

**THE DYNAMIC NEW ENGLAND LANDSCAPE:
INTERACTIONS AMONG DISTURBANCE,
ENVIRONMENTAL CHANGE, AND ECOSYSTEM
PATTERN AND PROCESS**

HARVARD FOREST LTER III 2000 – 2006

David R. Foster, Principal Investigator
Harvard Forest, Harvard University

Co-Investigators

Emery Boose Glenn Motzkin John O'Keefe David Orwig Julie Pallant	Harvard Forest, Harvard University
Carol Barford William Munger Steven Wofsy	Earth and Planetary Science, Harvard University
Fakhri Bazzaz	Organismic and Evolutionary Biology, Harvard University
Peter Del Tredici	Arnold Arboretum, Harvard University
John Aber Glenn Berntson Alison Magill Scott Ollinger	Complex Systems Research Center University of New Hampshire
Jerry Melillo Knut Nadelhoffer Paul Steudler	The Ecosystems Center Marine Biological Laboratory
Rebecca Field David Kittredge Mitch Mulholland	Department of Natural Resources Conservation University of Massachusetts Department of Archaeological Services
Cathy Langtimm	Biology Department, Holy Cross University

Project Summary

Temperate forests, such as those that dominate the Eastern US, are critically important ecosystems at regional to global scales. These forests harbor a diversity of species and habitats, provide essential resources, offer important amenities to densely populated regions, and comprise key elements in global carbon budgets. Understanding the structure, function, and patterns of these ecosystems and anticipating their response to natural disturbance, environmental change, and anthropogenic disturbance and stress are therefore critical societal goals that depend on a sound knowledge of fundamental ecological processes. Such insight can only be gained through long-term, inter-disciplinary research that integrates field studies, measurements, experiments, and modeling over a range of temporal and spatial scales.

The Harvard Forest LTER program seeks to interpret ecological pattern and process in New England forests and to apply this knowledge to regional and global issues in forest conservation, land restoration and protection, public policy, and the environment. Over the past decade, HF LTER has matured into a collaboration that applies unique approaches in historical and community ecology, ecophysiology, atmospheric chemistry, and ecosystem studies to the interpretation of long-term, large-scale experiments and measurements, mechanistic studies, and retrospective research. In **LTER I**, we used primarily site-based annual and static measurements to interpret current conditions and to evaluate the comparative response of forest ecosystems to natural disturbance (hurricanes) versus anthropogenic stress (N deposition and soil warming). Long-term measurements from these studies enabled **LTER II** to associate inter-annual variation in processes and environment, to examine land-use impacts at site to sub-regional scales, and to incorporate an understanding of historical landscape transformations into interpretations of modern pattern and process. This research produced major accomplishments: >300 publications; a synthesis volume linking 1000 years of forest dynamics to ecosystem structure, function, and composition; an annual Research Program for 35 students; and innovative approaches to regional, national, and international cross-site studies.

In **LTER III** we seek to make major advances in our understanding of the interactions among disturbance, environmental change, and ecosystem pattern and process at site to regional and even global scales. We propose to: (1) extend measurements, modeling activities, and historical studies to regional scales; (2) interpret landscape development, vegetation and wildlife dynamics, and ecosystem patterns in relationship to millennial-scale climate change, land-use, and disturbance; (3) evaluate ecosystem response to critical ongoing disturbances and stresses (e.g., forest cutting and conversion, ozone and N deposition, and invasions by pests and non-native plants); (4) interpret long-term measurements and responses to experimental treatments mechanistically and in relation to inter-annual and inter-decadal variation and history; and (5) apply these results to understanding the current and projected role of this region in global carbon storage. In these efforts we will (1) continue our long-term experiments and measurements; (2) strengthen our inter-disciplinary connections and cross-site comparisons; (3) add new mechanistic studies, disciplines, and co-investigators; and (4) leverage major additional support from NSF, DOE, NASA, EPA, USDA, The Nature Conservancy, and private foundations.

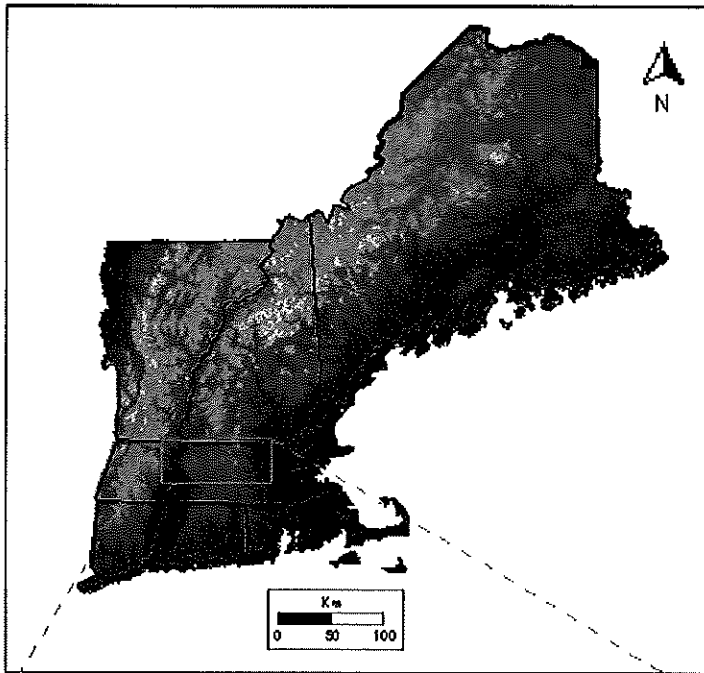
I. Prior Results and Background to the Harvard Forest (HF) LTER

The Harvard Forest LTER has developed into an integrated research program addressing fundamental and applied ecological questions in temperate forest ecosystems that are dynamic as a consequence of disturbance and environmental change (Fig. 1; Foster & Aber 2000). **LTER I** emphasized site-based investigations in which static and annual estimates of forest pattern and ecosystem process were interpreted in relation to current mean conditions. Long-term experiments contrasted natural disturbance (hurricanes) vs. anthropogenic stresses that are indirect consequences of current land use (N deposition and soil warming). Major findings included: (1) historical land use conditions modern ecosystem structure, process, and dynamics; (2) ecosystem function and trajectories exhibit large inter-annual variation; and (3) interpretations of ecosystem pattern and process require investigations across broad spatial and temporal scales (Fig. 2). Consequently, in **LTER II** we added retrospective (historical/paleoecological) studies; incorporated land-use history and inter-annual variation into experiment and measurement design; and broadened our investigations to sub-regional (Central Massachusetts) scales. A decade of research has produced major accomplishments: > 300 publications including 22 theses, 12 books, two video presentations; a synthesis volume linking 1000 years of forest dynamics and natural and human disturbance to ecosystem structure, function, and composition (Foster & Aber 2000); a Summer Research Program for 35 students annually; unique methodological and experimental approaches to ecological, atmospheric, and historical research; and regional, national and international cross-site studies.

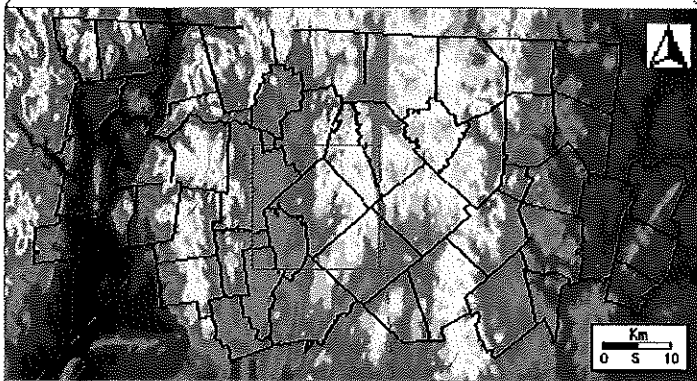
We are poised in **LTER III** to (1) expand many studies to regional (New England-wide or larger) scales; (2) evaluate inter-decadal dynamics of key processes and responses; (3) pursue new mechanistic studies of ecosystem, population, and atmospheric processes to interpret long-term trajectories of major experiments; (4) incorporate critical disturbance and stress phenomena (major forest pathogens, forest logging and conversion, ozone, Little Ice Age climate change, exotic species) with ongoing studies of land-use, hurricanes, fire, N deposition, and drought; and (5) apply results to local, regional, and global issues in climate change, water and air quality, forest management, land protection, and conservation. Results below, reported primarily from **LTER II**, set the stage for these new studies.

Specific objectives of Harvard Forest **LTER II** included: (1) contrasting pre-European and historical forest dynamics and disturbance; (2) using these histories to interpret vegetation patterns at sub-regional scales; (3) evaluating controls (land-use, climate, vegetation, soils) on C and N dynamics; and (4) synthesizing results through integration and model development.

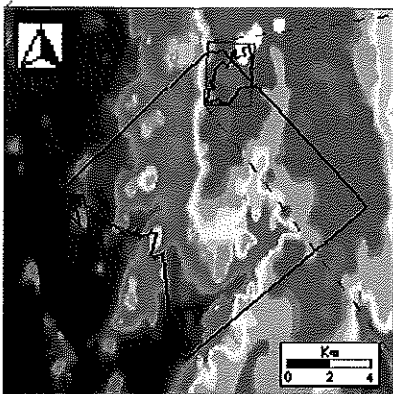
Retrospective Studies using paleoecological and historical approaches enabled us to analyze dynamics over millennia to understand fundamental ecological processes, to identify key factors shaping modern forest conditions, and to provide management and conservation insights (Foster et al. 1996; Foster & Motzkin 1998). In **LTER II**, we sought to interpret the impact of New England's history of deforestation, agriculture, farm



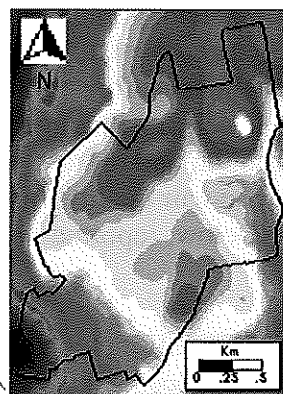
Region - New England



**Subregion -
Central Massachusetts**



**Landscape -
Petersham, Massachusetts**



Site - Harvard Forest

Figure 1. The major spatial scales of investigation in the Harvard Forest LTER program. In LTER I the main emphasis was on site-based measurements, field studies, and large experiments. In LTER II many important processes and ecological patterns were investigated at a landscape scale, which coincides approximately with a township (10 x 10 km), or sub-regional scale in Central Massachusetts, which embraces the Central Uplands and Connecticut Valley physiographic regions. In LTER III our studies will increasingly place site-based and other studies in the framework of the entire New England region. We will scale-up by: (1) sampling on a regional scale, (2) conducting cross-site studies, (3) investigating additional sub-regions and physiographic regions (e.g., the Coastal region), and (4) using remote sensing, GIS analysis, and modeling. Colors indicate elevation.

abandonment, and reforestation on modern forest patterns with a focus on Harvard Forest and the C. Massachusetts sub-region. Important findings include: (1) at the time of European settlement, tree distributions were correlated with regional climate, whereas modern vegetation is more homogeneous as a consequence of historical land use and is not reverting to pre-settlement patterns (Foster et al. 1998b); (2) pre-European vegetation was dynamic as a consequence of climate change (Little Ice Age), fire, and Indian activity (Fig. 3; Fuller et al. 1998); (3) historical decreases in long-lived, shade-tolerant trees (e.g., beech, hemlock) and increases in sprouting/successional species (e.g., birch) were driven by land-use and lagged response to the Little Ice Age (Foster 2000); (4) pre-European forest communities were controlled by site conditions, climate change, and fire; modern assemblages are novel and reflect specific land-use histories (McLachlan et al. 2000, Foster et al. 2000).

Hurricane Modeling and Reconstruction enables us to interpret the landscape and regional impacts of important storm events based on historical data (Boose et al. 1994, 2000). The technique provides meteorological data, regional maps of actual damage, and estimates of wind speed, direction, and damage for each storm and compilations of spatial and temporal gradients for all storms. Landscape damage variation is examined with a simple exposure model. This technique can be applied to any region and allows incorporation of hurricane disturbance regimes into research and management (Foster et al. 1999). Results for New England since 1620 include: (1) hurricanes are key factors regionally, decreasing in frequency and intensity from SE to NW due to weakening over land and cold ocean water (Fig. 4); (2) landscape-level gradients of exposure exist due to topography, whereas stand-level damage is dependent on land-use and stand history; and (3) hurricane impacts varied widely on annual and decadal scales.

Community, Population, and Ecosystem Studies are used to evaluate the role of history vs. site conditions in controlling modern species distributions and assemblages. Separating the influence of these factors is complicated by: (1) inter-correlated environmental gradients, (2) paucity of historical data, and (3) confounding of disturbance history with environment. To address these problems, we used three approaches. Intensive studies of vegetation on homogeneous sand plains allowed assessment of disturbance effects in the absence of site variation. Applicability of the results was evaluated on all similar sites in our C. Massachusetts sub-region. Studies were then extended to complex uplands where variation in environment and disturbance coincide. Results include: (1) modern sand plain communities are more strongly related to past land-use than fire or current site factors (Fig. 5; Motzkin et al. 1996; 1999a). (2) on heterogeneous uplands, species respond individualistically to site factors and disturbance, but distributions are most strongly related to moisture and land-use history (Motzkin et al. 1999b); (3) constraints on dispersal/establishment prohibit some species from re-colonizing sites for centuries (Motzkin et al. 1996; Donohue et al. 2000); and (4) prior land use exerts long-term effects on forest C and N dynamics that varies with site and vegetation (Compton et al. 1998; Compton & Boone 2000).

Long-Term Experiments enable us to evaluate critical ecosystem processes and to contrast forest response to natural disturbance and anthropogenic stress. The

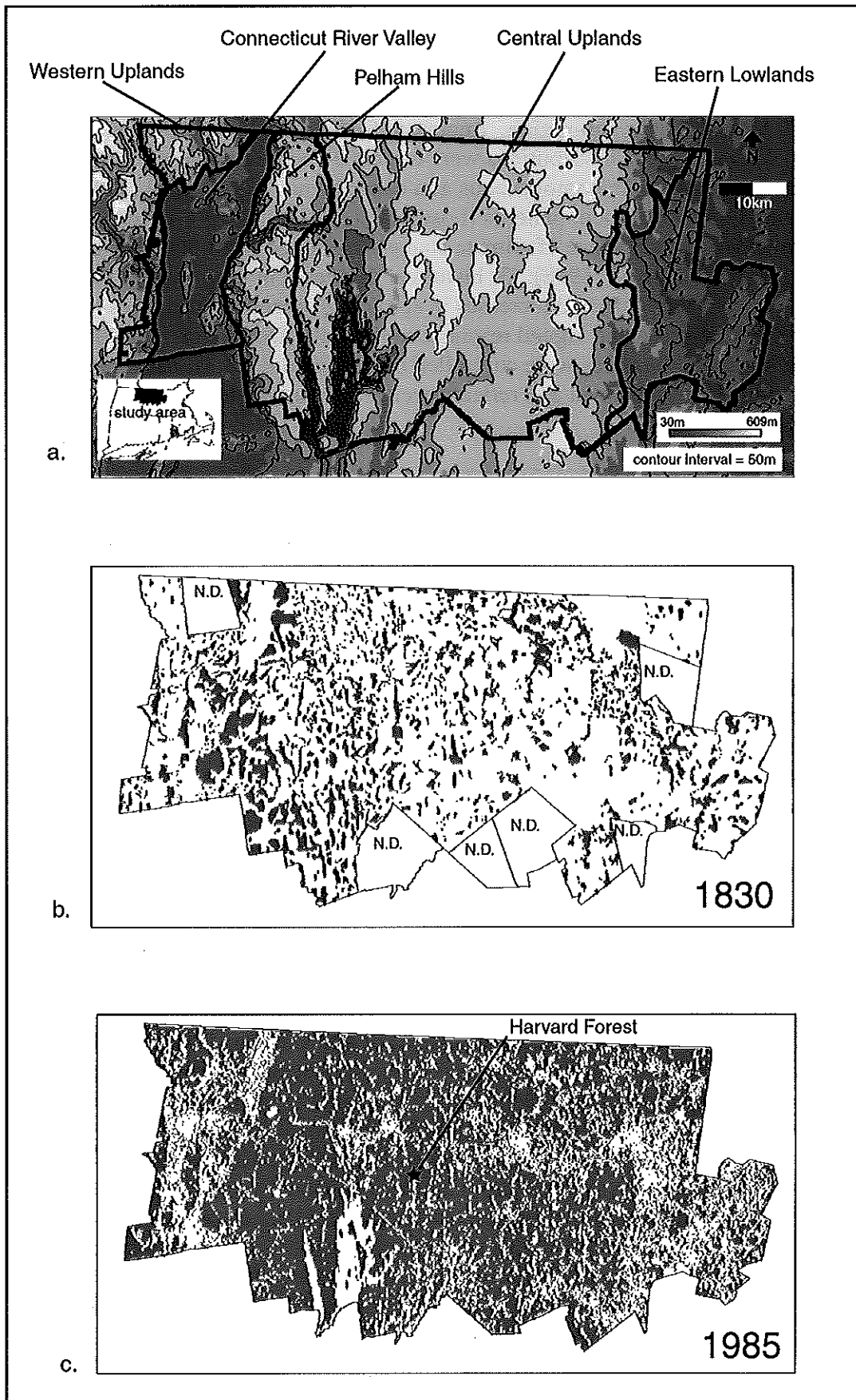


Figure 2. The Central Massachusetts sub-region showing topography, the major physiographic areas (a) and forest cover in 1830 (b) and 1985 (c). Patterns of land cover change strongly influence modern ecosystem structure and function and vary with physiography. The Quabbin Reservoir, created in 1938 to supply water to metropolitan Boston, appears in the lower center of maps a and c.

Experimental Hurricane mimics the 1938 storm and was stimulated by recognition of the importance of hurricanes and the lack of integrated studies that address forest recovery and reorganization following wind disturbance (Foster 1988a,b; Cooper-Ellis et al. 1999). Results include: (1) most uprooted and damaged trees re-leafed, died in 2-6 years, and were replaced by sprouts, leading to only minor change in microenvironment or composition (Fig. 6); (2) due to continuity of LAI and the soil environment, changes in nutrient cycling and soil C effluxes were minor (Bowden et al. 1993); (3) seedling regeneration was controlled by resource congruence (water, light, nutrients); species success varied across five microsite types; seed dispersal of major tree species varied considerably: heavy-seeded oaks accumulated in uproot pits while light-seeded birch occurred on all microsites (Carlton & Bazzaz 1998a,b); and (4) the study forced re-evaluation of the 1938 hurricane (Foster et al. 1998a). Stands damaged in 1938 were mostly pine on old fields, which were subsequently salvaged; thus, increases in river flows and changes in forest composition in 1938 were more a consequence of land-use than natural disturbance.

The **Soil Warming Experiment** evaluates the effect of a 5° C rise in soil temperature, similar to that predicted by many global models, on ecosystem processes. Results include: (1) over 7 years, CO₂ flux-increases due to warming dropped from 30-40 % to ~9 % (Peterjohn et al. 1994, 1995). Annual decreases occurred in dry and cold years; (2) net N mineralization rates in the soil increased 106-140% in most years, but dropped to 31% during a drought year (Fig. 7). Nitrification was consistently low, < 5% of annual net mineralization; and (3) trenched plots indicate that growing season microbial respiration was 69-74% of total respiration; root respiration was 26-31%. Heating increased microbial respiration (20-32%) more than root respiration (9-15%), with annual variation due to drought (Melillo et al. 1995).

The **N Saturation Experiment** tests hypotheses on the response of N-limited ecosystems to increases in N deposition (Aber et al. 1989). Plots in adjacent hardwood and red pine forests are subjected to 0 (control), 5 (low) and 15 (high) g N·m⁻²·yr⁻¹ additions of NH₄NO₃ from May to October. Major N fluxes are measured (net mineralization and nitrification, aboveground uptake, litter fall, decomposition, leaching loss of DON (dissolved organic N), N₂O emissions) along with aboveground NPP, foliar N, and soil CO₂ flux. Results include: (1) Increases in nitrate leaching occurred as predicted with N additions, but the timing differed strongly between sites with differing histories (Fig. 8; Magill et al. 2000). The pine stand on fields fertilized in the 19th C has lower N demand and immediate nitrate loss with high N. The hardwood stand, originally low in N cycling due to prior pasturing, cutting and fire, retained N and showed nitrate loss only in year 9 under high N; (2) N retention occurred without increased soil CO₂ efflux (Aber et al. 2000) or apparent microbial nitrate immobilization (Berntson & Aber 2000), suggesting the importance of abiotic or mycorrhizal N retention (Aber et al. 1998). Soil and decomposing litter are greater sinks for N inputs than tree biomass, but the proportions of N uptake by trees vs. soils increased with deposition (Nadelhoffer et al. 1999a); (3) elevated nitrate losses in the pine stand are associated with declines in biomass production (Magill et al. 2000) despite large increases in foliar N. Needle retention time and total LAI declined and net rates of photosynthesis per unit leaf area are unchanged. In

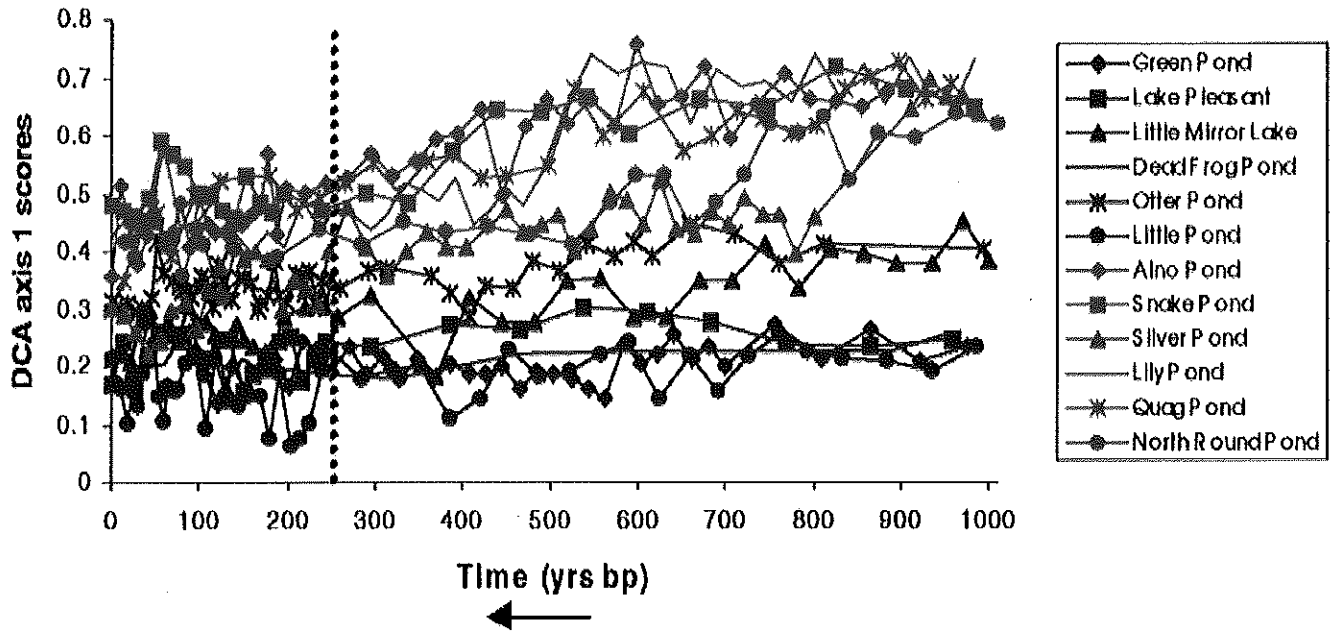


Figure 3. Detrended correspondence analysis (axis-1 scores; 32% of variation) for pollen samples from 11 lakes in C. Massachusetts over the last 1000 years (Fuller et al. 1998). Compositional changes occur before and following European settlement (dashed line), driven by climate (Little Ice Age) and land-use activity. The relative importance of these factors, including Indian activity and fire, remains a major question for LTER III. Upland sites are shown in red, lowland sites in blue.

