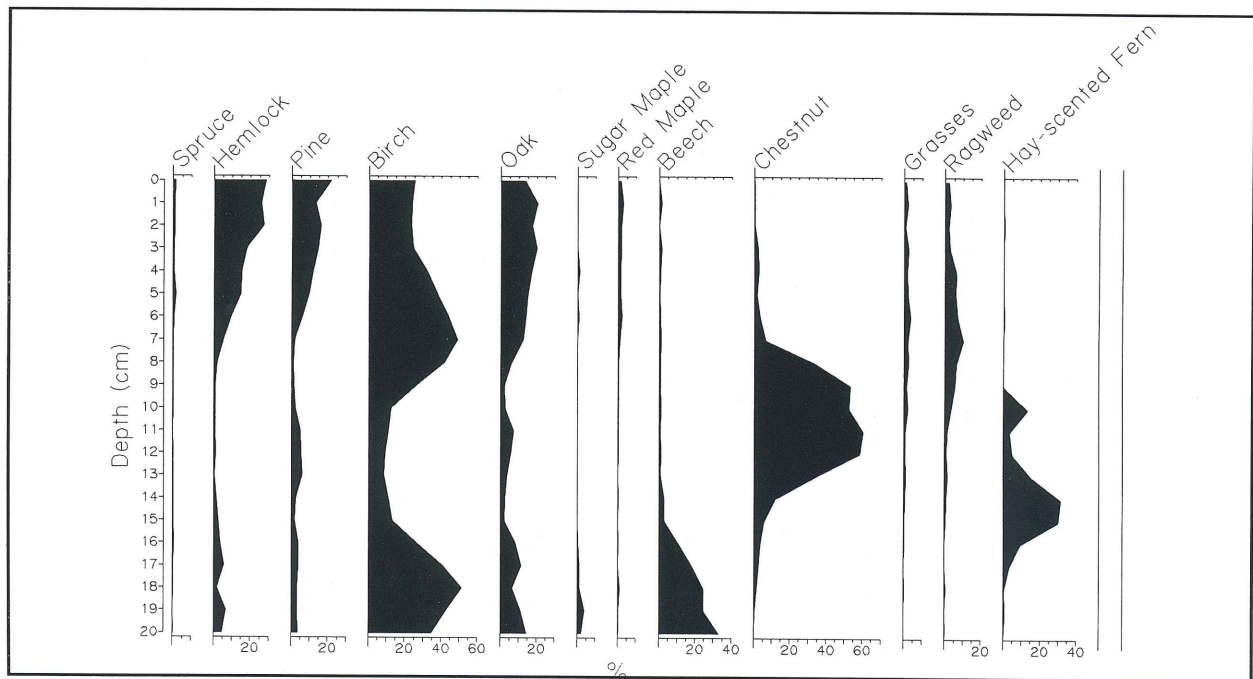
Unlike the bulk of the New England landscape, in which hemlock declined as a result of agricultural land-use such as plowing and pasture, these stands developed into a virtual monoculture of hemlock. This local pattern that

differs from the regional trend is a result of the specific disturbance history of these stands in which disturbances, such as cutting, wind and forest pathogens, favored the understory of hemlock saplings and seedlings. This result also highlights the flexibility of hemlock to a variety of disturbance types and challenges the notion that hemlock is simply a late-successional species. The study further indicates that, while the last 300 years of anthropogenic disturbance have drastically changed the character of New England's forests, in some cases, ecological attributes associated with old-growth forests, such as open park-like stands of large, old, late-successional trees, can be produced by direct human influence.

