HARVARD FOREST LONG-TERM ECOLOGICAL RESEARCH PROGRAM

FOREST ECOSYSTEM DYNAMICS IN CENTRAL NEW ENGLAND

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PROJECT SUMMARY

Forest ecosystems worldwide are changing in response to direct and indirect human activities. Evaluation of current and anticipated impacts presents a significant challenge requiring interpretation of the driving variables and components of change across temporal, spatial, and ecological scales. These dynamics also present the opportunity to evaluate the mechanisms underlying ecosystem response to changes in external forcing functions.

Harvard Forest LTER I comprised an integrated analysis of temperate forest response to important human (atmospheric deposition and climate change) and natural (wind damage) disturbances. The research was structured around five primary areas: (1) retrospective studies of long-term changes in forest composition, disturbance, and environment; (2) studies of forest conditions and processes that are critical to an understanding of ecosystem responses; (3) experimental manipulations to evaluate forest response to disturbance processes under controlled or replicated conditions; (4) modeling studies that synthesize our understanding of ecosystem characteristics and responses to disturbance over a range of temporal and spatial scales; and (5) cross-site studies to generalize and broaden the context of our work.

To address our broad objectives, we assembled an interdisciplinary research group representing diverse fields of biological, physical, and cultural science. Studies have utilized novel technologies and extended existing capabilities including high spectral resolution remote sensing of canopy chemistry, eddy correlation measurements of atmospheric-gas exchange over periods of hours to years, ecosystem-scale ^{15}N tracer studies, modeling of broad-scale meteorology and hurricane impacts, and application of ecosystem models to landscape and regional scales. In support of these activities, we developed extensive external and institutional funding and added a permanent site data-manager, who is involved with all aspects of project design, analysis, data storage, and distribution. Results from our long-term experiments and measurements have been widely disseminated and have been incorporated into a program of research, training and education at the undergraduate, graduate, and post-doctoral levels, as well as education for the general public.

Results from LTER I have transformed our understanding of forest response to disturbance and have emphasized the importance of integrated studies across ecological scales and disciplinary boundaries. In particular, our results document that temperate forest structure and function must be interpreted in the context of past disturbance, particularly land-use. Consequently, in LTER II our research is integrated in the study of legacies of human land-use on modern forest processes and the extension of results from mechanistic and empirical studies to a regional scale. We will continue our keystone long-term experiments and measurements with our focus on the five LTER core areas. We will initiate studies to: (1) strengthen the temporal and spatial context of the research; (2) evaluate mechanisms underlying population response to disturbance and broad-scale patterns of species distribution; (3) assess human-induced alteration of ecosystem function, especially C and N dynamics; (4) evaluate controls on C exchange at leaf to stand levels; and (5) synthesize our work across scales through continued modeling, inter-site, and comparative studies.

A. OVERVIEW AND RESULTS FROM PRIOR RESEARCH

Harvard Forest LTER I focused on the comparative analysis of temperate forest ecosystem response to human disturbance (atmospheric deposition and climate change) and natural disturbance (wind damage). The research has been structured in five parts: (1) retrospective studies of long-term changes in forest composition, disturbance processes, and environment; (2) studies and long-term measurements of forest structure and process that assess current forest condition and basic ecosystem functions; (3) experimental manipulations to evaluate the range of ecosystem responses to disturbance under closely controlled or replicated conditions; (4) modeling studies that synthesize our understanding of ecosystem dynamics and expand our results in time or space; and (5) comparative cross-site studies in which similar measurements, models, or experiments are used to generalize and broaden the context for our work.

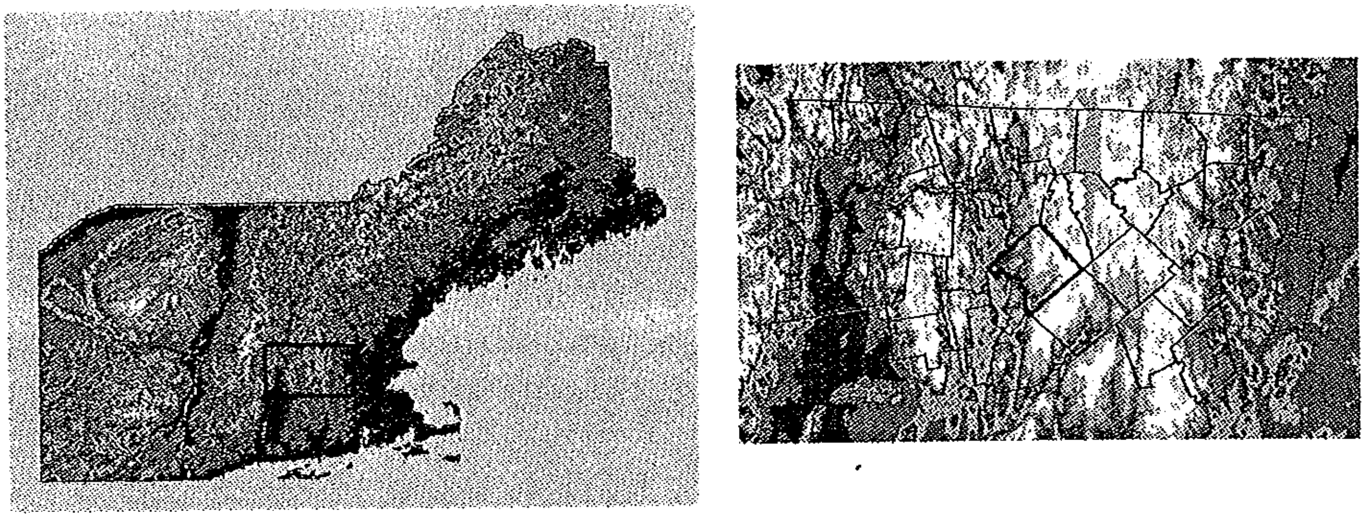
Using this research structure we have established a set of long-term experiments and measurements that integrate the central theme of our program and the five LTER core areas (Table 1). Through comparative studies of key processes at several scales we have provided cross-checks and validations of many measurements. Results have been integrated into simple, data-based models of ecosystem function and disturbance regimes, and extrapolated over different spatial scales using GIS and remote sensing (Figs. 1 and 2).