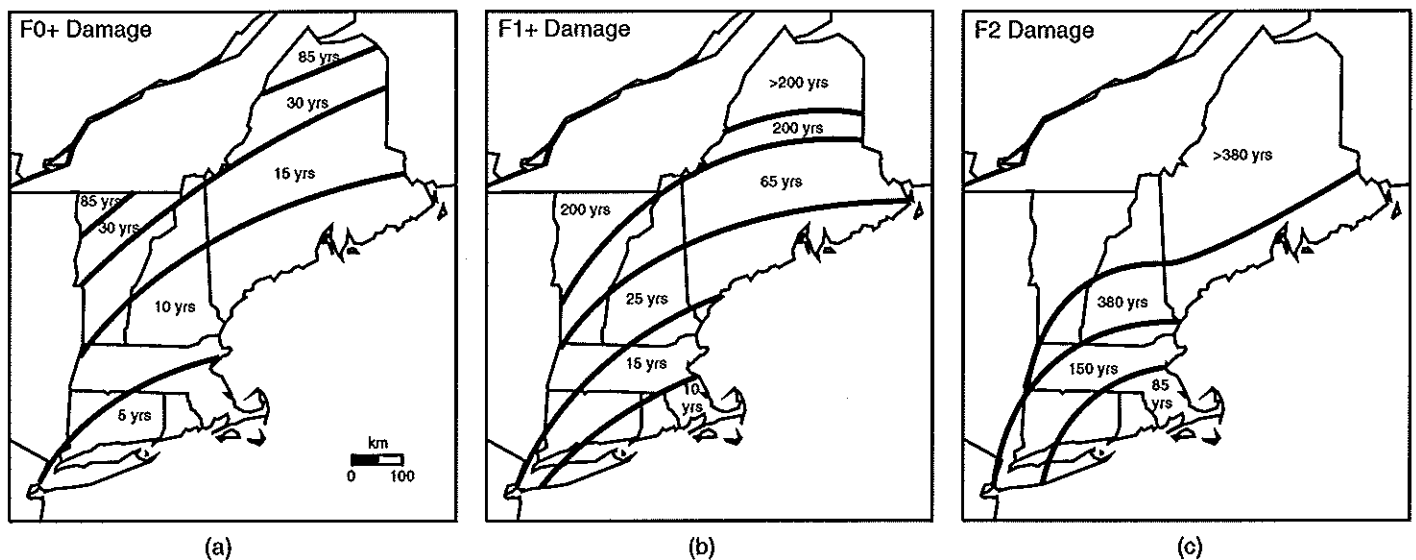


Figure 4. Smoothed regional gradients in reconstructed hurricane damage for New England using the HURRECON model (Boose et al. 2000). Average return intervals for (a) F0+ damage (loss of leaves and branches), (b) F1+ damage (scattered blowdowns, small gaps), and (c) F2 damage (extensive blowdowns and large gaps).

the hardwood high N plot, there is an increase in foliar N and woody biomass production; (4) decomposition of litter is depressed with high N additions, supporting hypotheses on the suppression of enzyme decomposition systems with abundant mineral N. N accumulation in litter continued in the absence of mass loss, suggesting chemical interactions between organic substrates and N. Up to 30% of leaf mass loss occurred through leaching dissolved organic carbon; (5) ¹⁵N tracer studies were consistent with studies at 6 European sites showing that soils are the dominant sink for N saturation inputs to temperate forests and that N deposition does not dramatically increase C uptake (Nadelhoffer et al. 1999c,d); and (6) variation in plant performance is related to availability of nitrate or ammonia. Tree species differentiate between these N forms, the spatial distribution of ammonia and nitrate affect seedling growth, and growth increases with nitrate deposition.

Comparison of ecosystem response to natural disturbance versus anthropogenic stress showed that although hurricane impacts appear catastrophic, many key ecosystem processes are relatively unchanged and stands recover structure and function rapidly, in keeping with the cyclic history of disturbance and recovery. By contrast, N addition and soil warming have no visible impact yet measurements of ecosystem function suggest serious imbalances with long-term implications for ecosystem function (Foster et al. 1997).

The **Environmental Measurement Station (EMS)**; Wofsy et al. 1993) is a unique eddy covariance system that we developed in order to evaluate carbon exchange in relationship to environmental variables. Major results include: (1) over 75,000 hourly rates of Net Ecosystem Exchange of CO₂ (NEE) provide 9 years of annual NEE estimates (Goulden et al. 1996a, b); this spurred creation of flux measurement networks in the US (AmeriFlux) and abroad to examine pattern and process at ecosystem to continental scales (Fig. 9); (2) C uptake (mean ~2.1 t C ha⁻¹ yr⁻¹; Goulden et al. 1996a,b; Frohking et al. 1996) is a consequence of recovery from prior land use and the 1938 hurricane; (3) annual variation in NEE is controlled by growing season length, cloudiness, precipitation, and winter soil temperature (Goulden et al. 1996a).

Measurements of **atmospheric exchanges of reactive trace-gases** at the EMS include dry deposition for nitrogen oxides, deposition of ozone, and emission of hydrocarbons (isoprene and terpenes) that influence ozone and nitrogen oxides in the regional and global atmosphere. These observations help define how biogenic hydrocarbons mediate N deposition by the formation of hydroxyalkylnitrates (Fig. 10) and elucidate the mechanisms, including local forest processes, that facilitate the escape of nitrogen oxides from regional sources to continental and global scales.

The **DIRT (Detritus Input and Removal Treatments) Experiment** investigates the mechanisms of carbon dynamics in forest ecosystems and seeks to characterize the role of plant inputs in determining soil properties and organic matter dynamics. Treatments over 10 years include: doubling of leaf litter inputs, no leaf litter inputs, no root inputs, no leaf or root inputs, and soil "impoverishment" by replacing O and A horizons with B horizon soil. Results include: (1) soil respiration measurements estimated fine root

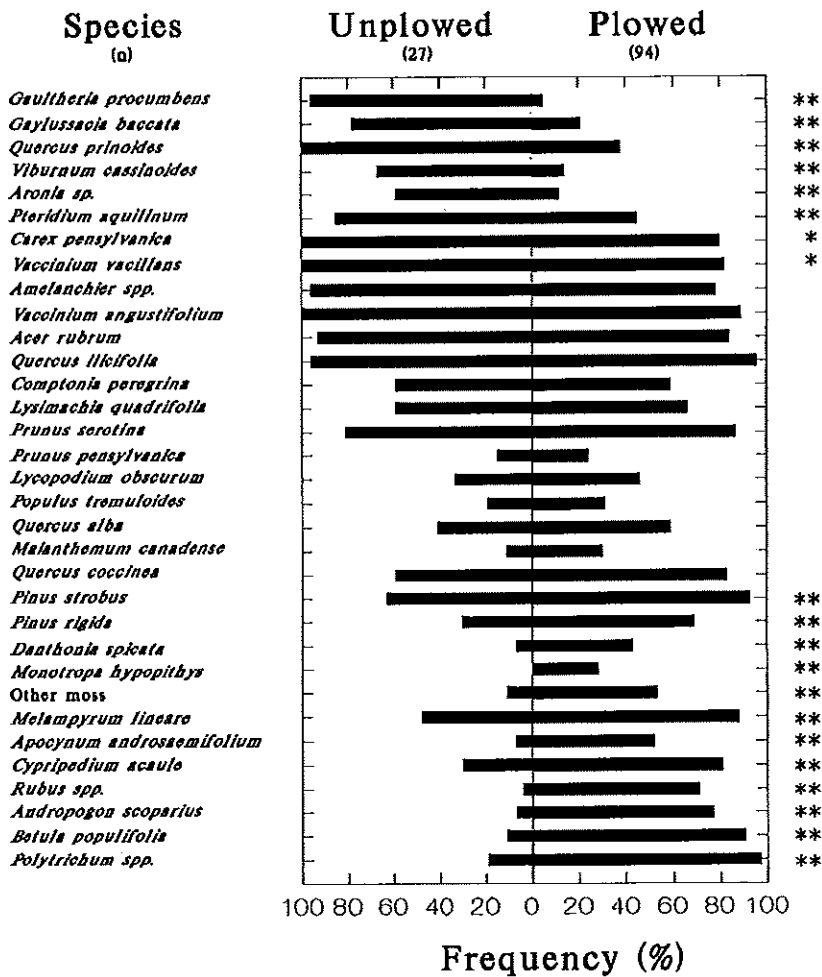


Figure 5. The frequency of occurrence (%) of common plant species on historically plowed vs unplowed sites on an edaphically homogeneous sandplain in the Connecticut Valley (Motzkin et al. 1996) that reforested naturally following land use in the 19th C. Significance of G tests is indicated at the $P < 0.05$ (*) and $P < 0.01$ (**) levels.

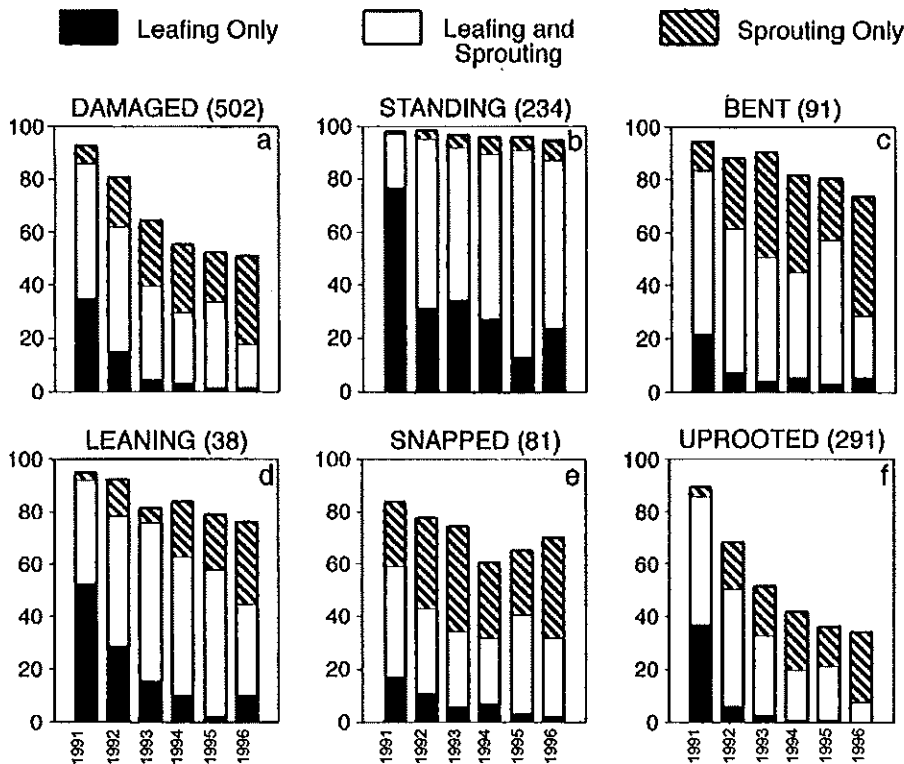


Figure 6. Survival rates and mechanisms for trees on the experimental hurricane according to different types of damage. Vegetative regeneration through sprouting is a very important mechanism for survival and proliferation and is a major focus of LTER III studies (Cooper-Ellis et al. 1999).

production (Bowden et al. 1993b); roots and associated rhizosphere soils are much more responsive to temperature variations than are bulk soils (Fig. 11; Boone et al. 1998); and (2) soil C and N contents, humus turnover, net N mineralization, nitrification, dissolved organic C and N production, and microbial communities are strongly influenced by litter and root inputs (Nadelhoffer et al. in review).

Collaborative Modeling with the Hubbard Brook (HB) LTER and U.S. Forest Service enables spatial extrapolations of ecosystem function based on HF and HB LTER research. We developed spatial data sets for climate (Ollinger et al. 1993,1995), soils and vegetation, and a simple model of forest C, water, and N dynamics (Aber et al. 1995, 1996, 1997, Aber & Driscoll 1997) validated against NPP and water yield at the site and regional (Ollinger et al. 1998) scales, and nitrate leaching losses at HB (Aber & Driscoll 1997). The model includes ozone effects on photosynthesis and forest production (Ollinger et al. 1997) and responses to climate change and N deposition in terms of NPP, water yield, and nitrate leaching in streams. Results include: (1) ambient ozone is reducing forest NPP by ~10%; (2) climate change is predicted to increase regional forest production by about 30% and decrease water yield by 15% due to change in precipitation inputs; (3) annual climate variability exerts a large effect on watershed nitrate losses; and (4) responsiveness to climate variability may make it very difficult to detect changes in nitrate leaching due to N deposition (Fig. 12). At current levels of deposition, more than 100 years of stream chemistry data would be required to demonstrate predicted increases.

Cross-site Research is a growing part of HF LTER research; it provides insight into the range of variation in fundamental processes, strengthens our ability to develop generalizations, and supports our efforts at spatial extrapolation. Controls on C sequestration in forests are examined through comparison of annual and interannual rates of C flux at Howland ME (USFS, DOE), Morgan, IN (DOE), Thompson, Manitoba (NASA), other AmeriFlux sites, and the Brazilian Amazon. Our results indicate that conifer forests (Maine, Manitoba) have a longer season of uptake but lower efficiencies for photosynthesis than Harvard Forest (Goulden et al. 1997), whereas the deciduous Indiana forest acts much as Harvard Forest does. The 90-year old stand at Howland takes up C at similar rates, but the old forest in Manitoba releases C due to warming and ablation of permafrost.

Interactions among land use, climate variation, and natural disturbance in controlling forest landscape patterns and dynamics are being compared in New England, Ireland, Puerto Rico (LUQ LTER), and the S Yucatan (Mexico), with support from LTER, NSF-International, NASA, and University College, Dublin (Boose et al. 2000; Foster et al. 1999, 2000). In all areas, historical and modern land use are more important drivers of vegetation structure, composition, dynamics, and function than natural disturbance such as hurricanes or fires or environmental variability. This research confirms similarities among very different landscapes, has re-oriented major research programs in each region, and has been a very successful means of exchanging faculty, scientists, and students.

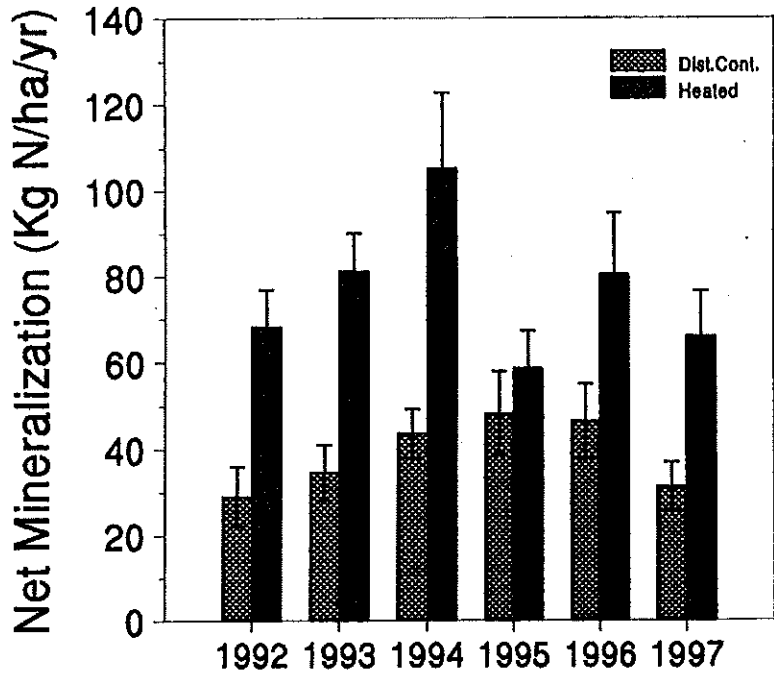


Figure 7. Response of soil N mineralization rates to soil warming 5° C above ambient, in comparison with control plots (disturbed by insertion of heating cables, but not warmed). The dip in mineralization rate in 1995 corresponded to severe summer drought (Peterjohn et al. 1993, 1994; Melillo et al. in press).

Sequential NO₃ Breakthrough

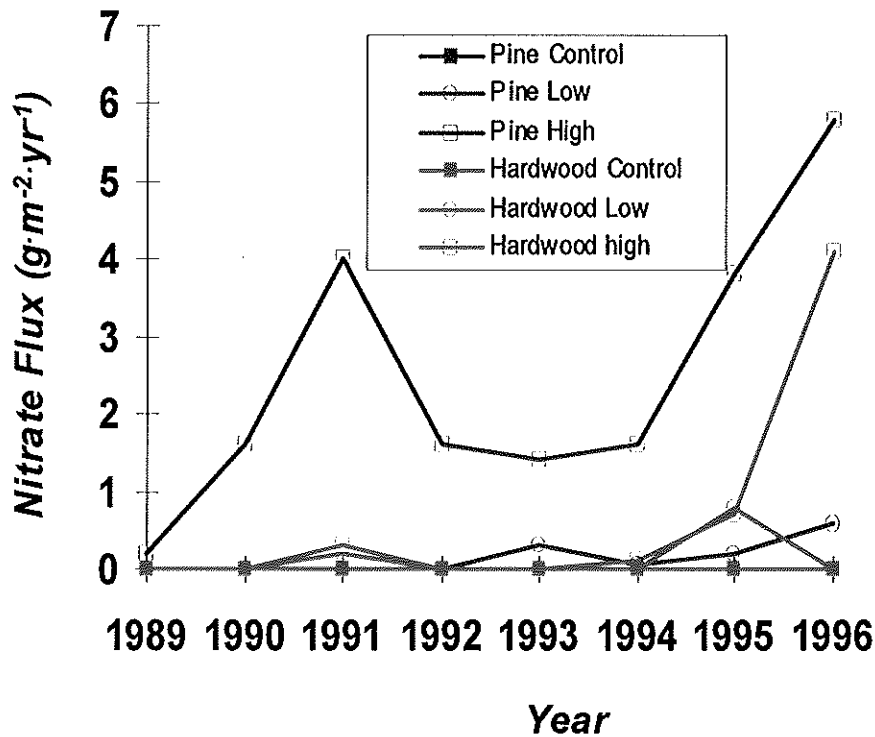


Figure 8. Nitrate flux below the rooting zone in the N saturation experiment. Response varied tremendously with land-use history, forest type, and the level of N additions (Aber et al. 1998). Pine and hardwood controls had consistent values of zero for all years.