Hemlock on the Modern Landscape

Glenn Motzkin and David Foster

The current distribution of hemlock in central New England reflects the interplay of site conditions and disturbance history. Although hemlocks may grow on a wide range of sites from swampy lowlands to rocky ridges, many of the mature hemlock stands that we find on the landscape today occur in rocky lowlands or steep ravines and hillsides. In contrast, understory hemlocks are found in a much broader range of site conditions. Why are young hemlocks becoming established on sites where we rarely



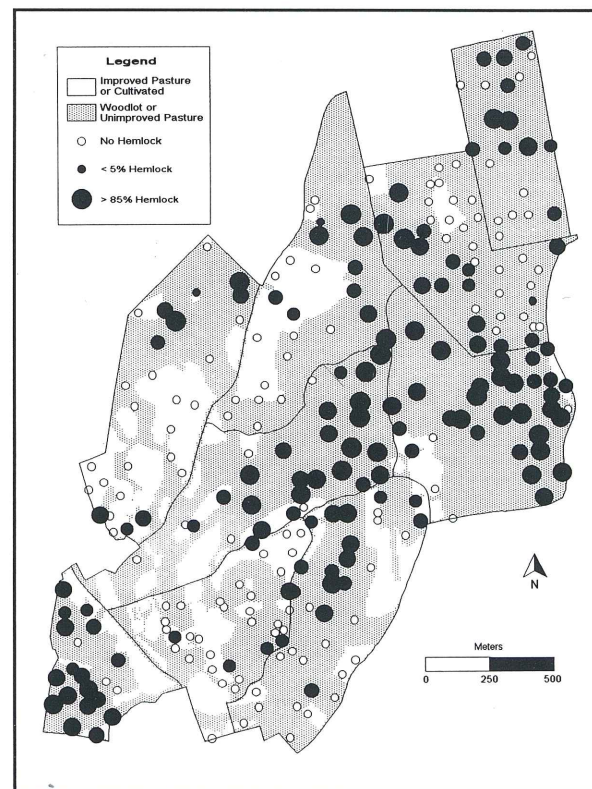
Hemlock currently is the dominant tree in this mature forest in the center of the Prospect Hill tract. Pollen analysis of the soil shows, however, that the pre-settlement forest was composed of beech, birch, hemlock and oak and was replaced by chestnut after repeated cutting in the 18th and 19th C. Only with a cessation of logging activity and the demise of chestnut from blight did hemlock come to dominate this forest.



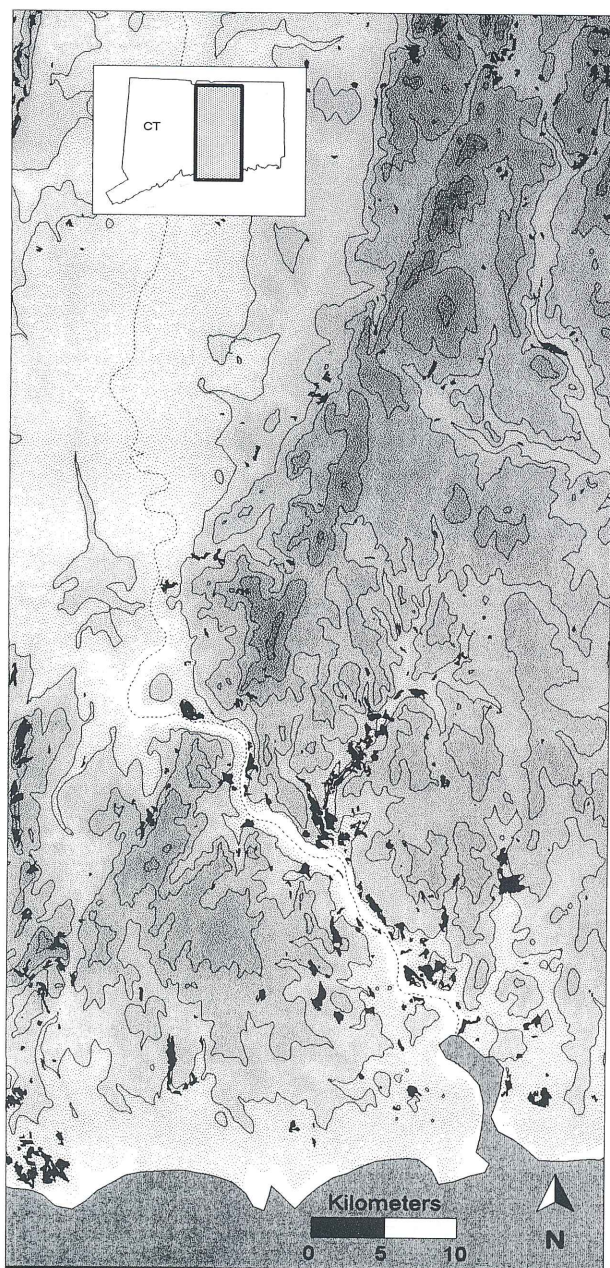
Julian Hadley in the canopy tower of the Prospect Hill hemlock forest