A. HARVARD FOREST LTER II BIBLIOGRAPHY

DISTRIBUTION OF HARVARD FOREST LTER PUBLICATIONS

	LTER I	LTER II
Total	90	236
Books	3	9
Book Chapters	12	36
Theses	11	13
<i>Oecologia</i>	5	18
<i>Ecology</i>	7	14
<i>Ecological Applications</i>	4	10
<i>Journal of Geophysical Research</i>	2	10
<i>Global Change Biology</i>		8
<i>Global Biochemical Cycles</i>		7
<i>Ecosystems</i>		7
<i>Nature</i>	2	5
<i>Journal of Ecology</i>	6	5
<i>Canadian Journal of Forest Research</i>	10	5
<i>Plant and Soil</i>	1	5
<i>Arnoldia</i>		5
<i>Soil Biology and Biochemistry</i>		5
<i>Biogeochemistry</i>	2	4
<i>Journal of Soil Science Society of America</i>	1	4
<i>Journal Torrey Botanical Society</i>		4
<i>Plant Cell & the Environment</i>		3
<i>Bulletin Ecological Society of America</i>		3
<i>Climate Research</i>		3
<i>Tellus</i>		3
<i>Science</i>	1	3
<i>New Phytologist</i>	2	2
<i>BioScience</i>	1	2
<i>Ecological Monographs</i>	1	2
<i>Water, Air & Soil Pollution</i>		2
<i>American Journal of Botany</i>		2
<i>Environmental Monitoring Assessment</i>		2
<i>Oikos</i>		2
<i>Remote Sensing of the Environment</i>		2
<i>Journal of Biogeography</i>		2
<i>Trees</i>		2
<i>Trends in Ecology and Evolution</i>	4	1
<i>Canadian Journal of Botany</i>	3	1
<i>Ambio</i>	1	

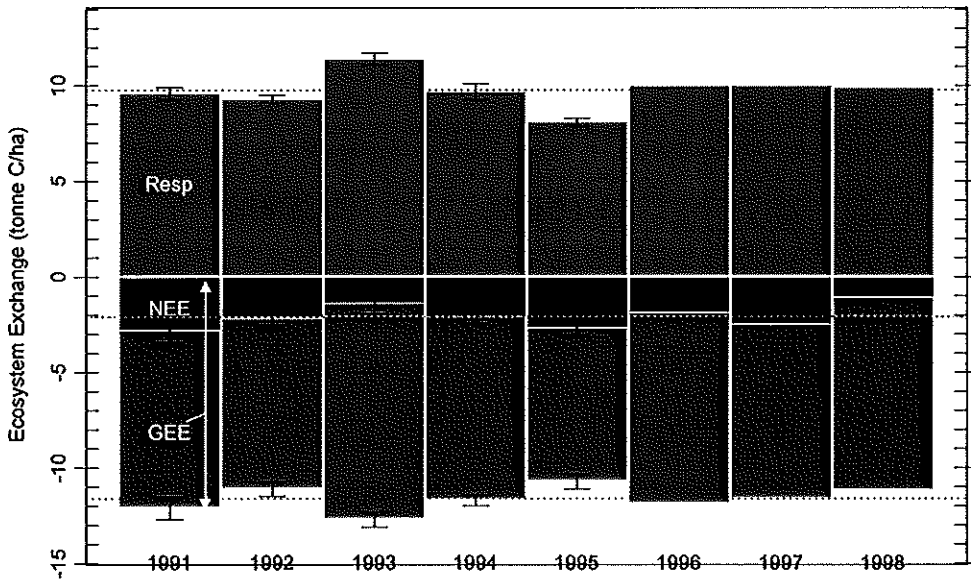


Figure 9. Annual integrated values for *Net Ecosystem Exchange (NEE)* (black bars) from 1991-1998, the sum of hourly net fluxes measured by the flux tower at the Harvard Forest Environmental Measurement Site in the Prospect Hill tract. *Ecosystem respiration (R)* is derived from nighttime data, interpolated into daytime using a function dependent on soil temperature. *Gross Ecosystem Exchange*, defined as $R - NEE$, approximates the quantity of carbon fixed by the forest canopy in the year. Note that R and GEE tend to co-vary, but differential variations are responsible for changes in annual NEE . For example, in the drought year of 1995 both R and GEE were depressed, but R declined more than GEE and thus net carbon uptake was relatively high.

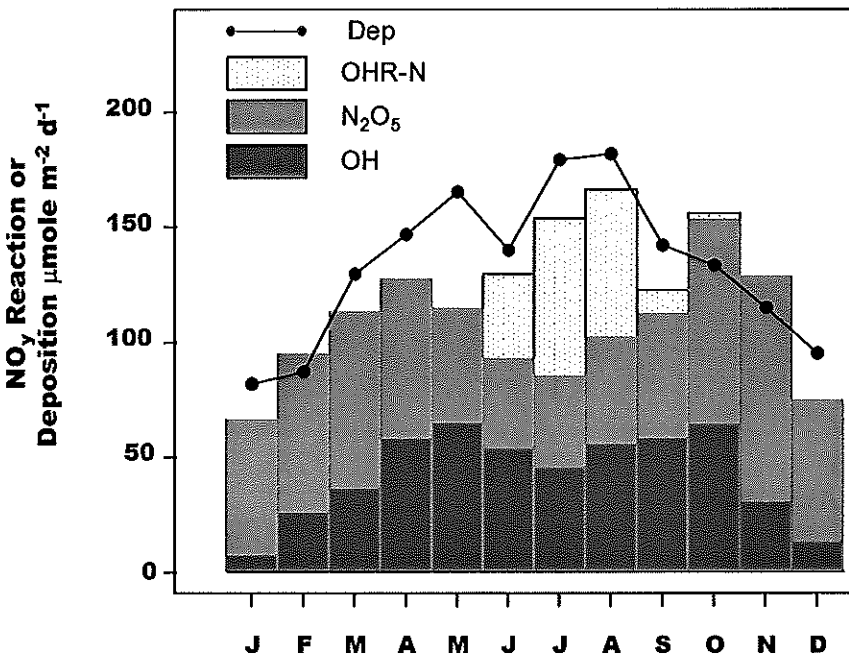


Figure 10. Monthly mean input of nitrogen oxides by wet and dry deposition (shown by solid line) is approximately balanced by formation of nitric acid and hydroxy-organic nitrates that are derived from biogenic isoprene and terpenes. The estimated production rates are inferred from observed concentrations of NO_x and O_3 and measured isoprene emissions at Harvard Forest.

<i>American Naturalist</i>	1	
<i>Annual Review of Ecology and Systematics</i>	1	1
<i>Botanical Review</i>	1	
<i>Ecological Modeling</i>	1	1
<i>Forest Ecology and Management</i>	1	1
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<i>Climatic Change</i>		1
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<i>Acta Phytoecologia Sinica</i>		1

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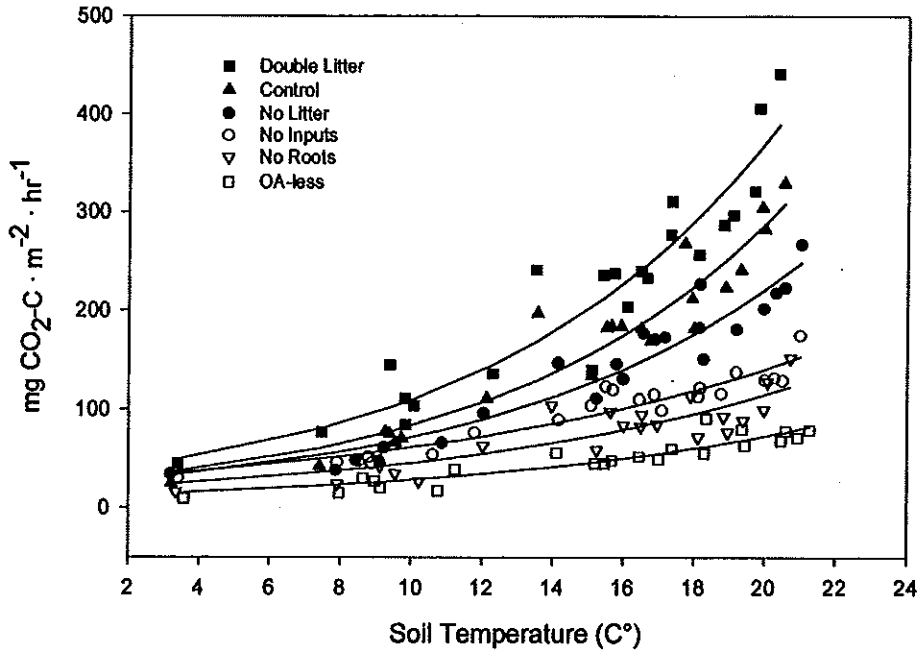


Figure 11. Relationship between mean daily soil CO₂ flux and soil temperature at 5cm soil depth from 16 June 1994 through 14 June 1995 for each of 5 DIRT plot treatments plus controls. An exponential function of the form $y = \beta_0 e^{\beta_1 T}$, where y = flux, β_0 and β_1 are fitted constants, and T = temperature, was fitted to the data. Reprinted from Boone et al. (1998).

PnET Predictions Future Changes in Nitrate Loss

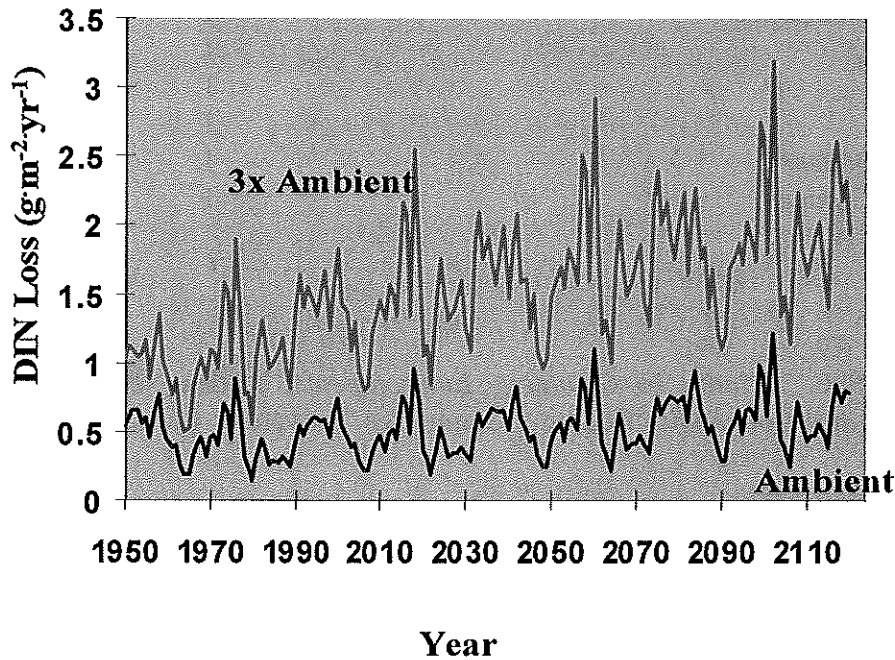


Figure 12. Effect of N deposition rate (ambient vs. 3 x ambient) on future changes in nitrate leaching losses from watershed 6 at Hubbard Brook using the PnET model. Over 100 years of data are required to detect a significant increase in nitrate losses with ambient N deposition (Aber et al. 2000).

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Foster, D. R., D. A. Orwig and J. F. O'Keefe. 1997a. Impact of development on the forests of Wachusett Mountain. Department of Environmental Management, Commonwealth of Massachusetts. 15 pp.

- Foster, D. R., D. A. Orwig and J. F. O'Keefe. 1997b. Old-growth forest monitoring on Wachusett Mountain. Department of Environmental Management, Commonwealth of Massachusetts. 12 pp.
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B. HARVARD FOREST ON-LINE DATASETS

1. List of On-line Data Sets

The following data sets are currently available on the Harvard Forest web page (see <http://lternet.edu/hfr/data/catalog.html>). Starting dates for active projects begun before 1992 are indicated in brackets. Recent projects for which complete data are not yet posted are marked with an asterisk.

Atmospheric Exchange & Biogeochemical Cycling

- Environmental Measurement Site (EMS) [1989]
- Methane Data at EMS
- Soil Respiration, Temperature, and Moisture at EMS
- Meteorological Back Trajectories for EMS
- Canopy Chemistry Study
- CO₂ Exchange by Hemlock Forests in Central New England*

Climatology & Phenology

- Harvard Forest Climate Data [1964]
- Phenology of Woody Species [1990]

Experimental Manipulations

- N Saturation Amendment Experiment [1988]
- Simulated Hurricane Experiment [1990]
- Trace Gas Fluxes & Soil N Dynamics in Simulated Hurricane Experiment
- Microsite Environments in Simulated Hurricane Experiment
- DIRT Experiment (Litter Manipulation) [1990]
- Soil Warming Experiment [1991]
- Phenology and Growth of Vegetation at Soil Warming Experiment

Forest Dynamics & Land-Use History

- Forest Change and Human Populations in New England
- Land Use and Forest Dynamics in Central Massachusetts
- Land Use and Forest Dynamics at Harvard Forest
- Vegetation Patterns of a New England Sand Plain (Montague, MA)
- Demography and Morphology of Ericaceous Species on Montague Sand Plain
- Plant Life History and Land-Use History (Montague, MA and Harvard Forest)*
- Dynamics of Old-Growth Forests on Wachusett Mountain (Princeton, MA)*
- Forest Ecosystem Response to Hemlock Woolly Adelgid in Southern New England
- North Quabbin MA Conservation Study
- North Quabbin MA Timber Harvesting Study*

- Land Use and Land Cover Change on the Massachusetts Coast*
- Land Use and Land Cover Change in the Yucatan (Mexico)*
- Landscape-Scale Forest Dynamics in the Luquillo Experimental Forest (PR)

Hurricane Studies

- Forest Damage Patterns in the 1938 Hurricane
- Reconstruction of 1938 Hurricane (New England) and Hurricane Hugo (Puerto Rico)
- Landscape and Regional Impacts of Hurricanes in New England*
- Landscape and Regional Impacts of Hurricanes in Puerto Rico*

Long-term Plots

- Hemlock Mapped Tree Plot [1990]
- Lyford Mapped Tree Plot [1962]
- Overstory Mapped Tree Plots [1990]
- Hurricane Recovery Plots (Harvard Forest) [1940]
- Hurricane Recovery Plots (Pisgah Forest) [1984]
- Regeneration Following Clearcut Study [1990]
- 1937 Vegetation Inventory (3000 acres)
- 1986 Vegetation Inventory (3000 acres)

Models & Software

- PnET: Modeling Carbon, Water, and Nitrogen Dynamics
- INTERPNT: Mapping Trees Using Distance Measurements
- EXPOS: Modeling Topographic Exposure to Wind
- HURRECON: Modeling Hurricane Wind Speed, Direction, and Damage

Paleoecology

- Vegetation Patterns Over Recent Centuries in Northeastern North America
- Long-term Dynamics of Vegetation and Environment in Central Massachusetts
- Long-term Stand Dynamics in Central Massachusetts
- Paleolimnology of Lakes in Central New England*

Physiological Ecology

- Gap Partitioning Among Maples in Central New England
- Canopy Photosynthesis Study
- Fern Understory as an Ecological Filter
- Leaf Display Flexibility in Forest Trees*
- Linking Community Dynamics and Ecosystem Function*
- Plant Functional Pools of C and N for Ecosystem Carbon Cycling*

Species Lists

- Vascular Plants
- Bryophytes
- Breeding Birds

Wildlife Studies

- History of Wildlife in Massachusetts
- Bird Nest Predation in Eastern Oak Forest*
- Vertical Activity of White-Footed Mouse in Oak Forest*
- Effects of Acorn Production on White-Footed Mouse Populations
- Influence of Abandoned Stonewalls on Small Mammal Distributions*

2. Use of On-line Data Sets

At the present time, downloading of Harvard Forest data sets is not recorded electronically, and prospective users (though encouraged) are not required to notify us of their intended or actual use of our data. We are able to track some uses through the questions and acknowledgements that we receive. Several projects also actively submit their data to regional and national databases. Below are examples of use of our on-line data by other scientists.

- Environmental Measurement Site. Data from the EMS project are integrated into the NIGEC and AmeriFlux data systems via hot links at the CDIAC and NIGEC web sites. There have been hundreds of hits and several modeling papers using these data. The data structure has been adapted for widespread use in the AmeriFlux network. The Harvard Forest EMS site and data set were also a component of the NARSTO-NE regional air quality study sponsored by a consortium of EPA, state agencies and industry.
- N-Saturation Data. Foliary chemistry, soil chemistry, litter decomposition, and PnET-predicted N deposition data have been downloaded and used by scientists from NIWOT LTER, Inst. Of Arctic Biology, Syracuse University, Marshall University, and Mt. Holyoke College; and a joint publication is in review with scientists from the Swedish University of Agricultural Sciences.
- Climate Data. The Harvard Forest climate data set has been used in numerous modeling studies and is probably the most frequently downloaded data set. Recently we prepared and submitted our data for inclusion in the LTER Network ClimDB project (<http://sql.lternet.edu/climdb/climdb.html>), which provides tools for data selection and reduction.
- Pollen Data. Pollen data sets from several projects have been submitted to the North American Pollen Database (<http://www.museum.state.il.us/research/napd/>), where they are easily accessible to other paleoecologists and have been used by many

European and North American scientists. For example the IGBP Biome 300 project will continue to use these and other historical data regularly.

- **Models & Software.** Numerous acknowledgments have been received for the Interpnt and Expos programs, along with some requests for source code.
- There has been wide international use of results and data from the DIRT and Soil Warming Experiments.

In addition the following data sets, recently posted, are expected to attract users in the coming year: Phenology of Woody Species (10-year record), North Quabbin Timber Harvesting Study (15-year record), and various long-term Mapped Tree Plots.

II. THE DYNAMIC NEW ENGLAND LANDSCAPE: INTERACTIONS AMONG DISTURBANCE, ENVIRONMENTAL CHANGE, AND ECOSYSTEM PATTERN AND PROCESS

A. CONCEPTUAL FRAMEWORK AND THEME OF THE HF LTER PROGRAM

Temperate forests, such as those that dominate the Eastern US, are critically important ecosystems at regional to global scales. These forests harbor a high diversity of species and habitats, provide essential resources such as water, air, and wood products, offer important amenities to some of the most densely populated parts of the globe, and comprise key elements in global carbon budgets and atmospheric trace gas concentrations. Understanding the structure, function, and patterns of temperate forests and anticipating their future responses to natural disturbance, environmental variation, and human-imposed disturbance and stress are therefore critical societal goals that are dependent on a sound understanding of fundamental ecological processes. Such insight can only be gained through long-term study that integrates inter-disciplinary approaches through field studies, measurements, experiments, and modeling over a range of temporal and spatial scales.

The Harvard Forest LTER program seeks to interpret ecological pattern and process in New England forests that have been and will continue to be highly dynamic as a consequence of disturbance and environmental change and to apply this knowledge to regional and global issues in forest management, conservation, land restoration and protection, public health and policy, and the environment. Over the past decade, HF LTER has matured into a program that applies unique approaches in historical and community ecology, ecophysiology, atmospheric chemistry, and ecosystem studies to the interpretation of a suite of long-term, large-scale experiments and measurements, mechanistic studies, and retrospective research at site, regional, and global scales. In **LTER I**, we used primarily site-based annual and static measurements to interpret current conditions and to evaluate the comparative response of forest ecosystems to natural disturbance (hurricanes) versus anthropogenic stress (N deposition and soil warming; Fig. 13). Long-term measurements and insights from these initial results enabled **LTER II** to associate inter-annual variation in processes and environment, to examine direct land-use impacts at site to sub-regional (Central Massachusetts) scales, and to incorporate an understanding of historical landscape transformations into interpretations of modern pattern and process.

In **LTER III** we are poised to make significant advances in our understanding of the interactions among disturbance, environmental change, and ecosystem pattern and process at local to regional and even global scales. In particular, we propose to (1) extend many measurements, modeling activities, and historical studies to regional scales, (2) interpret landscape development, vegetation and wildlife dynamics, and current patterns in relationship to millennial-scale climate change, land-use history and natural disturbance, (3) evaluate ecosystem response to critical current disturbances and stresses (e.g. forest cutting, forest conversion, ozone and N deposition, and biological invasions by insect pests and exotic plants), (4) interpret long-term measurements and responses to experimental treatments mechanistically and in relationship to inter-annual and inter-

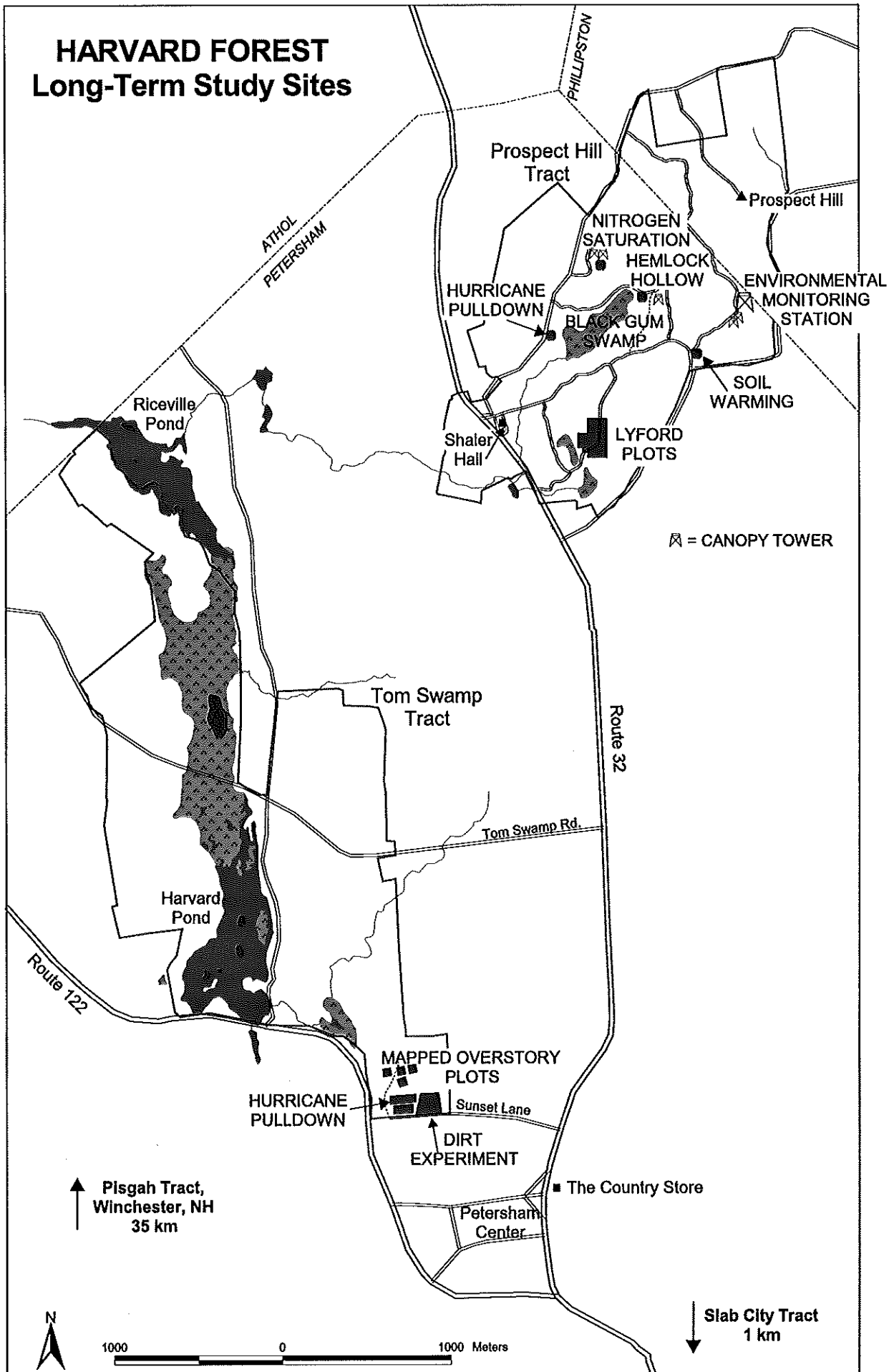


Figure 13. The northern part of Petersham, Massachusetts showing major study sites in the Harvard Forest LTER program.

decadal environmental variation and landscape history, and (5) apply this information to understanding the current and projected role of this vast forest region in global carbon budget storage. In these efforts we will (1) continue our long-term experiments and measurements, (2) strengthen our inter-disciplinary connections and cross-site and cross-regional comparisons, (3) add new mechanistic studies and disciplines (e.g. wildlife biology, plant morphological response to disturbance, social dimensions of land-cover change), and (4) address new processes while adding additional co-investigators to our long-term science team and leveraging major additional support from NSF, DOE, NASA, EPA, USDA, The Nature Conservancy, and private foundations.