find mature stands? To help us answer this question, we developed a map of the distribution and abundance of hemlock on the Prospect Hill Tract of Harvard Forest. Although hemlock is widespread on Prospect Hill, we see that it is not abundant everywhere. In particular, hemlock is generally absent from sites that were used intensively for historical agriculture, such as former cultivated fields and improved pastures. In contrast, hemlock is abundant in the historical woodlot and on former unimproved pastures. Once removed from a site by disturbance such as agricultural clearing, hemlock is slow to become re-established. Thus, although young hemlocks are slowly becoming established on agricultural fields that were abandoned from 60 to >100 years ago, we still see few overstory hemlocks on these areas. In addition, hemlocks, especially when young, are very susceptible to fires. Until 40 or 50 years ago, when methods of fire detection and suppression improved, fires were widespread in much of central New England, and this also served to limit hemlock to low-lying areas that were not burned frequently.

Has hemlock always been abundant in the old woodlot? Stand and historical reconstructions suggest that although hemlock has been present at this site for millennia, its abundance has changed dramatically. Heavy cutting throughout the 18-19th centuries for a variety of wood products, including tanbark for the tannery that once operated on Harvard Forest land, encouraged the development of a dense, sprout chestnut stand with understory hemlock. When the chestnut blight killed the chestnut trees in the 2nd decade of the 20th century, previously established understory hemlocks grew to dominate the woodlot. Thus, the ~110 year-old stand that we see today developed only after intensive disturbance by both humans and pathogens.



Distribution of hemlock on the Prospect Hill tract. Due to its slow rate of spread and preference for moist sites, hemlock is most common and abundant on old woodlots and unplowed areas.



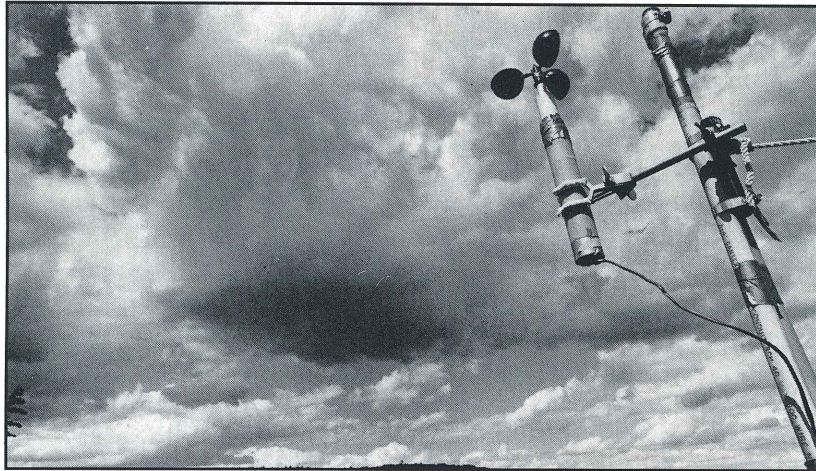
Our central Connecticut study region extends from Long Island Sound to the Massachusetts border. Each hemlock stand was mapped from aerial photographs and is being sampled in the field. The topographic contours and study show a preference of hemlock for ridge tops, narrow valleys and steep hillsides.