The proposed work comprises two integrated initiatives that are explored below: assessing the role of disturbance and environmental change in controlling vegetation and landscape dynamics (Part B) and extending these results through additional studies and experiments to the interpretation and projection of carbon and nitrogen dynamics in forest ecosystems (Part C).

B. FOREST AND LANDSCAPE DYNAMICS IN RESPONSE TO DISTURBANCE AND ENVIRONMENTAL CHANGE

Over the past 350 years, the New England landscape has been transformed by human activities interacting with environmental change and natural disturbance (Foster & O'Keefe 2000). The forested landscape was extensively deforested and cut over, then farmed intensively through the mid 19th C, and subsequently allowed to reforest naturally over the past 150 years as agriculture shifted to the Midwestern US and Eastern populations concentrated in urban and suburban areas (Fig. 14; Foster 2000). Today, the region is 60-95% forested; in structure, wildlife, and many ecosystem, landscape, and regional processes, it is more natural than at any time since the American Revolution. HF LTER research highlights the major conclusion that interpretations of modern ecosystem pattern and process are dependent on integrating detailed knowledge of this history of landscape changes with an understanding of changing disturbance processes and environmental conditions. Such an integrated perspective is essential if we are to meet our major objectives of interpreting modern conditions and anticipating future ones while contributing to policy discussions in conservation, forest and land management, and the environment (cf. Fig. 15).

The challenges confronting an interpretation of modern landscape pattern and process in the context of this history are relatively large, despite past research activities. Central questions that follow directly on results from LTER I and II studies include:

- 1. How have broad patterns of forest composition been driven by interactions among long-term climate variation, land-use, and natural disturbance?**
- 2. What are the relative contributions of history versus site factors in controlling community composition and landscape variation?**
- 3. How have wildlife populations responded to these changes in land cover and human activity?**
- 4. What role do ongoing disturbances by invasive organisms, notably pathogens that selectively eliminate dominant trees species and exotic flora, exert on forest ecosystem structure, composition and function?**

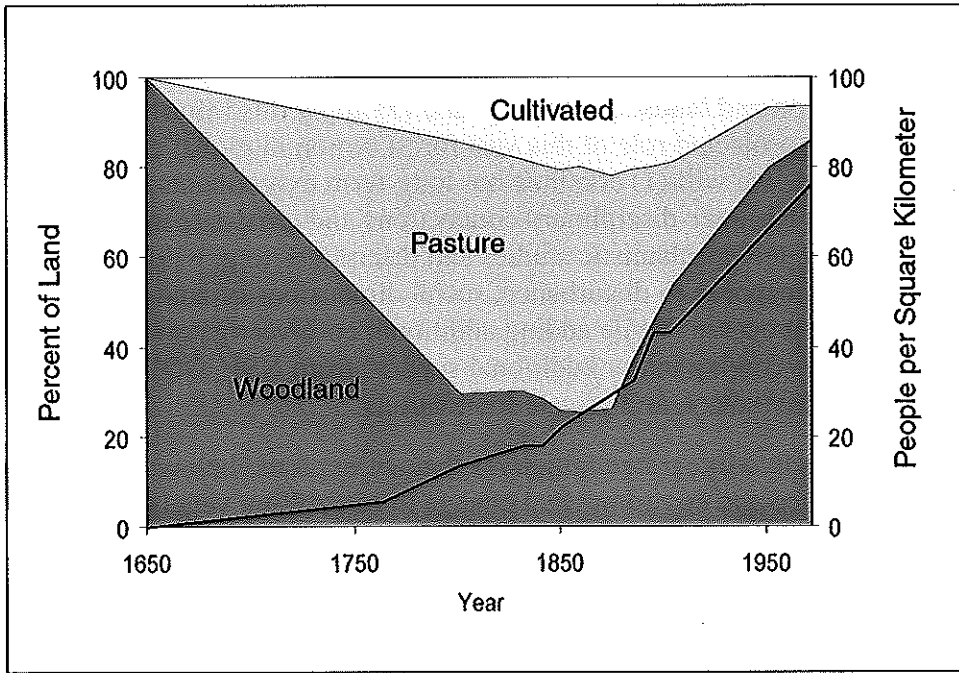


Figure 14. Changes in land use (green, woodland; gray, pasture; tan, cultivated) and human population (dark line) through the historical period in central Massachusetts. Population increases in slope in the mid-1700s, mid-1800s, and early 1900s, whereas land use exhibits three contrasting phases: deforestation through 1800, intensive agriculture (1800-75), and rapid reforestation (1875-1985). Importantly, all current forest areas are derived from one of three distinctive historical land uses: woodland, pasture, or plowed field.

Why does Harvard Forest take up carbon?

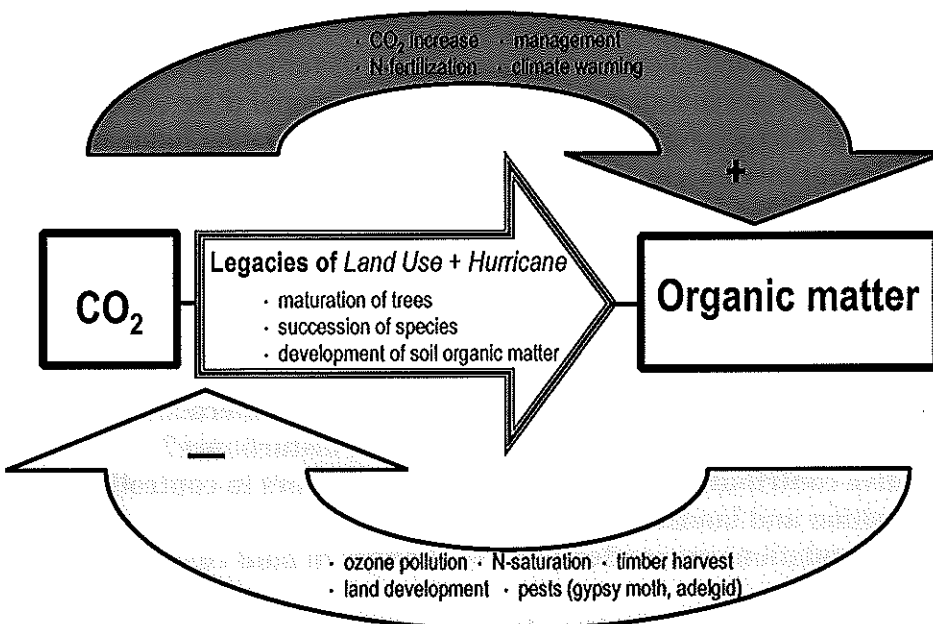


Figure 15. Conceptual diagram of the factors driving sequestration of CO_2 at Harvard Forest. The forest is aggrading due to the legacies of prior land use and the hurricane of 1938. Factors such as lengthening of the growing season, atmospheric nutrient inputs, forest management, and higher atmospheric CO_2 accelerate uptake of CO_2 . Air pollution, introduced pests, and timber harvest reduce CO_2 sequestration.

5. What are the important long-term mechanisms for plant survival, recovery, and regeneration following disturbance, including hurricanes, logging, and insect outbreak?

Our past studies provide us with the information and skills necessary to address and answer these questions and to relate the results to our understanding of pattern and process in New England forests. **Question 1** emerges from our research in Central Massachusetts and is appropriately addressed at a regional scale across New England using paleoecological, historical, and field techniques. **Question 2** has previously been addressed at only two sites and in the C Massachusetts sub-region; in order to evaluate variability across New England, detailed studies are necessary in other physiographic regions that vary considerably in environment, land-use history, and conservation imperatives. **Question 3** has never been comprehensively addressed for New England and yet is essential background for detailed wildlife studies and for addressing current ecological, social, and conservation issues. We will focus on a statewide (Massachusetts) assessment where excellent historical records complement our studies of forest dynamics. **Question 4** addresses one of the central processes that has shaped New England forests historically and is of immediate concern due to the arrival of the hemlock woolly adelgid and many exotic plant species that are expected to alter forest composition and function. It will be studied using landscape analyses and field and controlled-environment studies. **Question 5** emerges from our hurricane experiment and other studies that identify vegetative reproduction as a key forest process that requires morphological, comparative, and field investigations.

This research plan develops logically from LTER studies and represents a major expansion to derive broader generalizations. It addresses fundamental ecological issues that will enable us to contribute meaningfully to important societal concerns.

1. Regional Analyses of Vegetation and Wildlife Patterns and Dynamics

Little Ice Age and Land-use as Drivers of Regional Vegetation Change

Our LTER studies indicate that the vegetation of northeastern North America was changing in pronounced ways 300-500 years before European arrival (ca. 1620-1700) and that dynamics after European settlement were driven by interactions among climate (Little Ice Age; LIA) and human land use (Fig. 16; Foster et al. 1998; Fuller et al. 1998; Francis & Foster 2000). Building on our substantial LTER database for C. Massachusetts, we will extend these studies across New England to interpret pre- and post-European vegetation change in light of independent data on climate history and Indian and European activity. With LTER and other NSF support, we will use multi-proxy approaches from paleoecology, paleolimnology, archaeology, and history to reconstruct climate, vegetation, and cultural dynamics over the past 1500 years at 8 sites arrayed across the climatic and forest gradients of New England (Fig. 17; methods follow Fuller et al. 1998, Foster et al. 1998). Analysis of records from the North American Pollen Database (NOAA) will place these results in a truly regional framework for the entire northeastern US (Fig. 18). Specific methods will include: high resolution pollen records to reconstruct vegetation; chironomids, stable isotopes, geochemistry, diatoms, tree-ring records and historical reconstructions to interpret climate history; charcoal and

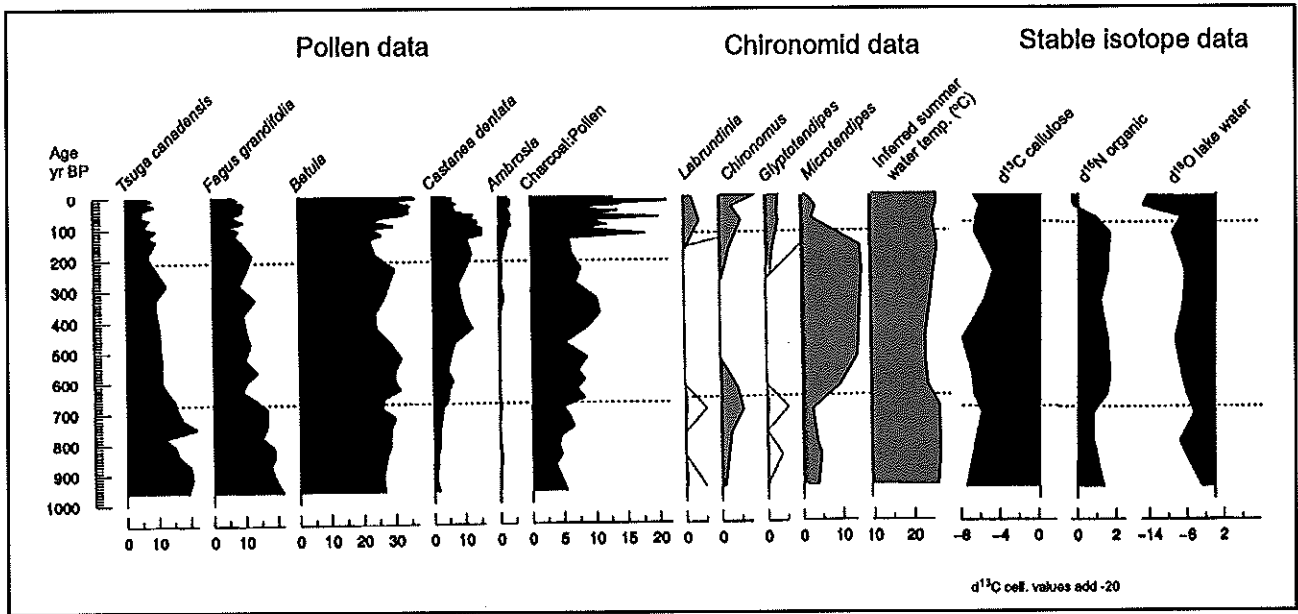


Figure 16. Preliminary analysis of the stratigraphic record over the last 1000 years from North Round Pond, one of our study sites in southwestern New Hampshire. Pollen, chironomid, and stable isotope data were each zoned objectively and independently as indicated by the broken horizontal lines; each shows similarities, particularly with regards to the onset of changes approximately 650 years bp. Major changes at that time are suggestive of broad-scale environmental change include declines in *Tsuga* (hemlock) and *Fagus* (beech) and an increase in *Castanea* (chestnut); major increase in *Microtendipes*, decline in other chironomids, and decline of 2.5 degrees in chironomid-inferred summer water temperature; and increase in ^{15}N . In contrast, changes between 100-200 years bp are consistent with anthropogenic disturbance: increases in *Ambrosia* (ragweed), *Betula* (birch), *Castanea*, charcoal, and O and N isotopes. Chironomids change independently of the pollen and isotopes, and inferred summer temperatures become warmer over the past 150 years.

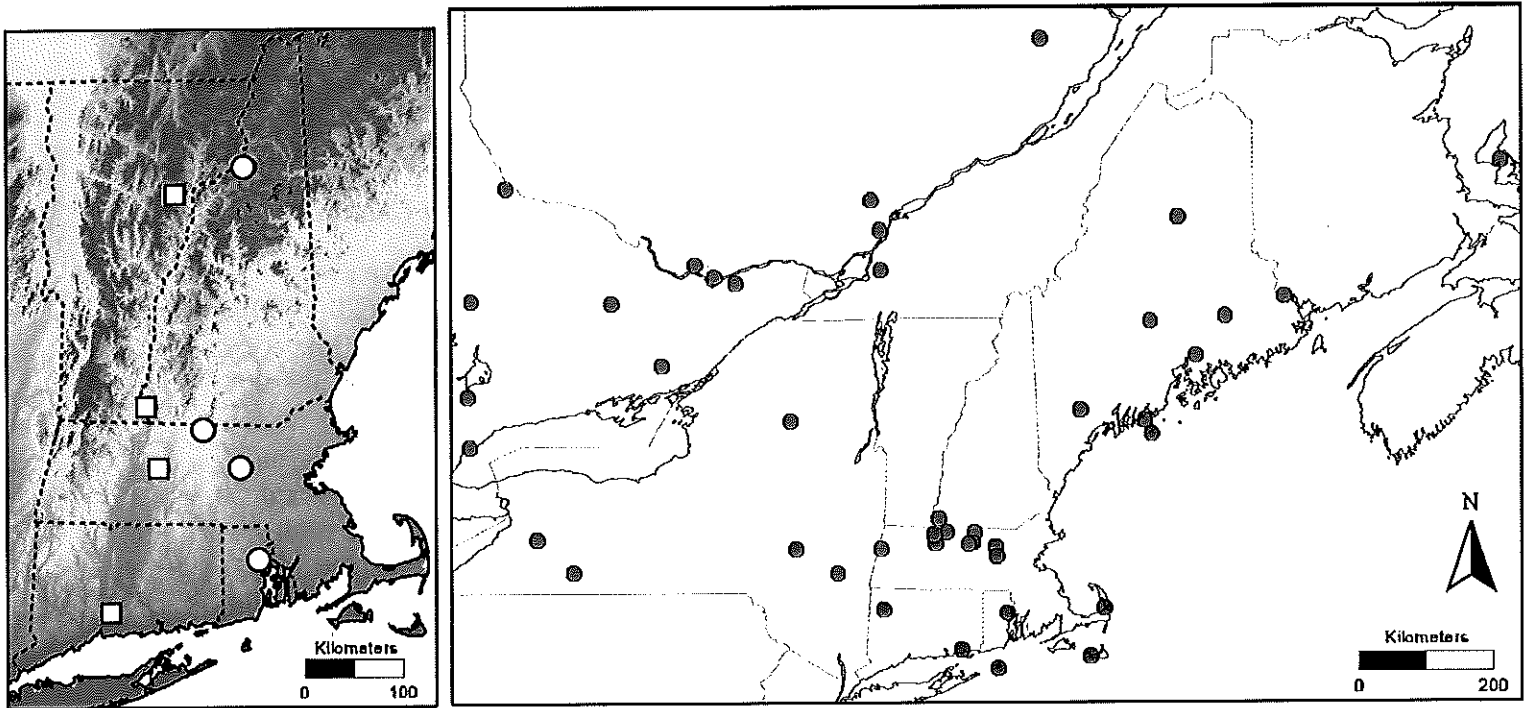


Figure 17. Location of eight lake sites (four latitudinal pairs) on a map of growing degree days in New England. Growing degree days range from 838 (purple) to 4233 (red). All eight sites will be analyzed for pollen, charcoal, and geochemistry. Four sites (squares; one of each pair) will also be analyzed for diatoms, stable isotopes, and chironomids. Each of the sites is a small, closed basin.

Figure 18. Map of Northeastern North America showing sites from the North American Pollen Database analyzed preliminarily for evidence of vegetational change before European settlement and coincident with the Little Ice Age. Sites in red had pronounced pre-European changes, whereas those in green did not.

land-use data to document fire and human impacts; and ^{210}Pb and ^{14}C for temporal control. Forest composition at the time of European settlement will also be determined independently from early Proprietor's records (cf., Foster et al. 1998), which contain tree species data for most of New England. We will develop a comprehensive Proprietor's database in collaboration with Hubbard Brook (HBR) scientists (C. Cogbill), which will add substantially to our knowledge of the early European landscape. Results from these investigations will provide: (1) an objective characterization of the LIA and climate history in New England over the past 1,500 years; (2) comparison of pre- and post-European forest dynamics in relationship to independent environmental and land-use histories; (3) re-examination of historical forest dynamics in light of prior climate and vegetation change; (4) a broad spatial and temporal context for site to regional studies and modeling in the LTER; and (5) interpretations of direct value to two other LTER sites: HBR and Plum Island.

Long-term Vegetation and Disturbance Dynamics of Coastal New England

A major focus of HF LTER research is to evaluate the relative importance of modern conditions versus historical factors in controlling stand and landscape-level vegetation composition and dynamics. LTER II showed that the relative influence of history versus site conditions on current vegetation patterns varies considerably among sites and physiographic regions. On edaphically homogeneous sand plains throughout the Connecticut Valley, land-use history is the primary determinant of modern vegetation (Motzkin et al. 1996, 1999a; Donohue et al. 2000). In contrast, across the heterogeneous Central Uplands, vegetation varies with historical factors and complex environmental gradients, especially soil drainage and C:N ratios (Foster et al. 1998; Motzkin et al. 1999b). As a result of such variation, a comprehensive understanding of controls on species distributions, vegetation patterns, and community dynamics must incorporate the full range of physiographic and historical conditions that occur across New England. Thus, we propose to augment past studies of two major physiographic areas (Uplands and Valley) with an integrated study of the history and dynamics of the Coastal region that extends from Cape Cod to Long Island, including Nantucket, Martha's Vineyard, and Block Island. This region is particularly appropriate for such investigations because: (1) the physiography and disturbance history contrast strongly with the Upland and Valley; (2) the coastal region is an international conservation priority that supports numerous uncommon species and communities and yet has never been studied comprehensively from a broad spatial and temporal perspective; and (3) previous coastal studies have failed to evaluate the effects of historical disturbance rigorously, despite the long and well-documented history of land-use and fire (Fig. 19; Foster & Motzkin 1999).

We propose integrated paleoecological, historical, and field studies to determine factors contributing to the development of modern vegetation patterns and dynamics. We hypothesize that prior to European settlement, vegetation was largely controlled by: (1) variation in soil fertility and drainage, which is strongly related to surficial landform; (2) fire history, which is correlated with surficial geology and human distribution; and (3) geographic location and exposure. We further hypothesize that the modern occurrence, composition, and dynamics of major coastal assemblages have primarily resulted from disturbance, especially land-use history. Although wind, fire, and pathogens have been

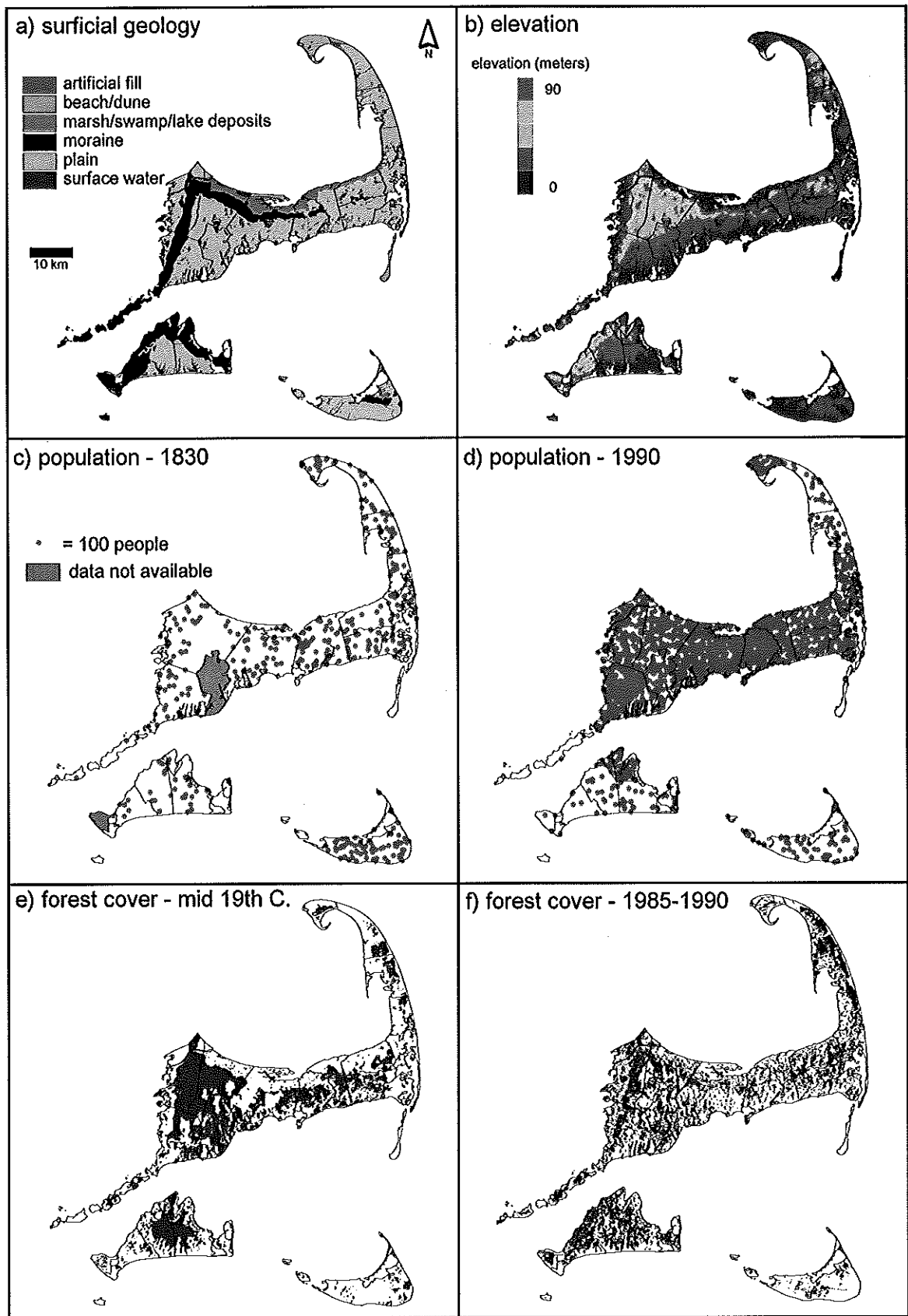


Figure 19. The Cape Cod and Islands portion of the Coastal physiographic region showing surficial geology and major landforms (a), elevation (b), population in 1830 (c) and 1990 (d), and forest cover in the mid 19th century (e) and 1985 - 90 (f).

important, we anticipate that they have not obscured land-use effects. In particular, we hypothesize that the distribution of rare species and communities is tightly linked with patterns of prior land-use.

To address these hypotheses, several approaches and data sources established in LTER II will be utilized to allow for direct comparison with our results from other sub-regions:

- (1) Fine-resolution pollen, charcoal and sediment analyses of 15 sites, stratified by geography, landform, and distance from centers of Indian and European activity, will provide decadal information on forest composition and dynamics at regional and landscape scales over the last 1,500 years (cf., Fuller et al. 1998).
- (2) Comprehensive historical data and maps on cultural features, vegetation, and disturbance (1650 to present) will be added to our large New England GIS database.
- (3) Sampling of vegetation and soils in random plots will relate regional vegetation variation to site conditions and historical disturbance (Motzkin et al. 1996, 1999a, 1999b; Donohue et al. 2000).

This research addresses the major HF LTER theme of evaluating the relative importance of modern conditions versus history in controlling forest composition and dynamics. It will also make significant contributions to biodiversity conservation and management (Foster & Motzkin 1998, 1999), expand our regional analyses, and add substantially to our growing GIS, paleoecological, historical, vegetation and soils data for New England.

Wildlife Dynamics in Response to Land Use, Cultural and Environmental Change

HF LTER studies have previously concentrated on vegetation dynamics. However, 400 years of land-use and land-cover change have also produced profound changes in wildlife populations (Foster 2000, Foster & O'Keefe 2000). Currently, many mammal and bird species (e.g., bear, beaver, fisher, moose, eagles and herons) that were uncommon during the past 200 years are expanding dramatically, whereas major declines are occurring in species characteristic of New England's agrarian past (e.g., bobolinks, meadowlarks, woodcock and open-land sparrows; Fig. 20). These changes have been driven by many ecological and cultural factors, including habitat availability, competitive interactions, climatic conditions, cultural perceptions, and management. However, few studies have attempted to detail the history of wildlife dynamics and relate these to shifts in ecological and cultural parameters. Such a perspective is critical in order to understand current wildlife dynamics and to address policy conflicts and ethical dilemmas that result from wildlife-human interactions in an increasingly suburbanized landscape (Deblinger et al. 1999).

The regional databases and historical perspective of the HF LTER present an unusual opportunity to address basic ecological questions about the factors controlling wildlife populations, the feedbacks between plant and animal species, and contrasts between the organization and dynamics of plant and animal assemblages. Consequently, we propose a historical analysis of New England wildlife to: (1) document major trends in populations since European settlement, (2) identify the loss or arrival of major species and analyze the long-term composition of wildlife assemblages, (3) identify the physical, biological, and cultural factors driving these changes, (4) integrate this information with vegetation

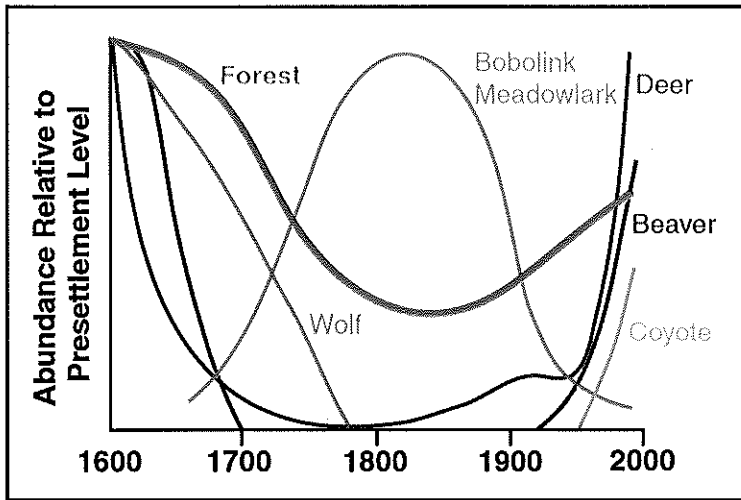


Figure 20. Changes in wildlife species showing different responses to changes in land cover and human activity in Massachusetts during the historical period. Though the curves are generalized they portray the broad dynamics accurately.

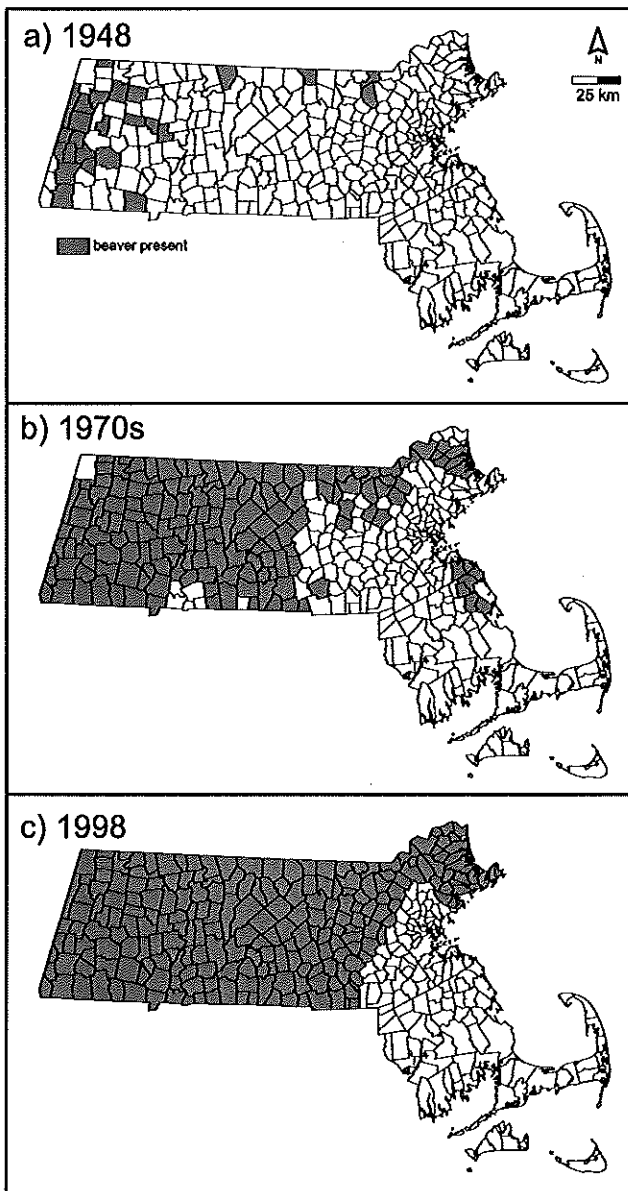


Figure 21. Increase in beaver distribution in Massachusetts since 1948. Although extirpated from the state in the early 1700s, there are currently approximately 20,000 beavers in the state (State of Massachusetts, unpubl.; Bernardos, Foster, and Motzkin in prep.).

data to increase our understanding of forest processes through time, and (5) provide a context for understanding recent changes and for guiding conservation policy. We will focus on the entire state (Massachusetts) where excellent historical records enable us to develop a semi-quantitative understanding of these dynamics and relationships (Fig. 21; Cardoza pers. comm., Bernardos, Foster & Motzkin in prep.). Results will assist species-specific investigations on the effects of suburbanization and land-use change on wildlife populations (Deblinger et al. 1999).

2. Biological Invasions: Population, Community, and Ecosystem Response

Invasive plants and animals cause significant changes in forests at population to ecosystem levels through competition with and predation on native species, and by influencing resource availability and forest structure and process. Exotic insect pests have been particularly important historically, resulting in substantial change in forest composition and function across the Eastern US and the near elimination of several dominant trees in the past century. Non-native plant species are increasingly altering forest composition in ways that are largely unknown. Due to the importance of such events in forests worldwide and their historical and current significance to New England, we propose investigations of recent invasions by a major forest pest and by exotic plants in order to determine effects on species interactions, community composition and structure, and nutrient dynamics.

Regional, Landscape, and Forest Dynamics due to Hemlock Woolly Adelgid (HWA)

Although the history of forest pathogen introduction in New England is well-documented, no studies address the factors controlling these infestations or forest ecosystem response to selective mortality of dominant species. Consequently, the introduction of HWA, a small, aphid-like insect from Japan, presents a unique opportunity and imperative to study forest damage and response to a major pathogen. HWA has caused extensive decline and mortality in parts of hemlock's range and looms as a major threat to eastern forests (Fig. 22). HWA reached southern New England in 1985, produced widespread mortality in Connecticut by 1988, and is now in >70 Massachusetts towns. Because hemlock is an important and abundant late successional species that strongly controls stand microclimate and soil conditions, many HF LTER studies have investigated the long-term dynamics and function of hemlock forests. Consequently, we are in a strong position to study HWA (Foster et al. 1992; Foster & Zebryk 1993; Compton & Boone 2000; Hadley in press, Orwig & Foster 1998).

We propose to expand studies initiated with USDA Forest Service support to undertake two related efforts: (1) stand to regional evaluation of HWA infestation and hemlock mortality (1985 onwards) and assessment of the physical, biological, and historical factors influencing damage and response; and (2) analyses of forest composition, structure, micro-environment and ecosystem responses to hemlock stress and mortality.

Regional Spread and Landscape Controls. In preliminary studies of a 5900 km² area of Connecticut, HWA occurred in nearly 90% of stands and was responsible for nearly complete mortality in many large hemlock forests (Fig. 23; Orwig & Foster 1998). Mortality decreased with latitude and duration of infestation and appears to be unrelated

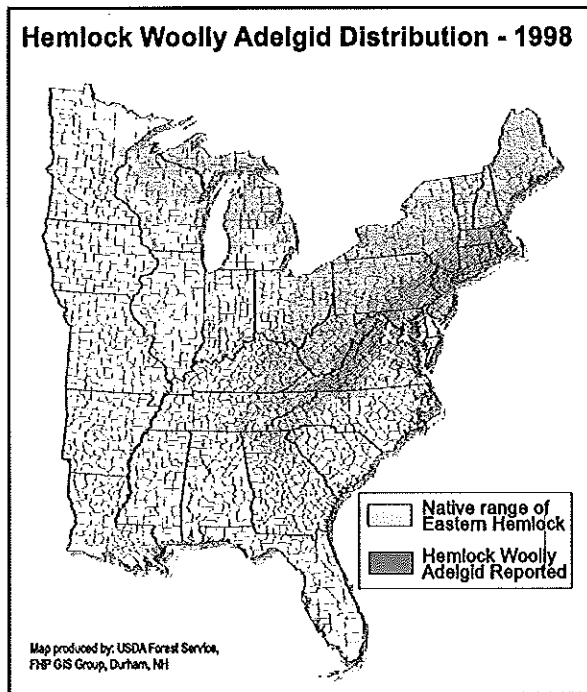


Figure 22. Distribution of the hemlock woolly adelgid with reference to the range of hemlock. There appears to be no physical or biological impediment to the spread of adelgid across eastern North America.

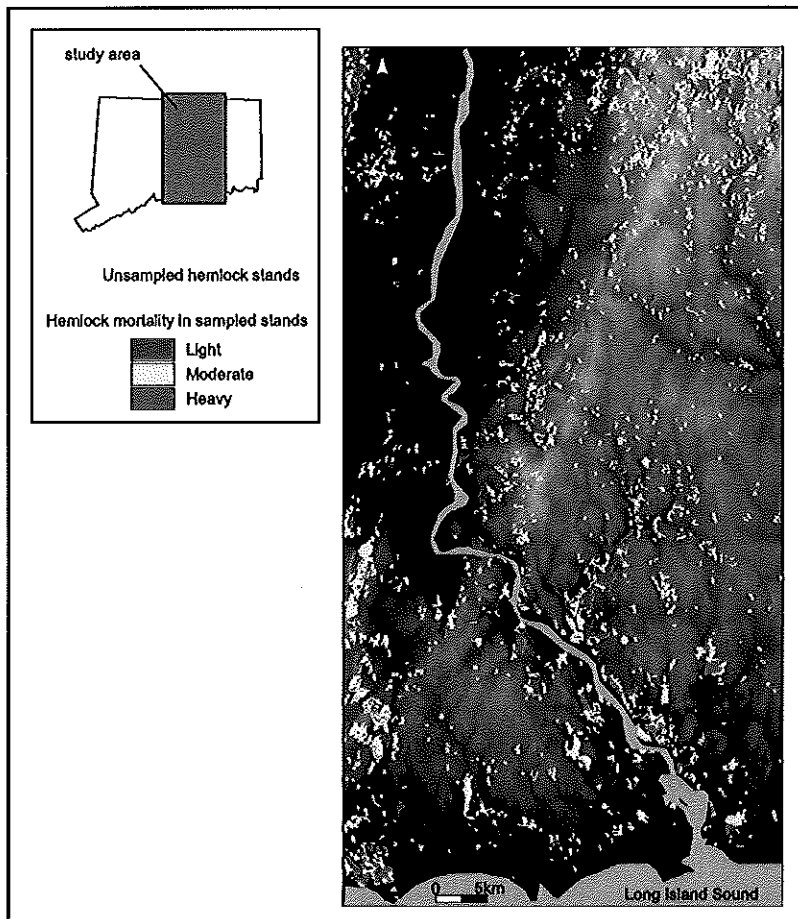


Figure 23. Hemlock stands and topography in central Connecticut. Hemlock stands are coded according to mortality from adelgid as documented in Harvard Forest studies. Note the heavy mortality of stands in southern CT, where the adelgid has occurred for the longest period of time.

to site or stand factors; therefore, we project heavy to complete mortality of hemlock across the region. We will extend our study to Massachusetts to utilize our extensive data on healthy hemlock forests and to document changes that relate to ongoing HF LTER studies.

Forest Ecosystem Response. As infested stands may suffer complete mortality in 4-8 years, the potential exists for major ecosystem impacts including nutrient loss, N export, and erosion. Our initial results indicate large increases in N mineralization and nitrification rates with mortality (Jenkins et al. 1999). However, many questions remain concerning the magnitude and duration of N changes and their relationship to soil conditions and biotic uptake. Consequently, we will initiate studies of N availability, mineralization, and nitrification rates in sites recently infested with HWA and will continue these long-term measurements to investigate temporal dynamics and driving mechanisms as mortality commences. We will then compare ecosystem response to pathogens with ongoing studies of hurricane damage, N saturation, soil warming, and logging (cf. Section C).

Invasive Plants: Community and Ecosystem Effects and Relationship to History

Although the spread of aggressive invasive plants in temperate forests is generating increasing concern, few studies have evaluated the influence of historical factors on the dynamics of these invasions. Because land-use frequently creates opportunities for plant establishment and exerts long-term impacts on site conditions and patterns of succession (Foster 1992), invasion and spread of exotics is likely to be influenced by past and current activity. In turn, biological invasions may alter community dynamics, species diversity, and ecosystem function. In LTER III, we propose studies to address the following questions: (1) Does variation in land-use history influence forest susceptibility to invasion and the distribution of exotics? (2) How do invasives affect the composition and dynamics of forests and influence ecosystem processes? And, (3) What relationships exist between physical disturbances, anthropogenic stresses, and biological invasions?

We will study the distribution and dynamics of the 5 most widespread invasive woody species in C. Massachusetts (*Berberis thunbergii*, *Rhamnus cathartica*, *R. frangula*, *Lonicera* sp. and *Celastrus orbiculatus*), each of which has the potential to cause major forest ecosystem changes. *Berberis* is an understory shrub that forms dense thickets and can alter soil characteristics (Kourtev et al. 1998), *Rhamnus* and *Lonicera* are shrubs that can displace existing vegetation (Weatherbee et al. 1998), and *Celastrus* is a vine that can grow densely on trees and the ground (Dreyer 1994). Species distributions will be determined through extensive mapping and existing data for the Harvard Forest and adjacent Quabbin Reservation. Detailed site histories will be determined from field and archival records following Motzkin et al. (1996, 1999b) to allow direct comparison with data from the Connecticut Valley, Central Massachusetts, and the Coastal region in order to determine broad patterns of variation in the distribution and abundance of invasive species. Edaphic and other resource variables will be sampled in adjacent sites with and without invasives to identify factors that may influence species distributions. Long-term plots will be established in areas with different land-use histories, in which establishment, abundance, and demography of invasives will be monitored. In addition, we plan to

Carbon Sequestration in Forests: Expectations vs Results, Harvard Forest

Expectations

- Uptake of CO₂ (photosynthesis): limited by light, water, nutrients; insensitive to T, short season (near optimum).
- Land cover change ⇒ small CO₂ uptake: reforestation after agriculture completed.
- Decomposition and respiration very sensitive to temperature ⇒ strong release of CO₂ with warming.

Carbon storage in temperate forests expected to cease after 50-100 years post-reforestation and to decrease in response to climate warming.

Results

- Uptake of CO₂ (photosynthesis) very sensitive to short season, light and water; large increase in CO₂ uptake in warm years.
- Land cover change ⇒ big CO₂ uptake: reforestation after agriculture creates a long-lasting legacy, amplified by warming.
- Decomposition and respiration temperature limited in winter, but water limited in summer ⇒ weak T ↔ respiration response.

Carbon storage in temperate forests persists for > 100 years post-reforestation and increases in response to climate warming.

Figure 24. Summary of the expected rates of carbon storage (low, nearing steady state) and modulating factors (summer temperatures and precipitation), in contrast to results from the first 10 years of our study (high rates of carbon uptake, sensitivity to winter and spring temperatures, cloudiness, and land use legacies).