Regional and Landscape Distribution of Hemlock and HWA Impacts in Southern New England

David Orwig

Hemlock woolly adelgid (HWA; *Adelges tsugae*), an introduced aphid-like insect from Asia, is expanding across the northeastern United States through the range of eastern hemlock and has the potential to severely reduce this important species. Consequently, while HWA infestation looms as a tremendous management problem and threatens to disrupt forest ecosystems on a very broad scale, it also represents an opportunity to examine an important evolutionary and historical process - the spread and impact of a new pathogen on the environment. In order to develop insights into these management, conservation and ecological issues we have initiated a study investigating forest dynamics and ecosystem processes resulting from HWA infestation. At the landscape level, we have mapped the distribution of all hemlock stands greater than 3 ha within a 5900 km² transect extending through southern New England in order to characterize the temporal and spatial patterns of damage generated by HWA since the time of its arrival in 1985.

The regional hemlock map was completed in the spring based on aerial photographs and during the summer of 1997, David Orwig along with students Jesse Bellemare and David Mausel have been visiting 100 hemlock stands throughout this transect to ascertain the extent of HWA damage, overstory mortality, and forest composition. This information is being incorporated into a Geographic Information System analysis of the spatial and temporal patterns of HWA spread across the landscape, to determine what physiographic, edaphic, and topographic factors may be important for the observed patterns. Permanent plots are being established in 10-12 of the stands in central and northern Connecticut to expand our study of stand and community response to HWA as it continues to migrate northward. In 1995 we initiated a detailed examination of stand response of eight hemlock stands in south-central Connecticut to differing levels of HWA infestation. Results from the second year of analyzing these plots suggest that stands continued to deteriorate, as annual mortality levels ranged from 5 to 15% in stands that had already lost 20 to 95% of all overstory hemlock. All remaining hemlock trees sampled in seven of the eight stands were infested with HWA and over 90 % suffered at least 50 % foliar loss. Understory vegetation exhibited an increase in species richness and percent cover from 1995 to 1996 in the majority of stands. The dominant response continues to be the prolific establishment of black birch. Average stand age, which ranged from 68-110 years, did not appear to affect hemlock mortality or seedling establishment. These stands are being monitored again in the summer of 1997 to examine the temporal trends in overstory mortality and understory recruitment.



Hemlock Stand Structure and Environment

Sebastian Catovsky

Many forests in New England and the Great Lakes states are composed of a mosaic in which the canopy is dominated by hemlock patches or individuals separated by patches of hardwoods. The patchwork nature of such forests creates a heterogeneous understory microenvironment, as a result of the influence of canopy trees on the light, temperature, humidity and soil conditions at the forest floor. Documentation of the specific characteristics of this microenvironmental mosaic and its relationship to the overstory pattern is essential to interpret the characteristics and dynamics of these forests. My doctoral thesis is examining this environment from the perspective of resource (light, nutrients, moisture) availability and addressing the consequences of this resource patchiness on seedling regeneration.

Mature canopy hemlocks have a large impact on the microclimate and light conditions at the forest floor, and on the chemistry and nutrient status of the soil beneath them. Hemlock creates very intense shade in the understory (often around 1% of incident radiation) because of its deep canopy and only allows a small fraction of direct radiation to reach the forest floor as sunflecks. These low light levels generally reduce soil and air temperatures in the understory. Soils underneath hemlocks tend to be relatively dry, perhaps because of their shallow rooting and high rainfall interception. The needles shed by hemlock and other conifers have high carbon to nitrogen ratios, and tend to decompose more slowly than leaves of hardwoods, which strongly affects soil properties. This slow decomposition reduces nutrient availability under hemlock, increases the depth of the litter layer and promotes podzolization. Hemlock needles are extremely acidic, and pH of surface soils sampled under hemlock are commonly below 4.0.

Although we understand the basic differences between hemlock- and hardwood-dominated stands, few studies have explicitly compared different stand types from the perspective of the many resources that are important for plant growth. My research addresses how differences in understory conditions in hemlock and hardwood-dominated stands may influence regeneration of tree species. Specifically, I am quantifying the spatial and temporal variation in environment and resources between hemlock and hardwood-dominated stands at Harvard Forest and measuring demography in these stands to relate variation in resource availability to patterns of seedling germination, growth and mortality. Understanding what environmental factors control seedling demography should allow investigation of how conifer and hardwood species differ with regard to their regeneration abilities and preferences.