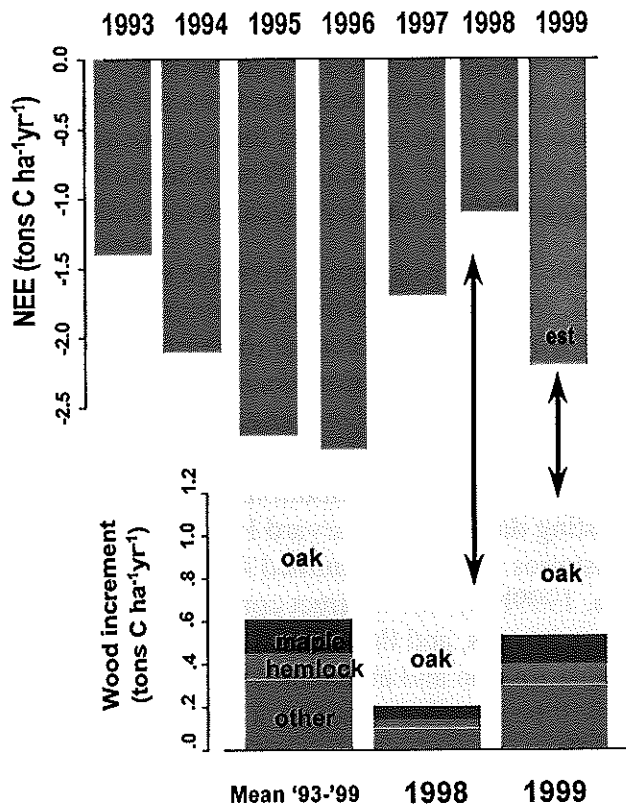


Figure 25. Legacies of prior land use and differential response to stress strongly modulate annual uptake (NEE). Woody increment accounts for 60-70% of annual NEE, reflecting the growth of red oak (>50% of woody biomass increment). The drought of 1997 had a strong, delayed effect on growth of red maple and hemlock, the next most abundant large trees. Weak uptake by these species was a major factor in the anomalously low observed uptake of carbon in 1998, as compared to the 5-yr mean and to an average year (1999). Wood increment was determined using stem circumference measurements and allometric equations [e.g. *Whittaker et al.*, 1974]. Wood volume measurements on 40 plots (each 30m diameter, total ~880 trees with diameters at breast height (DBH) greater than 10 cm) began in 1993. We fitted steel band dendrometers on 824 surviving trees in April, 1998 and monitored circumference weekly during the growing season and ~monthly in winter.

measure changes in resource availability, dynamics of indigenous species, and community structure.

To complement these and past studies on species interactions and responses to resource conditions (e.g., George & Bazzaz 1999b; Wayne & Bazzaz 1997; Catovsky & Bazzaz 1999), we also propose a set of controlled studies and introductions of common invasive species in the field. The goal of these experiments is to characterize competitive interactions between invasives and native plants as well as to measure the influence of altered resources on establishment of invasives and indigenous species. We will integrate these studies with controlled environmental (glasshouse) studies in which factorial experiments will further quantify competitive interactions among invasive and native species and determine mechanistic responses to resources, including resource-use efficiency and allocation patterns. Results will increase our understanding of the differential susceptibility of plant communities to invasion and thereby improve our ability to predict short and long-term population dynamics and community structure. Our results will also have direct bearing on public land management, including the Quabbin Reservation, where resource managers have identified the control of invasive species as a major objective (T. Kyker-Snowman pers. comm.).

3. The Mechanisms of Plant Recovery from Disturbance: Vegetative Reproduction

Our prior investigations of regeneration dynamics after disturbance have focussed on resource and microsite influences on seedling establishment or on demographic limitations to colonization after disturbance (e.g., Carlton and Bazzaz 1999a,b). It is increasingly clear, however, that vegetative regeneration is often the primary mechanism by which woody species respond to physical disturbance (Del Tredici 1998, Donohue et al. 2000). For instance, results of the experimental hurricane as well as our prior studies on logged areas and areas salvaged following HWA infestation demonstrate the critical importance of rapid vegetative regeneration in controlling ecosystem response to physical disturbance (Cooper-Ellis et al. 1999; Foster et al. 1998a). To date, few studies have explicitly addressed the differing morphological responses of individual species to the range of physical disturbances that are characteristic of temperate forests (Del Tredici, in review). As a result, the degree to which ecosystem response depends on pre-disturbance stand composition and structure versus seedling regeneration is largely unknown. Such an understanding is critical if we are to compare species responses to different disturbance types and if we are to understand the mechanisms by which individuals and species respond to dynamic landscapes and management regimes.

In LTER III, we propose to document the range of vegetative morphological responses displayed by the dominant tree species in New England to characteristic disturbances including windthrow, fire, logging, and pathogens. We are particularly interested in evaluating the change in regenerative capabilities of individuals of different life stages. For instance, although vegetative regeneration is well-documented for mature stems, morphological adaptations that allow even recently germinated seedlings to regenerate vegetatively are widespread and may be a primary mechanism for successful establishment in many species. Using long-term data from the experimental hurricane, our new logging study (see Section C, below), and ongoing HF studies of sites with known disturbance histories, our specific objectives are to: (1) describe the vegetative

Land-use History of the Central Massachusetts Region

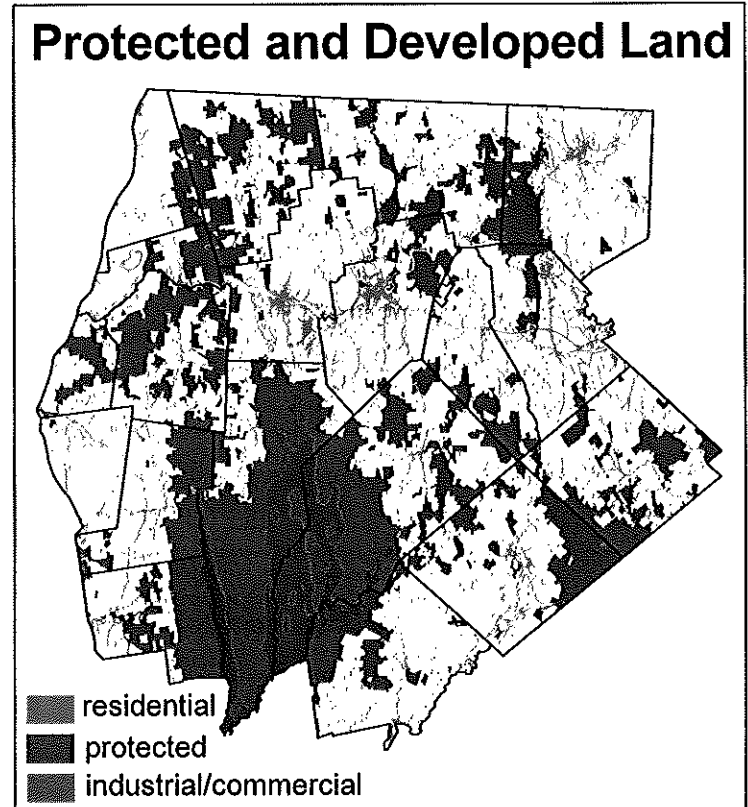
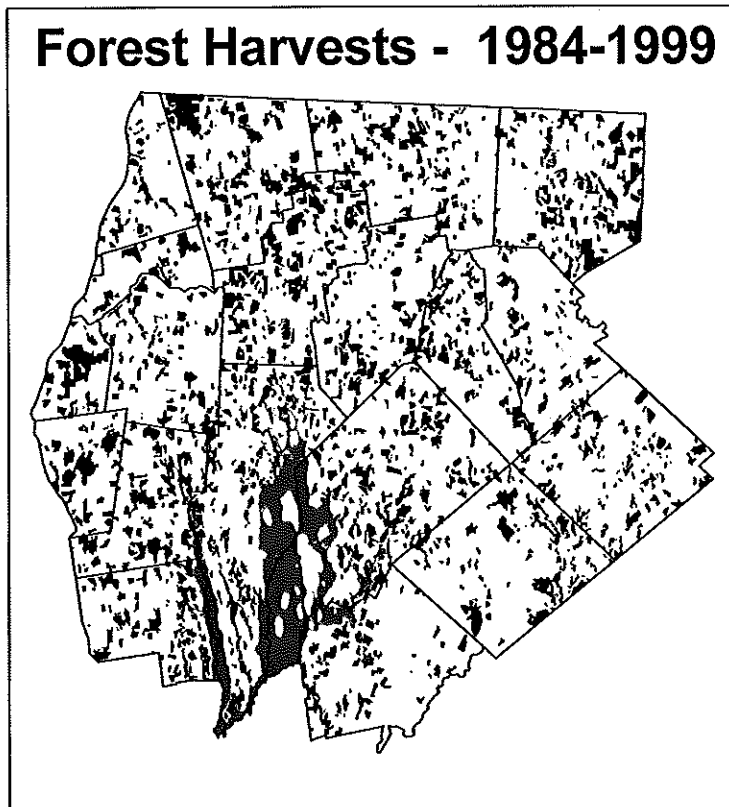
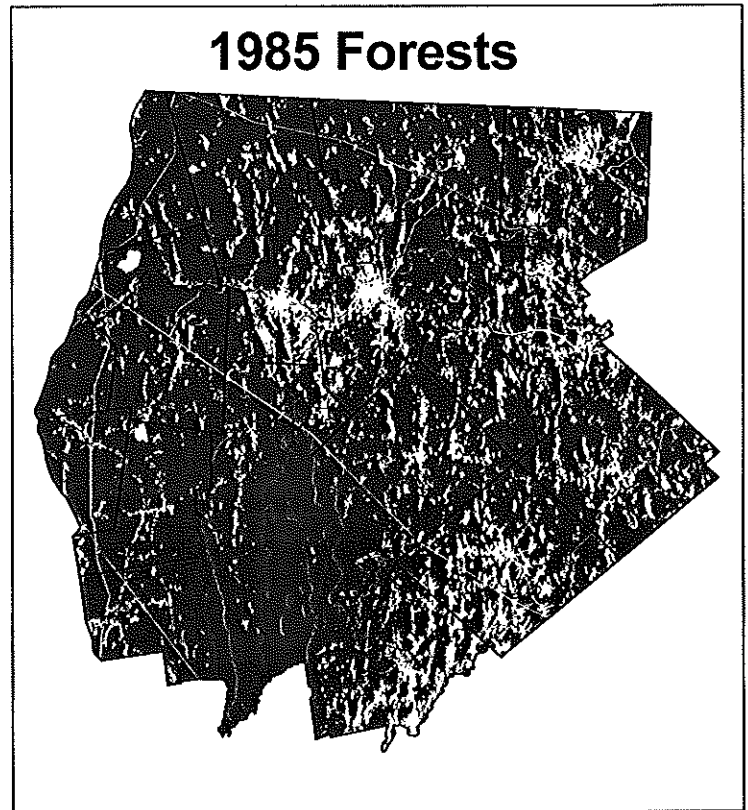
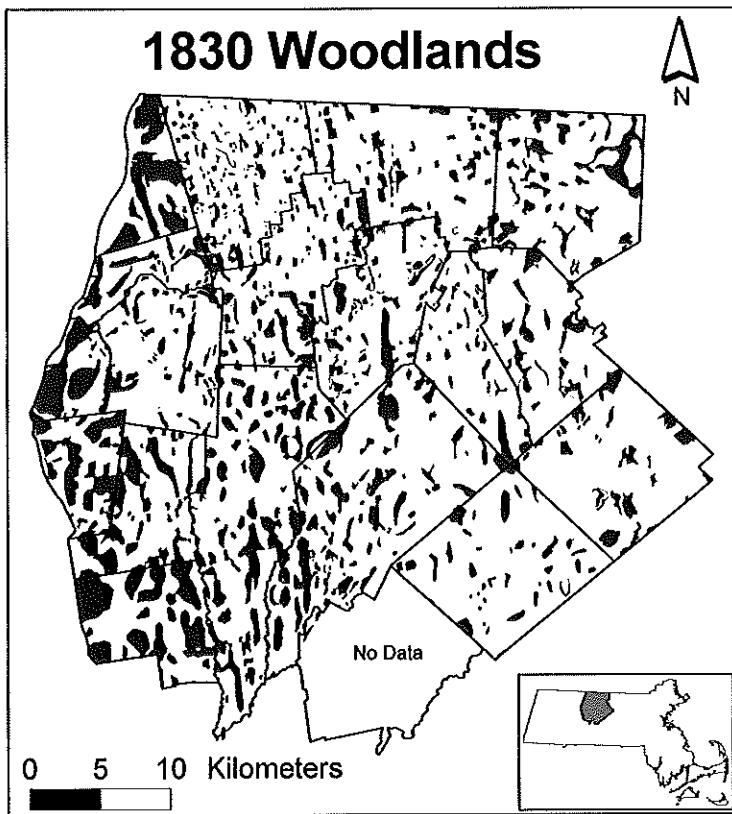


Figure 26. Central Massachusetts showing changes in forest cover from 1830 to 1985, logging harvests since 1984, and the current extent of protected and developed lands. Exploring these patterns, their social causes and ecological consequences will be a focus of LTER III studies.

morphological response of common tree species to dominant disturbances; (2) evaluate the regenerative capability of individual species relative to stem age; and (3) determine the importance of different regenerative strategies with increasing time since disturbance. We will develop a functional classification of damage types related to detailed morphological descriptions of mechanisms of vegetative regeneration. Results will contribute significantly to our understanding of biological and morphological constraints on species response to disturbance and our interpretations of forest ecosystem dynamics.

The **hurricane manipulation**, modeled after damage patterns from the 1938 hurricane (Rowlands 1941, Foster 1988a, Cooper-Ellis et al. 1999) and initiated in 1990, allows us to integrate our new studies of vegetative reproduction (LTER III) with our data on seedling regeneration (LTER II; Carlton & Bazzaz 1999a) in understanding mechanisms of ecosystem recovery. To accomplish this we will continue long-term measurements in the 0.8-ha manipulation and adjacent 0.6-ha control. All trees are mapped; data on damage, survival, and sprouting, recorded annually for each tree from 1991-1997, will continue every 3 years, as will assessment of regeneration via sprouting, new seedlings and advance regeneration. Herb and shrub cover, measured before the manipulation and in 1991, 1992, 1995, will continue every 5 years. Emphasis in LTER III will shift from initial forest recovery (Bowden et al. 1993a, Foster et al. 1997, Cooper-Ellis et al. 1999) to evaluation of long-term stand development in comparison with prior HF studies following the 1938 storm (e.g., Spurr 1956, Oliver & Stephens 1977, Henry & Swan 1974). The importance of sprouts, new saplings, and advance regeneration in forming the next forest canopy is becoming apparent as the new cohort of trees experiences severe competition and successful stems move into larger size classes. Consequently, we will focus on documenting modes of long-term regeneration and evaluating the contribution of tree population dynamics to community recovery.

The long-term continuation of this experiment is critical to understanding the mechanisms of forest vegetation recovery from a disturbance type that affects nearly every generation of New England forests (Boose et al. 2000a). Data on long-term forest recovery in the experimental hurricane will be directly comparable with our long-term data from plots established after the 1938 hurricane and with our new investigation of logging (below).

C. CARBON AND NITROGEN INTERACTIONS WITH LAND USE AND ENVIRONMENTAL CHANGE

As a consequence of the past three centuries of land-use and natural disturbance, the New England landscape, like much of the Eastern US, currently supports new and predominantly young forest that is growing rapidly and storing significant amounts of carbon (Foster & O'Keefe 2000, Wofsy et al. 1993, Aber et al. 1999, Irland 1999). The vast extent of this aggrading temperate forest (200-300x10⁶ ha in the US and Canada south of 51°N) makes these lands critical elements of global carbon dynamics with significant influence on future atmospheric CO₂ concentrations and landscape response to climate change (Wofsy et al. 1993).

PnET Predictions

Effects of Climate Change

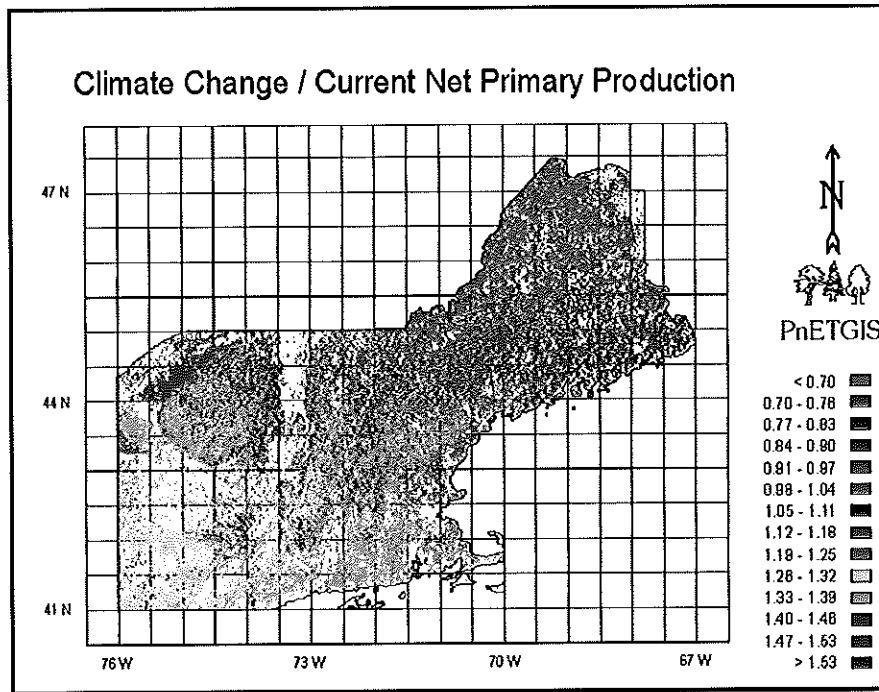


Figure 27. Predicted changes in NPP with a 2xCO₂, +6°C and -15% precipitation scenario.

PnET Predictions

Effects of Climate Change

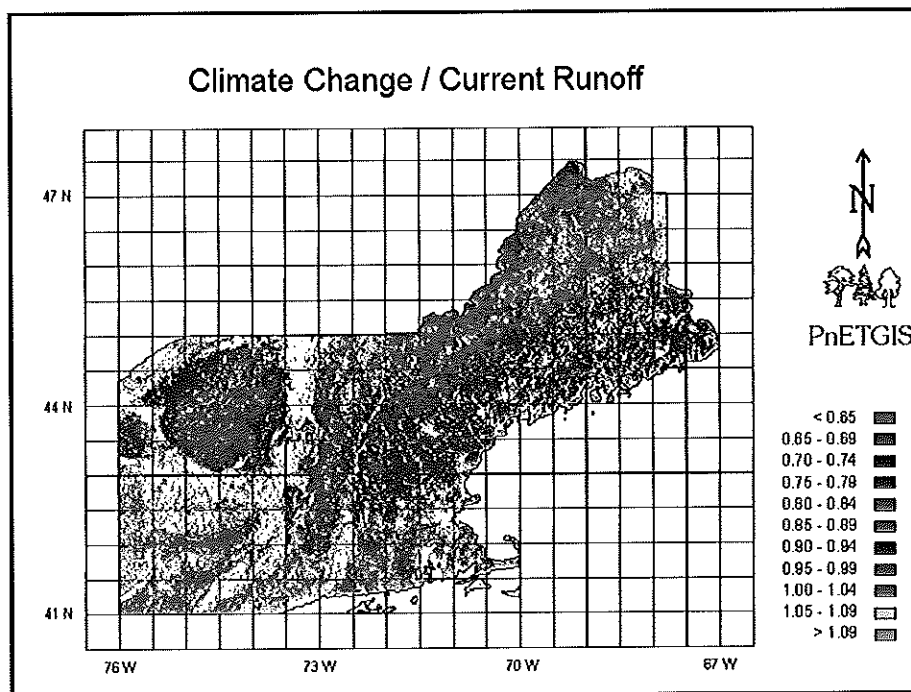


Figure 28. Predicted changes in water yield with a 2xCO₂, +6°C and -15% precipitation scenario.

The long-term trajectory and magnitude of forest growth and carbon storage in New England and the Eastern US are uncertain. To assess the current and future role of these forests in the global carbon cycle information is required defining: (1) the successional status of forests across the landscape, (2) current rates of C sequestration and evolution for the principal vegetation assemblages, (3) the potential effects of climate variation and human-imposed disturbance and stress (e.g., N deposition, logging, forest conversion), and (4) the mechanisms controlling C and N dynamics. Past LTER studies place us in an ideal position to address these issues through intensive site measurements, experiments, and regional analyses. Process-level and cross-site studies will, in turn, allow us to use of our ecosystem models to develop regional projections of forest-atmosphere carbon exchanges.

The challenges facing an assessment of current and projected carbon storage in New England are great. Traditional measurements of forest growth and carbon uptake such as forest inventories cannot define rates for such basic processes as soil organic matter accumulation or storage of carbon in woody detritus. This compromises our ability to link carbon storage to past land-use activity and ongoing environmental change. Although the New England states currently support greater forest area than at any time in the past 200 years (Irland 1999), increasingly these forests are being logged for wood products or converted to suburban uses that greatly alter local and regional carbon balances. Thus, one objective of our work in LTER III will be to assess the impact of forest management and land use change on carbon uptake. We plan to determine the regional extent of logging and forest conversion, and to study in detail the effects of a typical harvest on carbon stocks. The goal is to be able to compare carbon budgets of disturbed lands with patterns of carbon accumulation in forests growing on undisturbed lands.

Fossil fuel combustion and fertilizer production have greatly increased the deposition of fixed nitrogen (NO_x and NH_x) on temperate landscapes (Galloway et al. 1994, Melillo 1996). Increased deposition of these biologically reactive N forms can lead to eutrophication of terrestrial and downstream aquatic ecosystems (Aber et al. 1989, Stoddard 1994). Some studies have suggested that these N inputs stimulate significant C storage in mid-latitude forests (Townsend et al. 1996, Holland et al. 1997). However, more recent results from the N Saturation study (Magill et al. in press) and our cross-site comparison of ^{15}N tracer movements in temperate forests (Nadelhoffer et al. 1999c) suggest that *if* there is an effect of N deposition on forest C balance, increased soil C retention rather than N-induced increased tree growth is important.

Increasing temperatures may both increase the length of the growing season and fertilize forests as accelerating decay of soil organic matter increases N availability for uptake and storage in plants. These are probably more important influences on forest C accumulation than N fertilization effects (above). Since the C:N ratio in plants is substantially greater than in soil organic matter, warming may increase net C storage by transferring N from soils to vegetation, especially in forests (McKane et al. 1995, 1997; Melillo 1996, Townsend & Rastetter 1996). The magnitudes of such increases depends on how plant C balance is affected by other factors, including the potentially deleterious effects that increased N deposition may exert on tree growth and ecosystem processes

(i.e., N saturation; cf. Aber et al. 1989,1998) and other aspects of climate change (e.g., water availability, temperature effects on photosynthesis and respiration).