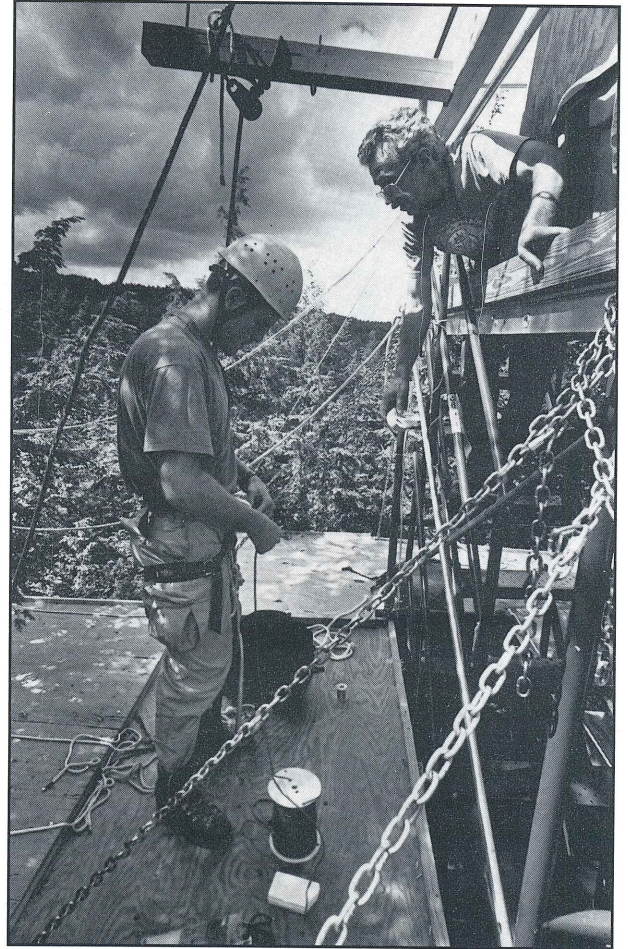
These descriptive studies relating seedling performance to microenvironmental conditions are being supported with experimental work in the glasshouse to separate the critical factors that influence seedling growth and survival. In an experiment addressing the factors influencing seedling regeneration underneath hemlock stands I am investigating how light, pH and nitrogen availability interact to influence conifer and hardwood seedling regeneration. Intact soil monoliths were collected along three 100m transects from a hemlock stand on Prospect Hill, in November 1996 and were kept in an experimental garden in Cambridge over winter. Seedlings were left to germinate naturally under different experimental treatments, which consist of 2 light levels (2% and 80%) and 3 soil treatments (control, liming, nitrogen addition). Germination, growth and survival of seedlings are being monitored through the season. So far, we have found large amounts of birch seedling germination, especially under high light, and some white pine emergence.

Ecophysiology and Carbon Exchange of Old-growth Hemlock Forests

Julian Hadley

Overall, and as a consequence of its ongoing recovery from intensive land use in the 19th and early 20th C, the New England landscape is a major sink for the accumulation of carbon as its forests continue to grow taller and larger. Because this ongoing storage of carbon serves to partially offset the global release of carbon through fossil fuel combustion, deforestation and other land-use practices, it is of great interest to scientists and policy makers evaluating scenarios for future changes in global environment due to atmospheric increases in carbon dioxide and other greenhouse gases. However, there are many questions about the details of carbon uptake and exchange in northeastern forests, particularly as they age and become older-growth stands comprised of large trees with large quantities of dead wood and thick soil organic layers. We have undertaken new studies of older forests, especially those dominated by hemlock, to begin to address these questions (cf. Wofsy *et al.* 1993).