Results from our long-term experiments underscore the fact that many fundamental mechanisms controlling N and C dynamics in temperate forest ecosystems remain poorly understood (Berntson and Aber 2000, Nadelhoffer et al.1999, Aber et al. 2000). Consequently, in LTER III we propose to expand our long-term measurements, experiments, regional comparative studies, and modeling activities to address central aspects of nitrogen and carbon cycles in New England forests, especially as they pertain to current and prospective environmental concerns and to the global C cycle. We will focus on the response of C and N dynamics to vegetation change and succession, climate variability, forest management, and stress, especially nitrogen deposition. At the heart of this work will be intensive site-based studies extended to pertinent sub-regional, regional, and even global scales through extensive measurement and modeling activity.

The proposed work expands HF LTER I and II activities in which we established a series of unique field measurements, large-scale experiments, cross-site studies, and modeling activities designed to increase our understanding of C and N dynamics in temperate forest ecosystems. Our permanent plot measurements are coupled with long-term eddy flux measurements of forest-atmosphere exchanges of CO₂, gaseous N compounds, other trace gases, water vapor, and energy made at the **Environmental Measurement Station (EMS)**; Wofsy et al.1993, Goulden et al. 1996, Hollinger et al. 2000). Large-scale and long-term experiments include: **DIRT** (Detritus Inputs and Removal Treatments), in which above- and below-ground litter inputs are manipulated to evaluate processes and mechanisms of organic matter formation; **Soil Warming**, in which soil temperature is raised 5 °C above ambient to assess the effect of warming on soil carbon and nitrogen dynamics (Peterjohn et al. 1994, Melillo et al. 1995, in press); and **N Saturation**, in which chronic N additions to forest plots are used to assess the effects of anthropogenic enhancement of N inputs on forest structure and function (Aber et al. 1993, Magill et al. 1997, in press, Nadelhoffer et al. 1999a). These intensive site-based activities are broadened through comparative studies at Hubbard Brook, Bear Brook and Howland Forest, ME, and international networks of ecosystem studies (e.g. AmeriFlux, Hollinger et al. 2000, NITREX, Wright et al. 1994).

In LTER III we will expand these efforts to address four primary questions:

1. **What are the current rates of C storage in temperate forests and how are they influenced by climate variability, succession, and forest logging and conversion?**
2. **How would direct (chronic N inputs) and indirect (within ecosystem N redistribution due to climate warming) influences on the Northeast's N cycle affect the C storage in the region's forests?**
3. **What above- and below-ground mechanisms mediate the ability of temperate forests to store carbon and to process fixed nitrogen?**
4. **What is the regional pattern of forest productivity in New England and how is it affected by past and current land-use, forest stresses, and N deposition?**

Question 1 will be addressed using the eddy-covariance measurements that have been taken continuously in HF LTER since 1990, combined with intensive biometry and

measurements of soil flux on permanent plots in the footprint of the tower. This work will be complemented by assessments of logging and forest conversion at site, sub-regional, and regional scales. **Question 2** will be addressed through analyses related to the N Saturation and Soil Warming experiments. **Question 3** will be explored through ongoing and new studies on the DIRT, N Saturation, and Soil Warming experiments. **Question 4** will be examined through comparative studies across New England and through regional ecosystem modeling based on intensive and extensive measurements at the Harvard Forest and regionally.

1. Long-term Measurement of Carbon Storage in Relation to Climate Variability and Forest Harvesting and Conversion

Environmental Measurement Station (EMS)

We plan to enhance long-term measurements of Net Ecosystem Exchange (NEE) using the EMS eddy-covariance system, extending the longest continuous time series for NEE in the world. The flux data, in combination with comprehensive ecological measurements, provide the foundation for interdisciplinary investigations of carbon balance, legacies of prior land use, effects of logging, and biosphere-atmosphere exchanges of pollutants and greenhouse gases by addressing the following questions (Figs. 24, 25):

- 1) What are the important biological processes controlling NEE in temperate forests?
- 2) How do these processes vary with climate over annual to decadal time scales?
- 3) What are the quantitative relationships between NEE, forest structure (e.g. canopy nitrogen content, LAI, coarse woody debris, stand age), species composition, and climatic variations over longer time scales (inter-annual, inter-decadal)?
- 4) Do seasonal anomalies in climate affect photosynthetic capacity or pools of short-lived organic matter, thus affecting annual carbon sequestration in subsequent years?

Measurements in permanent plots of C cycle processes, including aboveground wood increment, soil respiration, and production of litter and coarse woody debris, will complement ongoing eddy-covariance measurements of fluxes of CO₂, H₂O, sensible heat, O₃, and NO_y and observations of environmental parameters (e.g., net radiation, PAR, soil and air temperatures, wind profiles; Wofsy et al. 1993, Goulden et al. 1996a, Munger et al. 1996). Individual biological C fluxes will be summed and reconciled with the forest NEE. Our 10-year data record provides a very accurate measure of average seasonal fluxes and defines mean ecosystem response to environmental forcing by incident light, temperature, length of the growing season, etc. Seasonal and interannual anomalies in NEE and its component fluxes will be compared in detail to climate anomalies (e.g., drought) and disturbance (e.g. defoliators, ice or wind damage) to test concepts of causal relationships.

The proposed work will deliver basic biometric data, detailed carbon budgets, observations of the sensitivity of CO₂ exchange to environmental forcing and to past land use, and integrated synthesis of ecosystem control over temperate forest NEE, including:

- i. Process measurements and compartment inventories (see table below).
- ii. Integration of biological/ecological measurements with climate and NEE data.
- iii. Determination of control over long-term patterns of CO₂ exchange from i and ii.

PROCESS MEASUREMENTS AND COMPARTMENT C INVENTORIES.

Process	Observation
NEP	Annual sum of NEE
GEE + Tree Respiration	Species-specific wood increment data
GEE + Tree Respiration	Leaf litter production data
Soil Respiration	Direct soil collar measurements
Tree mortality and decay	Annual tree and coarse woody debris surveys

Our focus on defining quantitatively the implications of past and ongoing human and natural disturbance (prior land use and hurricanes) for C dynamics is a new direction for the EMS that addresses major questions in HF LTER. The measurements of leaf and wood production, respiration, and net C storage in wood track seasonal and inter-annual feedbacks between climate and C allocation in major forest compartments and define the variable contributions of different tree species. These observations will provide a unique opportunity for direct, quantitative assessment of the influence on the carbon cycle of prior land use, and interactions between land cover change and climate in the temperate region.

The Role of Forest Management in Carbon Dynamics in Central New England

Forest management plays a key role in sequestration or release of atmospheric CO₂ by forests. Although there are many models of logging effects on biomass and carbon balances, accurate observations of carbon fluxes associated with harvests are lacking for both short and long time scales. In central New England, logging has increased as a consequence of forest growth and market conditions, to become the pre-dominant forest disturbance. Determination of harvest impact on C storage and the pattern of forest cutting in the landscape is therefore a critical imperative for research. Thus we will expand on past efforts to include a detailed assessment of the fate of carbon following logging in a typical forest. We will also analyze the intensity, distribution, and impacts of logging and forest conversion in central Massachusetts, in the entire state, and across New England. In addition to providing direct information on forest disturbance and C storage, these analyses will provide essential input for regional modeling activities and vegetation studies.

Dynamics and fate of carbon following commercial logging. Logging impacts will be assessed in a commercial harvest in a mature hardwood forest, adjacent to and structurally very similar to those at the EMS and other LTER experiments. The proposed logged and control areas have been sampled since 1993 in 46 300 m² plots (9 harvest and 37 control), including litter by species, LAI, soil respiration, soil moisture, and high-frequency dendrometry on ~800 trees. In 1999 we surveyed coarse woody debris. In order to maintain an accurate carbon budget, **harvest-related measurements** will carefully account for removals by weighing all product and inventorying woody residue

and slash. Long-term **post-harvest measurements** will pay particular attention to soil moisture, temperature, respiration, and organic matter profiles (total carbon and C/N ratio). We will also measure species-specific growth increments, including new growth into the >5 cm size-class, tree mortality, and decay.

The proposed work on logging will deliver the following products:

1. Detailed accounting of the short-term C balance on the timber harvest compared with adjacent undisturbed sites (for which NEE is measured by eddy correlation).
2. Accounting of the initial fate of below-ground soil carbon following harvest.
3. Integrated understanding of how both ecological and climate responses to forest harvest control subsequent evolution of forest carbon balance.
4. Quantification of the relative magnitudes of the effects of human and long-term (10-year) natural disturbance within the ecosystem.

Regional Assessment of Forest Management and Conversion. To place our site-based measurements in a broad context and to ascertain the impact of forest harvesting and conversion on C storage regionally, we will: (1) develop a spatially explicit, long-term (1984 onwards) assessment of logging activity in central Massachusetts and (2) analyze Massachusetts and New England-wide patterns of forest cutting, forest conversion to other land uses, and forest growth versus removals.

Massachusetts is unique in requiring Forest Cutting Plans for all commercial timber harvests. These reports enable development of databases and GIS overlays characterizing the spatial characteristics, intensity, motivation, landowner, and volume of all logging activities in our central Massachusetts sub-region (Fig. 26). In LTER III we will assemble this database and undertake field sampling of areas harvested in the past 15 years in order to confirm the accuracy of the data and to evaluate the compositional and successional response of forests to logging. These data will be analyzed to:

1. Determine the extent and geographic pattern of harvesting in relationship to cultural, natural, ownership, and land-use factors.
2. Assess temporal trends in wood volumes and species and quality removed in relationship to regional economic factors.
3. Evaluate land-use patterns and behavior in a landscape predominantly owned and controlled by non-industrial, private forest owners (Kittredge 1999).
4. Make current our regional analysis of forest disturbance developed in LTER I and II and include natural and human factors by including dominant land-use practices.
5. Generate sub-regional and regional estimates of forest growth and impacts of forest harvesting conversion on carbon storage.

USDA Forest Service Forest Inventory Analysis (FIA) will be used to compare these detailed and spatially explicit data with state- and New England-wide assessments of forest cutting, conversion, and forest growth versus removal. FIA provides state-level average estimates of growth, removals, and total forest area. Our detailed data enable us to estimate harvest rates for extensive non-industrial private forest lands, to compare this to FIA removal rates, and to develop factors to apply to FIA removal rates elsewhere. This will be combined with land change data to better characterize changes in timber

volume and C storage due to harvesting versus change in land use. Other New England states have varying degrees of timber harvesting regulation and data that can provide indirect data on harvest and conversion. In addition, FIA crews recently measured the EMS footprint, providing a baseline for comparison of data from the Eastern US with eddy flux data and forest composition and stand characteristics at HF LTER.

2. Mechanisms of Carbon and Nitrogen Dynamics in Relation to Climate Change, Land Use and Nitrogen Deposition – Long-term Experiments

Long-term experiments initiated in LTER I to follow the course of carbon and nitrogen dynamics in relation to disturbance, climate change, and nitrogen deposition become increasingly important as we extend our research to investigate the effects of land use and the mechanisms of C and N cycling, and as we pursue a broader geographical scope. As these studies continue well into their second decade, they enable us both to evaluate the sensitivity of C and N dynamics to climate variability and to investigate above- and below-ground processes that control N and C cycling in temperate forests. Equally important, these experiments have critical cross-linkages with our land-use studies, hurricane experiment, permanent plots, and measurements made at the EMS and in the proposed logging assessment. They also provide key input to the regional and global comparative studies that we undertake and to the synthetic modeling approaches described later in this proposal. Thus, we will continue and expand these experiments in LTER III as described below.

DIRT– Plant Litter Influences on Soil Organic Matter Genesis and Function

We will continue chronic manipulations of above- and below-ground litter inputs to forest soils by maintaining and expanding the DIRT (Detritus Input and Removal Treatments) experiment, which is developing an understanding of the long-term (years to centuries) influences of plant inputs on soil organic matter development and dynamics. Treatments are conducted on replicate ($n = 3$) 3m \times 3m plots and include doubling of leaf litter inputs, preventing leaf litter inputs, preventing root inputs (with root-ingrowth barriers), and preventing all (leaf and root) plant inputs. A fifth treatment involves experimental “impoverishment” of soil by replacing the top 20 cm of O and A horizons with B horizon soil.

We will conduct our third post-treatment sampling in the early summer of 2001 after 10 years of manipulations. Sampling in years 0 (pre-treatment), 1, and 5 provided information on C and N contents, basic soil properties (CEC, base saturation, pH, texture), and potentially mineralizable C and N pools (methods of Stanford & Smith 1972, as modified by Nadelhoffer 1990). Year 5 sampling and analyses (Nadelhoffer et al. submitted) were expanded to include soil microfauna, bacteria and fungal counts and measurements of dissolved organic N and C dynamics (Aitkenhead et al. in prep), which will be repeated in 2001. In addition, we are collaborating with Dr. Maura Meade, a molecular ecologist at Allegheny College, to explore the use of molecular probes for assessing how variations in plant inputs to soil influences microbial functional groups.

Field measurements of soil respiration (Bowden et al. 1993, Boone et al. 1998) and soil solution chemistry (Aitkenhead et al. in prep) will be continued during alternate growing seasons, or more often if resources allow. Our accumulated field C flux and soil solution data will complement our existing data on temporal changes in soil properties and mineralizable organic matter pools. Our combined field and laboratory studies will provide information needed to test simulation models of plant-soil interactions (e.g., GEM; Rastetter et al. 1991) and soil organic matter dynamics (e.g., DOCMOD; Currie & Aber 1997).

In addition, we plan two new, related activities. First, we will install 'impoverished' soil plots to document soil development (see above) in three additional forest types dominated by red pine, white pine, and sugar maple. Once installed, these O-A Less plots require no maintenance as natural rates of root ingrowth and litter deposition are allowed. Periodic sampling (Years 0, 1, 5, 10, 20, 30...) and assaying of soil properties and mineralizable C and N pools will allow us to characterize patterns of soil process and property recovery under different forest types.

Second, we will expand linkages to related experiments in other regions. Currently we collaborate actively with the H.J. Andrews LTER (temperate conifer forest; Drs. Kate Lajtha, Phil Sollins, etc.) and Allegheny College, PA (base-rich sugar maple forest; Dr. Richard Bowden), which have modified DIRT experiments. We have begun discussions with collaborators working at the Coweeta (GA) and Luquillo (PR) LTERs (January 2000), Hungarian investigators (lead by Kate Lajtha at the June 1999 East European ILTER symposium in Budapest), and Korean and other East Asian ILTER investigators (Nadelhoffer, October 1999 East Asia ILTER meeting in Seoul), who are considering similar experiments. Ultimately, we anticipate an array of DIRT-type experiments in a variety of climatic and vegetation zones to provide information needed to build a process-level understanding of soil organic matter genesis and function at local and global scales.

Nitrogen Saturation Experiment

We will continue treatments and core measurements on N Saturation with the primary goal of assessing the complete, long-term sequence of responses. Of particular interest is documenting the timing and extent of increased nitrate loss to determine whether this ecosystem response is driven by the concentration or the cumulative dose of additions. If cumulative dose is the key driver, then the low N plots should take three times longer to show elevated nitrate leaching than the high N plots. We will also continue the N+S plots without the S addition, making them a replicate for low N treatment. Such replication is rare in long-term, large-plot experiments.

LTER support allows continuation of the experimental manipulation and core measurements. However, we are pursuing support for two additional process-level initiatives (G. Berntson, PI).

Effects of N Deposition on Kinetics and Magnitude of Soil N Immobilization. We have developed new short-term ¹⁵N tracer methods to quantify the kinetics and magnitude

of N immobilization and to quantify more clearly the contributions of "fast" and "slow" processes to gross N immobilization. In hardwood and conifer stands, rapid immobilization accounted for a significant fraction of total N immobilized (1/3-2/3 of the total), and long-term N deposition led to a reduction in N immobilization. For the conifer forest, this reduction was due to a loss in the amount of N immobilized during the fast phase, whereas in the hardwood stand it was due to slow phase immobilization. A strong relationship exists between NO_3^- leaching losses and measured N immobilization rates but only when both rapid and slow phases of N immobilization are included. We plan to quantify fast vs. slow N immobilization in a larger number of sites, over longer periods of time, with greater replication, and with coupled field and laboratory experiments. We plan to characterize the biotic and abiotic components of these different immobilization phases through manipulation (soil sterilization) and analysis of the linkage between C and N dynamics during immobilization (soil CO_2 flux, microbial uptake).

Effects of Long-Term N Deposition on Canopy Structure and Photosynthesis.

Preliminary measurements from access towers in the high N pine plots suggest that treatments have changed canopy production, turnover rate, and a critical foliar $\text{N}:\text{A}_{\text{max}}$ relationship. Collaborating with the USDA Forest Service, we found that while foliar N has increased by more than 100% and soluble protein has increased by 85% in the pine high N treatment canopy, maximum photosynthesis did not change. We also found that needle retention times were reduced by 40%, and LAI reduced by 16%, while litterfall rates increased by approximately 20%. These data suggest that increased N deposition has severely reduced the pine forest's gross photosynthetic capacity through reductions in standing foliage with no physiological compensation, providing an explanation for observed reductions in tree diameter increments and soil respiration rates. We will extend these measurements to low N pine plots and all hardwood plots.

Soil Warming Experiment

We will continue to study the effects of soil warming on soil and plant processes by maintaining our extant soil-warming experiment and by adding a new one during the next six-year LTER period. Our current study, established in 18 six by six meter plots in 1991, was designed to explore the consequences of temperature increases on soil processes including soil respiration, organic matter decomposition, methane production and consumption, net nitrogen mineralization and net nitrification, and nitrous oxide production (e.g., Peterjohn et al. 1994, Melillo et al. 1995). The plots are grouped into six blocks, each with three plots assigned to one of three treatments. The treatments are: (1) heated plots in which the average soil temperature at 5cm is elevated 5°C above ambient using buried heating cables; (2) disturbance-control plots that are identical to heated plots except that they receive no electric power; and (3) control plots that have been left in their natural state. For at least the first three years, 2001 through 2003, we will continue to measure soil respiration, trace gas fluxes, nitrogen mineralization and nitrification, and nitrogen leaching to extend our documentation of the effects of warming on soil carbon and nitrogen stocks and cycling rates.

In addition, we are planning a new warming experiment to address a central question: Can soil warming change ecosystem N distribution and thereby change the capacity of forests to store C? We will directly test the idea that warming can result in the redistribution of N from the soil to plants and thereby enhance net ecosystem carbon storage (Melillo et al. 1995). Using our warming protocol in Sweden, Professor Sune Linder (pers. comm.) has observed a 30% increase in wood increment in response to a 5°C soil warming over five years. In our new, larger, long-term soil-warming experiment, we will make a series of plant and soil measurements that will quantify changes in C storage to provide insight as to how these changes may be related to N redistribution from soil to plants. The larger plots are required to include enough trees in a treatment to capture the plant-soil interactions. Beginning in 2001, we will establish three 30x30 m plots adjacent to the current soil warming study and will make 3 years of baseline plant and soil measurements on all plots. In 2004, we will initiate a single treatment on each plot - one heated, one disturbance-control, and one control, following the protocols in our initial warming experiment. We will use baseline time-series data in place of plot replication to determine treatment effects in the same way that whole-watershed studies do.

Plant measurements will include: (1) annual woody increment, (2) C:N ratio in the woody increment, roots and leaves, and (3) natural abundance ^{15}N content in the various plant parts. Measurements of woody increment will provide an estimate of the degree to which soil warming and the acceleration of the N cycle stimulate C storage in trees. The measurements of C:N ratio in woody increment, roots and leaves will give insight into how "plastic" the stoichiometry of various plant tissues is in response to acceleration of the N cycle through warming. We will also measure ^{15}N in plant tissues (wood, roots, leaves) on all plots to determine whether plants on the warmed plots are acquiring N that has been mineralized from more refractory (^{15}N -enriched) soil organic matter pools.

Soil measurements in the new study will include: (1) C and N stocks in the bulk soil and in the light density (LD) and heavy density (HD) soil fractions; (2) the ^{14}C and ^{15}N content of the bulk soil, the soil fractions and the fine roots; (3) CO_2 and $^{14}\text{CO}_2$ efflux from the soil surface; and (4) lignase enzyme activity in the various soil horizons; and (5) net nitrogen mineralization and nitrification rates. Measurements of C and N stocks in the soil and respired CO_2 are essential background information for developing budgets using ^{14}C and ^{15}N . We propose to use ^{14}C (Trumbore et al. 1996, Paul et al. 1997, Trumbore et al. 1997) and lignase enzyme activities (Sinsabaugh et al. 1991, 1992) to determine whether soil warming has increased or decreased the decomposability of meta-stable soil organic matter. Measurements of N mineralization and nitrification will provide insights into the effects of warming on the N cycle and essential background information for interpreting our ^{15}N natural abundance study.

3. Regional Modeling of C and N Dynamics in Relation to Land Use, Climate Change and Forest Stress

We have applied PnET models to Harvard Forest sites and across the New York/New England region and have validated these against measurements for gross ecosystem C

flux, net primary production, and water yield at HF and Hubbard Brook LTER and regional data for NPP and water yield (Figs. 27, 28). The individual effects of several components of global change (CO₂, temperature, precipitation, tropospheric ozone, N deposition and land use) have been analyzed separately, and predicted responses have been published in conjunction with US Forest Service Northern and Southern Global Change Programs.

In LTER III we will extend this analysis spatially and integrate the separate effects of the different stressors listed above into a single model to provide an integrated analysis of the response of Eastern US forest ecosystems to the full suite of major environmental change factors. This work will continue in cooperation with the US Forest Service through the following steps.

First, we will improve PnET's photosynthesis routine to integrate the combined effects of CO₂ and ozone based on studies of the relationship between internal leaf CO₂ concentration and maximum photosynthetic rate. This relationship can be described by a Michaelis-Menten-type equation that can be used to predict the maximum rate of photosynthesis achievable at a given foliar nitrogen concentration. This approach is compatible with the realization of ozone effects on photosynthesis currently in the model and offers the potential for alternative descriptions of stomatal response to both ozone and CO₂ concentrations.

Second, we will extend the spatial extent of our study to include all forests in the Eastern US using the data from the VEMAP program, which provides interpolated climate time series data from 1895 at 0.5x0.5° resolution. Due to discrepancies between the VEMAP I radiation data set and a spatial interpolation based on direct measurements within the northeastern US (Jenkins et al. 2000), we have developed and will use a summary relationship based on the limited number of actual observations made over time.

We will also develop data planes for N deposition and tropospheric ozone concentration. N deposition will be estimated using the NADP data base, with records for over 100 stations in the eastern US, along with the detailed measurements of speciated dry deposition at the EMS tower to confirm the assumed relationship between dry deposition and total (wet + dry) deposition. We will use three USEPA sources to derive a spatially explicit, monthly time-step representation of ozone dose over the Eastern US for the period of measurement: documents on mapping and forecasting ozone concentrations (EPA/454/R-99/009 and EPA/625/R-99/007), daily ozone forecasts from the Hysplit_4 model, and the AIRS data set (set of surface ozone measurements from 1982 to the present). The Northeast States for Coordinated Air Use Management (NESCAUM) also compiles and maps ozone concentrations that we will use. These regional estimates will be linked to the more detailed understanding of chemical, physical, and biological processes that are inferred from the detailed measurements at the EMS tower.

Observations and modeling of reactive nitrogen deposition, and monitoring and analysis of concentrations of selected trace gases that influence the energy balance or oxidant

capacity of the atmosphere will complement the nitrogen addition, ozone impact, and carbon cycling studies.

D. SYNTHESIS AND INTEGRATION IN THE HF LTER PROGRAM

Over the history of the HF LTER program, synthesis of results and integration of interpretations have been achieved through: a system of regular science team meetings, the Annual HF Ecology Symposium and combined LTER and NIGEC (National Institutes of Environmental Change - DOE) workshop, joint lectures and articles (e.g., AAAS 1999; Foster et al. 1998), and regular collaboration among LTER co-investigators on other projects and agency proposals. Most importantly, synthesis and collaboration have been motivated by the results and conclusions that emerged from LTER I: information from apparently unrelated subjects (e.g., historical ecology and atmospheric chemistry) proved to be indispensable in interpreting modern ecosystem pattern and process. For example, the initial design of the N Saturation experiment and Environmental Measurement Station paid no attention to the details of history. Nonetheless, it became apparent that the results from each became interpretable only with a knowledge of 19th C land-use activity and 20th C impacts by hurricane and fire (Aber et al. 1998, Wofsy et al. 1993). Thus, exchange of information and integration of results have become essential parts of the design, methodological approach, and interpretation of all aspects of the HF LTER program. Recognition of this fact can be seen in the synthesis volume that has emerged (Foster and Aber 2000) and in the design of LTER III.

In LTER III, synthesis of activities is imbedded in all aspects of the project. Forest cutting, forest land conversion, insect outbreaks, hurricane impacts and past land-use are essential variables for studies of biological invasions, modern vegetation patterns, and conservation biology as well as the dynamics of nitrogen and carbon. Vegetation dynamics and ecosystem function will also be related to environmental variation on annual to century scales. Ultimately, the complete integration of these factors will occur through the development of models that predict ecosystem responses to complex patterns of land use and environmental change. In developing the basic models, generating input variables, and verifying output, we use our complete array of results from long-term experiments and measurements, land-use, disturbance and environmental histories, and mechanistic understanding of ecosystem processes. Thus, modeling activities not only enable us to extend our results in time and space but also represent an essential tool in the integration of our long-term research.

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IV. MANAGEMENT OF THE HARVARD FOREST AND LTER PROGRAM

Administration. The LTER program is administered at the Harvard Forest, base for the PI, many co-investigators and students; the major experiments and research facilities; data management and archives; and the financial office. Harvard Forest is a department in the Faculty of Arts and Sciences of Harvard University, administers the Masters in Forest Science, and offers courses and the Ph.D. degree through the Department of Organismic and Evolutionary Biology. Funding for the Forest is derived from endowments, whereas research activities are supported with grants. As PI and Director, David Foster is responsible for project administration, coordination of science meetings and the Harvard Forest research group, and site representation in the LTER Coordinating Committee. Dr. John O'Keefe, Coordinator of the Fisher Museum, oversees public education and outreach programs through the Fisher Museum. The LTER science team of co-investigators focus much of their research on the LTER and Harvard Forest projects. The science team meets bi-monthly and is responsible for policy decisions, developing new research directions and inter-site collaborations, and representing the LTER in the scientific community. Dr. Emery Boose, Computer Information Specialist, serves as LTER Data Manager, assisted by Julie Pallant as well as HF Archivist John Burk. Forest and facilities management is undertaken by the Woods Crew of four, directed by the Forest Manager.

The emergence of an integrated research and education program in forest ecology at the Harvard Forest has been accompanied by a growing user group of national and international scholars; more than 100 outside scientists, representing more than 30 institutions, conduct research at the Forest annually. To enhance collaboration and use by non-LTER scientists, we advertise opportunities including Bullard Fellowships, visiting fellowships for cross-site LTER studies, the Summer Research Program for Undergraduates, and our Annual Ecology Symposium through our web page and venues including *Nature*, *Science*, *ESA* and *BES Bulletins*, *Conservation Biology*, and *Journal of Forestry*. The **protocol for review of new projects** includes: submission of a completed web-based form for research proposals; initial review at HF by the Forest Manager, Data Manager, and Director; and review and discussion among the LTER science team. All co-investigators are involved in major land and data management policy decisions.

The **Annual HF Ecology Symposium**, followed immediately by the joint LTER (NSF) and NIGEC (DOE) science workshop, provides a forum for all researchers working at HF to discuss progress and new directions. The symposium is widely advertised and is open to scientists, students, and professionals throughout the northeastern US, thereby advertising opportunities for collaboration very effectively. The symposium is also well attended by agency representatives, policy makers, and collaborators. Abstracts are published and distributed to all LTER sites, NSF program directors, and ecologists nation-wide. The schedule, whereby we follow the symposium with evening and then day-long workshops for LTER and NIGEC researchers, provides an excellent forum for synthesis, critical oversight of program development, and opportunities for interaction among scientific disciplines that usually do not interact (e.g., historical ecologists, atmospheric scientists, and population biologists).

Since 1985 the Harvard Forest has sponsored an exciting **Summer Research Program in Ecology** for a diverse and talented group of students centered around an NSF REU site grant (10 students) with additional support from Harvard University (5 students), the Mellon Foundation (2-3 students), and other agencies (5-6 students). The program provides independent research experience and promotes career development in ecology. We use an effective administrative protocol comprising: advertisement and recruitment; selection of diverse and productive students; advanced preparation; individual mentorship within research groups comprised of faculty, graduate students, post-doctoral associates and undergraduate students; weekly seminars and discussion groups on science, careers, graduate studies, and ethics in science; field trips to research sites and other institutions; an annual student symposium; program evaluation and discussion; and follow-up including publication, professional presentation, thesis development, and career tracking.

Land Base. The 1200-ha Harvard Forest has operated as Harvard University's main ecological research and educational facility since 1907, and consequently its historical records on land use and vegetation change are unsurpassed by any site in the US. The Forest also owns the Pisgah old-growth tract in the 5000-ha Pisgah Park, NH, which blew down in the 1938 hurricane and is the site of much historical and current research.

Research Laboratories and Library. The Harvard Forest provides a complete base for research in forest, ecosystem and historical ecology and biosphere-atmosphere interactions. Coincident with LTER I and II, the Forest has overseen phenomenal growth in scientists, educators, students, collaborators, research and education programs, and laboratory, computing, archival, teaching, and housing facilities. Shaler Hall contains offices, seminar rooms, a 23,000-volume library, dining facilities for 40, laboratories for paleoecological, tree-ring, morphological, computational and GIS studies, and a complete herbarium of the local flora. Torrey Laboratory includes two research greenhouses, offices, and physiology and nutrient analysis laboratories with fume hoods, gas chromatograph, Lachat autoanalyzer, CN analyzer, nano pure water, balances, and drying ovens. The Archive (2200 ft²) houses 100 years of data on the land and research, a sample archive with cold storage facilities, and air photo interpretation systems. Researchers also make extensive use of laboratory, controlled environment, and computing facilities in the Division of Applied Sciences and Biological Laboratories at Harvard, the Ecosystem Center at the Marine Biological Laboratory, the Complex Systems Research Center at University of New Hampshire, and the University of Massachusetts.

Fisher Museum and lecture hall (10,000 ft²) is devoted to public and formal education, has seating for 100, and displays the HF Dioramas, which portray the history, ecology and conservation of New England forests. **Residences** includes Fisher House, with room for groups of 26, and four houses and ten rental apartments for visiting researchers, graduate students, and post-doctoral fellows. **Equipment** for experimental manipulations, forestry, construction, and maintenance includes a back-hoe, bulldozer, crawler, skidder, tractor, dump truck, flat bed truck, 2 vans, 7 pick-ups, wood-working and machinery shops, and a sawmill.

V. Long-term Management of Data, Documents & Samples

Arguably, the single greatest strength of the Harvard Forest as a research and educational field laboratory for long-term studies is the phenomenal information base on the history, changes, and processes occurring in the forested landscape. Although initial studies and databases date to the founding of the Forest in 1907, these are augmented by historical, paleoecological, dendrochronological, and archaeological information that pushes the records back over centuries and millennia, and which have been greatly expanded by intensive studies in the LTER and NIGEC programs. Management of the electronic data and document and sample archives that make these invaluable information sets available to the scientific community is a major mission of the Harvard Forest and a priority for the LTER program.

1. Data Management

Computer Facilities. Computer and network facilities at the Harvard Forest have improved at a remarkable rate since the beginning of LTER I in 1988 with funding from Harvard University and NSF. The three main buildings (Shaler Hall, Torrey Laboratory, and Archives) are wired for data and connected via a T1 line to the Harvard University Faculty of Arts and Sciences computer network in Cambridge MA. FAS provides support for our connection to the University and the Internet. At present the Forest has nearly 50 Dell Optiplex computers running Windows NT 4.0 (most common configuration: 400-450 MHz Pentium II or III processor with 128 mb RAM and 10-20 gb hard disk). Electronic mail services are provided by FAS UNIX servers in Cambridge. Networking features of Window NT enable us to share local resources such as printers and storage devices and to create local ftp and web sites. The HF web page is prepared on a local PC and uploaded to its current host (LTERNET) at the LTER Network Office in Albuquerque.

Improvements scheduled for 2000 include: (1) installing 2-4 Windows NT servers, (2) moving the HF web page to one of these servers, (3) extending our network via optical fiber to two nearby residential / conference buildings (Fisher and Raup houses), and (4) extending our network via wireless link to the EMS Tower in the forest.

Electronic Data Archive. The HF Data Manager and Assistant maintain an Electronic Data Archive for all scientific projects since 1988 (beginning of LTER I), as well as selected earlier projects. The Archive can be searched and accessed using the HF Data Catalog. A copy of the Data Archive and selected information from the Data Catalog are maintained on-line as part of the HF web site.

The structure of the Data Archive follows closely the recommendations and practices of other LTER sites. Each project is assigned a project code, which serves as the directory name for project files. For each completed project, these files include an Overview file, an optional Methods file, and one or more Data files with accompanying Metadata files. All files are stored in plain ASCII or HTML format (except for spatial data, which are stored in ArcView or Idrisi format). A few projects are maintained on web servers at

Harvard's Atmospheric Sciences Department, The Marine Biological Laboratory, or the University of New Hampshire (project codes beginning with AS, MB, or UN, respectively), with links from the HF web site. Permanent copies of the entire HF web site, including the Data Archive and relevant files on the AS and UN servers, are created annually and stored at the Harvard Forest and an offsite location.

The Data Catalog is maintained using standard database software (currently Visual dBase). For each project, the Catalog contains the project code, title, list of investigators, contact person, keywords, current status (from a Data Management perspective), start and end dates, field sites, and access codes for relevant materials in the Document and Sample Archives (see below). Online search capability is provided through the LTER Network Data Catalog, which harvests information from our Data Catalog weekly. The HF Data Catalog is used to track the progress of current research projects and to ensure that files in the Data Archive are updated in a timely manner (see below).

Policy for Submission of Data. The HF LTER endorses the LTER Network Data Access Policy, which specifies that data for most projects (Type I) will be made available online within 2-3 years of collection, while in exceptional cases (Type II), such as a student thesis project, data may be withheld for longer periods.

The following guidelines must be followed for all research projects at Harvard Forest:

- Applications for new projects must be reviewed by the Director, Forest Manager, Data Manager, and LTER Science Team. Prospective researchers must agree to Harvard Forest policies for submission of data, documents, and samples.
- Before work on a new project begins, the PI must submit to the Data Manager a Project Overview suitable for inclusion in the Data Archive and posting on the web page. A project code is assigned at this time, and entries created in the Data Archive and Data Catalog.
- Overviews for current projects are reviewed annually and updates must be submitted to the Data Manager if requested.
- Data and Metadata files must be submitted to the Data Manager in the proper format within 2 years of collection. Exceptions to this rule must be approved by the Director.
- Format and content of the submitted files are checked by the Data Manager; however primary responsibility for data completeness and integrity (quality control) rest with the project PI.

Policy for Use of Data. Harvard Forest on-line data are freely available for downloading and subsequent use. Prospective users are asked to (1) notify the HF Data Manager before downloading, identifying the data set and its intended use, (2) direct questions about the project or on-line materials to the designated Contact person, and (3) notify the Contact person of any publication plans.

2. Documents

Document Archives. The HF Document Archives contains document records for nearly 100 years of research at Harvard Forest. The entire collection (more than 1700 published and unpublished studies) has been cataloged in the Archives database, which contains (for each study) an access code, list of investigators, project title, date, and list of keywords. All important datasheets, maps and records in this archive have been microfilmed with duplicate copies maintained on-site and in a secure off-site location.

Policy for Submission of Documents. All scientists conducting research at Harvard Forest are required to submit relevant research documents to the HF Archivist within one year of project completion, for cataloging and inclusion in the Archives collection. Such documents should include copies of funded proposals, publications, unpublished reports, field notes, maps, and analyses for the project.

Policy for Use of Documents. The HF Archives are available for public use. Interested parties should contact the Archivist or Director. Materials may not be removed from the Archives building. Facilities are available for copying or scanning Archives materials.

3. Samples

Sample Archives. The HF Sample Archives currently contain over 200 boxes of soil, litter, and tree core specimens. The entire collection has been cataloged in the Samples database, which contains (for each box) an access code, list of investigators, project title, study site, date of collection, description of material, and number of specimens.

Policy for Submission of Samples. Investigators who wish to submit samples for long-term storage in the Sample Archive must do so within one year of project completion. Researchers should contact the Archivist for information regarding sample preparation and cataloging.

Policy for Use of Samples. Use of samples by anyone other than project personnel must be approved in writing by the project PI or the Director.

VI. Education, Public Outreach and Impact on Public Policy

Integration of LTER Research and Education. The HF supports its strong commitment to formal education (K through graduate), professional training (post-doctoral and beyond), and public outreach through a series of extremely successful programs that are well-integrated with LTER activities. In the past six years, graduate students from five departments at Harvard (Organismic and Evolutionary Biology (6 PhD), Earth and Planetary Sciences (1 PhD), Graduate School of Design (2 PhD), Kennedy School of Government (1 PhD), and Harvard Forest (6 MFS), the University of New Hampshire (2 MS, 4 Ph.D.), University of Massachusetts (1 MS), and Antioch College (2 MS) have undertaken their thesis research at the Forest. Undergraduate involvement is diverse: Senior theses at Harvard, Smith, Hampshire, and Mount Holyoke Colleges, and by REU students (4), dozens of field trips and courses, including the Harvard Forest Seminar offered to a dozen first year students, and the Harvard Forest Summer Research Program. This 12-week research and educational program involves 25-30 students who work closely with faculty and senior scientists on long-term research. The program culminates in a student symposium at which each student presents the results of their summer work. The majority of students are undergraduates funded through NSF's Research Experience for Undergraduates (REU), Mellon Foundation (for minority students), NSF's Collaborative Research with Undergraduate Institutions (CRUI), and Harvard Forest's Fisher Education Fund. Students from this program have an excellent track record of conducting senior theses, entering graduate studies, and pursuing careers in ecology and conservation.

At the professional level, Harvard University offers 4-8 Bullard Fellowships annually to mid-career scientists for research on environmental issues. Fellows spend 6-12 months at Harvard Forest or Cambridge pursuing research and often collaborating on LTER studies. With international applicants, this program provides an outstanding opportunity for the synthesis of ideas across disciplines and ecosystems. In the past 6 years, 41 Bullard Fellows represent 19 states and 8 foreign countries. Individuals span a range of ecological interest: e.g., N. Brokaw, P. Harcombe, D. Knight, Jiquan Chen, S. Trumbore, D. Whigham, T. Spies, E. DeLucia, J. Aber, J. Wiener, E. Franz, K. Woods, R. Primack, M. Abrams, W. Romme, G. Brush, R. Waide, D. Godbold, T. Webb, A. White, D. Bowman, D. Ford, D. Janos, J. Silva, and C. Vaquez-Yanes. Post-doctoral opportunities are also actively supported with about 15 post-docs working with LTER scientists in LTER II.

The Fisher Museum is the focus for Harvard Forest educational outreach under the guidance of Dr. John O'Keefe, forest ecologist and Museum Coordinator. Each year 5,000-6,000 visitors visit the Museum to see the world-famous Harvard Forest Dioramas, which depict the land-use history of central New England and the ecology, conservation and management of these forests. Other exhibits present and interpret LTER research and its scientific and societal implications. Interpretive nature trails demonstrate and explain current research. John has developed two multi-image slide and video presentations that describe the importance of long-term research at HF and outline the NSF LTER program.

During 1999, 85 visiting groups included: youth/scout; elementary; secondary; college/undergraduate; university; and professional/continuing education. More than 35 volunteers staff the Museum on weekend afternoons from May through October. The Museum is also used heavily as a venue for meetings, seminars and retreats by environmental and conservation organizations, state and federal agencies, and departments from regional colleges and universities. Our facilities allow us to host small conferences and symposia including (in 1999), a national meeting of the Ameriflux Network, and a conference on Eastern Old-Growth Forests.

Each year the Forest collaborates with Eagle Eye Institute in Somerville, MA, a non-profit group that organizes environmental programs for city youth. In 1999 this program brought 12 groups of 15 youths for day-long environmental education programs.

Throughout the year we sponsor a seminar series for our staff and regional scientists, drawing on visiting scholars, Bullard Fellows, LTER researchers, regional faculty, and natural resource professionals as speakers. The theme for fall 1999 and spring 2000 is *Conservation and Management of the New England Landscape*.

Harvard Forest Impact on Public Policy. HF LTER activities have an impact on public policy and societal issues at a national and international scale, in that HF scientists have played key roles in Senate and Congressional hearings and IGCP programs regarding global changes issues (especially S. Wofsy, J. Melillo, F. Bazzaz, J. Aber and D. Foster). The most direct impacts on public policy occur at the state and regional level; publications emerging from HF LTER II research led to:

- Initiation of a statewide Forest Vision and Planning Process, headed by HF Forest Policy Analyst David Kittredge (Foster & Foster 1999)
- Formation of a Regional Partnership of 47 organizations and public agencies seeking to conserve New England landscapes (Golodetz & Foster 1996)
- Protection of the largest sandplain ecosystem in the Connecticut Valley by the state of Massachusetts in 1999 (Motzkin et al. 1996, 1999a)
- Recommendations for restoration of the largest conservation property on Martha's Vineyard and endorsement by the Natural Heritage program and Boston Globe as the "largest restoration proposal in Massachusetts' history" (Foster & Motzkin 1999)
- The only regional analysis of hemlock woolly adelgid impacts, which is widely used by public agencies, organizations and the public (Orwig & Foster 2000, Foster 2000)
- Protection for the largest old-growth stand in Massachusetts (Orwig et al. 2000)
- The N Saturation Experiment and related modeling have been instrumental in generating renewed interest at EPA in N deposition effects (Aber et al. 1998).

Harvard Forest Long Term Ecological Research Program

Personnel and Project Responsibilities

Harvard University

David R. Foster PI; Project Coordination; Paleoecology; Forest Ecology; Coastal Historical Ecology; Cross-site Studies: Puerto Rico, Yucatan, New England

Emery Boose Data Management; Hurricane Regional Modeling

Glenn Motzkin Coastal Vegetation Analysis; Historical Ecology; Conservation Applications

David Orwig Hemlock Woolly Adelgid Study; Dendrochronology

Julie Pallant Data Management; Web Site Management

Carol Barford Logging and Carbon Dynamics; Dendrometry

William Munger Eddy Flux Towers; Nitrogen Fluxes

Steve Wofsy EMS Coordination; Regional and Global Comparisons

Fakhri Bazzaz Invasive Plants; Carbon and Nitrogen Interactions; Plant Reproduction and Resource Use

Peter Del Tredici Morphology of Vegetative Reproduction

University of New Hampshire

John Aber N Saturation Experiment; Regional Cross-site Studies of Nitrogen Dynamics; Regional Modeling

Glenn Berntson N Dynamics; N Saturation

Alison Magill N Saturation Experiment; Regional Sampling of N

Scott Ollinger Regional Modeling

Ecosystems Center – Marine Biological Laboratory

Jerry Melillo Soil Warming Experiment; Global Modeling; Regional, Swedish and Amazonian Cross-site Studies

Knute Nadelhoffer DIRT Experiment; ¹⁵N Studies; Cross-site DIRT studies

Paul Steudler Soil Warming Experiment; Trace Gas Fluxes; Amazonian Comparisons

University of Massachusetts

Rebecca Field Wildlife Dynamics; Suburban Wildlife Issues

David Kittredge Regional Logging and Forest Conversion; Public Policy

Mitch Mulholland Archaeology; Coastal Regional Study; Paleoecology

Holy Cross

Cathy Langtimm Wildlife Dynamics; Statistical Analysis