Measurements of the ecophysiology and CO₂ exchange of hemlock forests have thus far concentrated on an old-growth hemlock forest (maximum age 230 years) on the Prospect Hill tract of the Harvard Forest near the Black Gum swamp. In 1996, it was found that photosynthesis in the forest understory was severely limited by the very low light levels. Hemlock saplings were found to be well adapted to shade but had sufficient light to achieve maximum photosynthesis during less than 1% of the daylight hours from late June through late October. In contrast to light, temperature was rarely a strong limitation to photosynthesis, at least through late September. Soil moisture was also non-limiting for photosynthesis, although this may have been a result of higher than normal



Jack McFarland and Julian Hadley above the tree tops



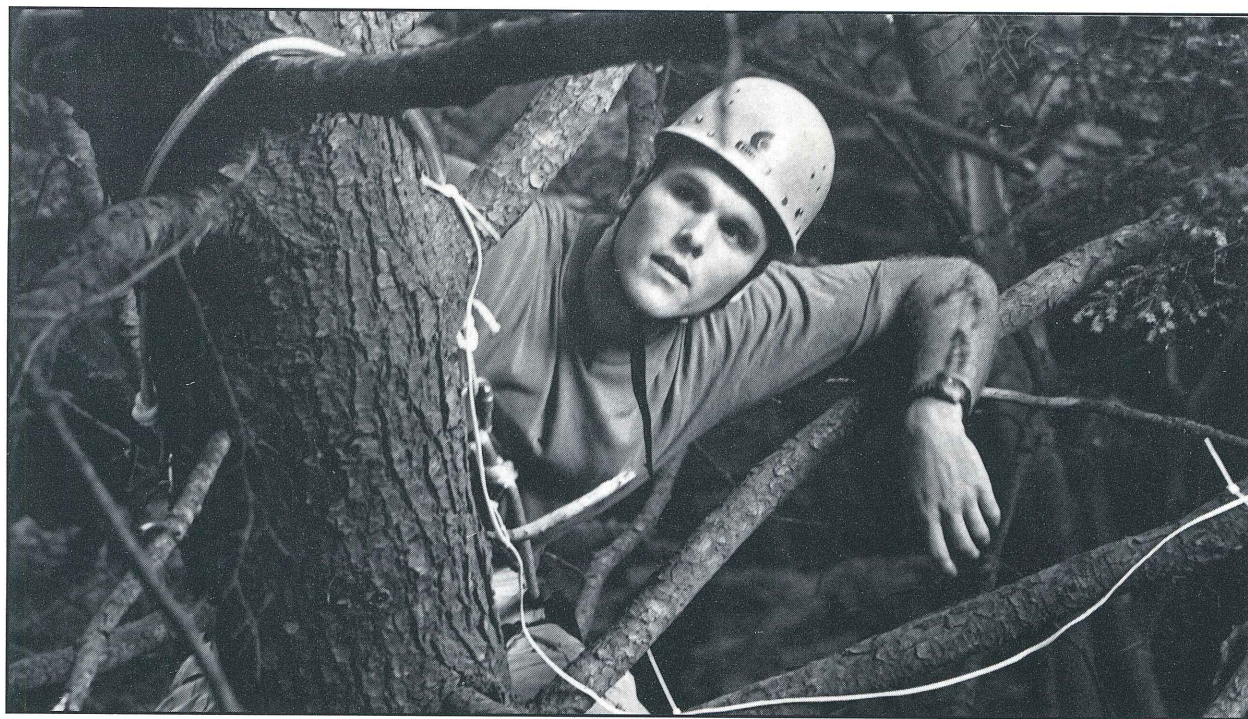
Cristi Braun and Julian Hadley

precipitation in June and July. These results quantify a frequent observation from hemlock forests and help to interpret the factors structuring these communities. The overstory of these forests is extremely efficient at intercepting and capturing light, which produces very low light levels in the understory. Small hemlocks are barely able to persist at these low levels and grow slowly. Almost none of the other tree species in the Northeast are capable of surviving in such a low light environment and consequently the understories of these stands are species-poor and characterized primarily by scattered small hemlock. As a result of the sparse understory vegetation and low light levels, we estimate that hemlock saplings, the dominant understory plants, are able to utilize only about 2% of the carbon dioxide that is released from the soil through respiration.

In order to sample this hemlock forest thoroughly from above as well as below, a 30-m tall canopy access tower was completed in October 1996. Microclimatic data for the hemlock canopy (including air temperature, humidity, wind speed, and available light) were collected beginning in March 1997, and measurements of CO₂ uptake by the canopy of old-growth hemlocks were begun in April, after platforms to access the trees from the tower were completed. Ecophysiological measurements of the

canopy from the tower will encompass all the elements necessary to understand and to produce a model of carbon exchange by these large canopy trees. Model parameters will include environmental variables (e.g. light, air temperature, humidity, and wind velocity), internal plant variables (e.g. foliar nitrogen content and water potential) and net photosynthesis and dark respiration of both foliage and woody tissues. Our measurements thus far have shown that foliage in the upper canopy has a slightly higher photosynthetic rate than sapling foliage. Light levels on leaf surfaces decline steeply from the top to the bottom of the canopy. Photosynthesis in lower canopy foliage must be limited by light most of the time.

Questions about the fate of CO₂ produced by soil respiration in the soil beneath snow and ice cover have led us to investigate dissolved CO₂ levels in streamflow beginning in January 1997. Downstream from a bog near the hemlock stand, CO₂ concentrations in water reached more than sixteen times atmospheric CO₂ levels in winter, and up to twelve times the atmospheric level during spring. In late April and early May, observations showed that these high CO₂ levels in the stream greatly stimulated photosynthesis by an abundant aquatic moss. We are continuing to measure streamwater CO₂ concentrations and the photosynthetic response of aquatic plants during the summer of 1997.



Jack McFarland checking the micromet sensors



Hemlock stand severely defoliated by hemlock woolly adelgid in Salem, Connecticut

Architecture, Morphology and Pollination of Hemlock

P. B. Tomlinson

Although hemlock is not the focus of intense morphological studies at the Harvard Forest, our fairly comprehensive studies of conifer genera enable us to place it within a comparative context of other taxa. This effort is made more interesting by the observation that *Tsuga* is distinctive within the Pinaceae, and among most conifers, in its architecture and pollination mechanisms. *Tsuga* is unusual in the Pinaceae in its pendulous leader and it has been widely described as having sympodial growth. An earlier study at Harvard Forest by Dave Hibbs (1981) demonstrated that the leader showed less than usual apical control over lateral branch expression and might best be described as an "unstable monopodium." The overall result of this growth form is still a tree with a single trunk and coniferous shape, although the branches are uniformly distributed and not in whorls or tiers, as in pines. How this apparent flexibility in leader development relates to stress response remains uninvestigated in detail, but is highly relevant to the activity of pathogens that may weaken the

leader. Experimental study is required in order to evaluate this issue in more detail.

Tsuga has a specialized method of pollen capture that relates to its pollen structure. In Pinaceae most genera have saccate pollen (i.e. pollen with bladder-like extensions). Conventionally this is said to facilitate wind dispersal by reducing the density of the pollen grain and so slowing the rate of pollen descent. This idea has been greatly challenged by research at Harvard Forest, which has adopted a broad comparative approach and considers in detail the southern coniferous family Podocarpaceae, which also has saccate pollen. In our studies sacci have been shown to be important in pollen capture rather than dispersal, and their function is hydrodynamic rather than aerodynamic. Part of the evidence for this interpretation is found in taxa like *Tsuga*, which lack sacci by evolutionary reduction and in which pollen germinates on the cone scales, away from the ovule. These comments suggest that where effort is concentrated on a single species, a broad comparative approach in a systematic context is highly relevant to biological understanding.

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VISITING RESEARCH SCIENTISTS AT THE HARVARD FOREST 1996-97

In addition to Harvard Forest researchers, a large number of Harvard University and outside scientists made use of Harvard Forest facilities and research sites. Many of these scientists were involved in the Harvard Forest Long Term Ecological Research (LTER) program or in Harvard University's Northeast Regional Center of the National Institute for Global Environmental change (NIGEC) project.

John Aber	University of New Hampshire	Doug Karpa-Wilson	Harvard University
David Ackerly	Harvard University	Shoichi Kawano	Kyoto University
Jeff Amthor	Lawrence Livermore Lab	Chris Kerfoot	Ecosystems Center - MBL
Peter Bakwin	Harvard University	David Kicklighter	Ecosystems Center - MBL
Dennis Baldocchi	NOAA/ARL, Oak Ridge, TN	Melissa Kibler	Gustavus Adolphus College
Diana Barnes,	Harvard University	Bruce Kindel	University of Colorado, Boulder
Susan Bassow	Harvard University	David Kittredge	University of Massachusetts
Fakhri Bazzaz	Harvard University	Otto Klemm	University of New Hampshire
Beth Belk	Woods Hole Research Center	Cathy Langtimm	U.S.G.S./Holy Cross College
Glenn Berntson	Harvard University	Xuhui Lee	Yale University
K. Boering	Harvard University	Barry Lefer	University of New Hampshire
Rich Bowden	Allegheny College	Manuel Lerdau	SUNY, Stony Brook
Frank Bowles	Ecosystems Center - MBL	Sue Leschine	University of Massachusetts
Jennifer Bravo	Brown University	Mary Ann Levine	University of Massachusetts
Sebastian Catovsky	Harvard University	Alison Magill	University of New Hampshire
Chris Catricala	Ecosystems Center - MBL	Mary Martin	University of New Hampshire
Jeannine Cavender-Bares	Harvard University	Charles McLaugherty	Mount Union College
Chaur-Fong Chen	Oregon State University	Ernesto Medina	Centro de Ecología y Ciencias Venezuela
Stephanie Ciccarello	Antioch New England	Jerry Melillo	Ecosystems Center - MBL
Rachel Clark	Gustavus Adolphus College	Jennie Moody	University of Virginia
Alan Coleman	Harvard University	Kathleen Moore	SUNY, Albany
Patrick Crill	University of New Hampshire	Mitch Mulholland	University of Massachusetts
William Currie	University of New Hampshire	J. William Munger	Harvard University
Peter Czepl	Harvard University	Christine Muth	Harvard University
David B. Dail	University of Georgia	Knute Nadelhoffer	Ecosystems Center - MBL
Eric Davidson	Woods Hole Research Center	Kathy Newkirk	Ecosystems Center - MBL
Bruce Daube	Harvard University	Fred Paillet	U.S. Geological Survey
Peter Del Tredici	Arnold Arboretum	William Patterson	University of Massachusetts
Michael Donoghue	Harvard University	Bob Pearcy	University of California, Davis
Marty Downs	Ecosystems Center - MBL	Marc Potosnak	Harvard University
Todd Drummey	Ecosystems Center - MBL	Ronald Prinn	M.I.T.
Bob Evans	U.S.D.A. Forest Service	Kurt Pregitzer	Michigan Technical University
Elizabeth Farnsworth	Harvard University	Michael Rogers	GA Institute of Technology
Rebecca Field	University of Massachusetts	Richard Rosen	AER, Inc.
David Fitzjarrald	SUNY, Albany	Brian Shelley	College of the Holy Cross
Son-Miao Fan	Harvard University	Timothy Sipe	Franklin and Marshall College
Richard Forman	Harvard University	Paul Steudler	Ecosystem Center - MBL
Steve Frolking	University of New Hampshire	Britt Stephens	U.S. Geological Survey
Lisa George	Harvard University	Peter Stone	M.I.T.
Alan Goldstein	Harvard University	Eric Sundquist	U.S. Geological Survey
Michael Goulden	Harvard University	Robert Talbot	University of New Hampshire
Dennis Gray	SUNY, Stony Brook	John Thomlinson	University of Puerto Rico
Robert Harriss	University of New Hampshire	Matt Thompson	Harvard University
Joseph Hendricks	University of New Hampshire	Susan Trumbore	UCLA, Irvine
Kristiina Hill	M.I.T.	Joannah Whitney	University of Massachusetts
Michelle Holbrook	Harvard University	Brayton Wilson	University of Massachusetts
David Hollinger	U.S. Department of Agriculture	Paul Wilson	University of California, Northridge
Lauren Interness	Woods Hole Research	Greg Winston	U.S. Geological Survey
Daniel Jacob	Harvard University	Richard Wilson	Harvard University
Henry Jacoby	M.I.T.	Maciej Zwieniecki	Harvard University

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David R. Foster
Director

Petersham, Massachusetts
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