A.1. Retrospective Studies

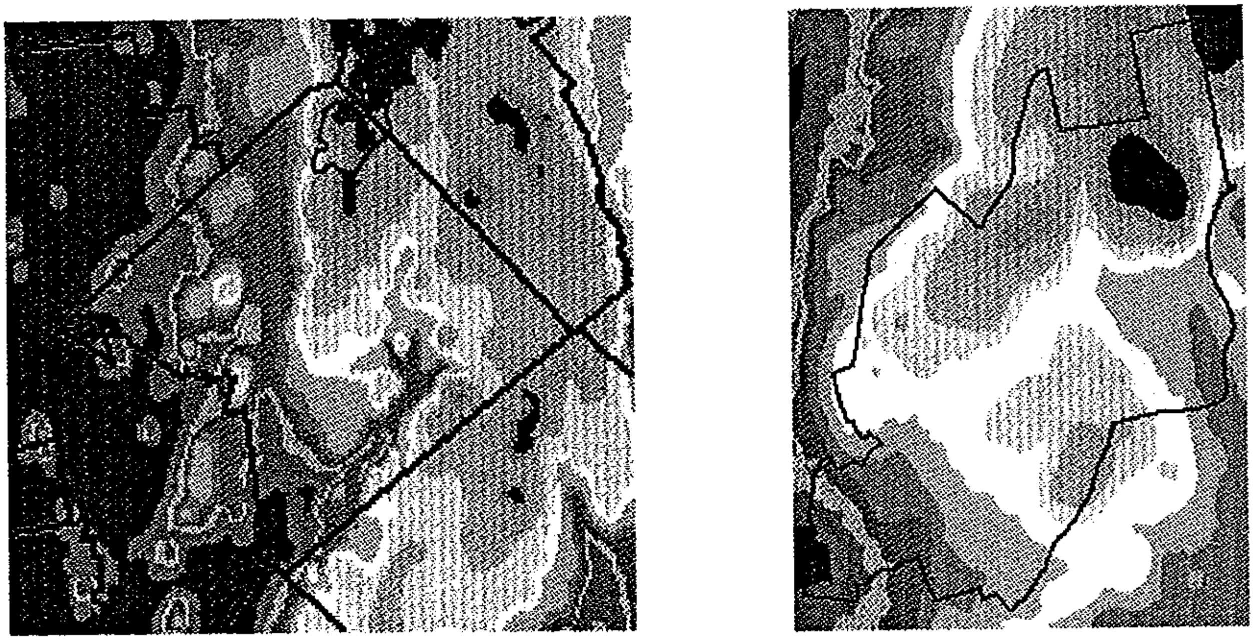
Retrospective studies evaluate ecosystem response to disturbance and provide a long-term perspective on the frequency of important processes and the development of modern forest ecosystems (Foster *et al.* 1990).

A.1.a. *Paleoecology and Historical Ecology* - We have assessed vegetation dynamics and disturbance at different spatial and temporal scales by combining fine-resolution pollen analysis of forest soils and lake sediments with historical analyses (Schoonmaker and Foster 1990). Objectives included characterizing regional forest response to climate change, landscape-level responses to human disturbance, and stand dynamics. These studies revealed contrasting patterns of forest dynamics at different scales. Regionally, composition has remained relatively stable over the past 5000 years; changes involved subtle shifts in species abundance resulting from climate cooling since 2000 BP (Fig. 3). Within forest stands, major species fluctuations resulted from windthrow, fire, and pathogens; vegetation response varied greatly with disturbance type and species composition. European settlement initiated the most dramatic vegetation change during the past 5000 years. Deforestation and agriculture transformed forest structure, composition and distribution; subsequent reforestation upon agricultural decline and the introduction of new pathogens produced a forest with no prior analogue (Fig. 4). These results indicate: (1) that recent human disturbance contrasts quantitatively and qualitatively with pre-European and historical disturbances and (2) that prior human activity strongly influences modern forest structure and dynamics.

A.1.b. *Hurricane Reconstruction* - Severe hurricanes impact New England forests every 100-150 years and have been shown to control forest ecosystem process and structure (Foster and Boose 1992). We developed an integrative approach for studying the patterns of hurricane damage on a range of spatial scales: (1) a meteorological model (HURRECON) that reconstructs site-specific wind



(a) New England (b) North Central Massachusetts



(c) Petersham township (d) Prospect Hill tract

Scale	REGION	SUBREGION	LANDSCAPE	SITE
Primary study area	New England	N.C. Mass.	Petersham	Prospect Hill
Approximate size	1000 km	100 km	10 km	1 km
Elevation range	0-1870 m	30-610 m	190-420 m	280-425 m

FIG. 1. Spatial scales of prior and proposed research. Maps show elevation of primary study areas at each scale. See Appendix 5 for more details.

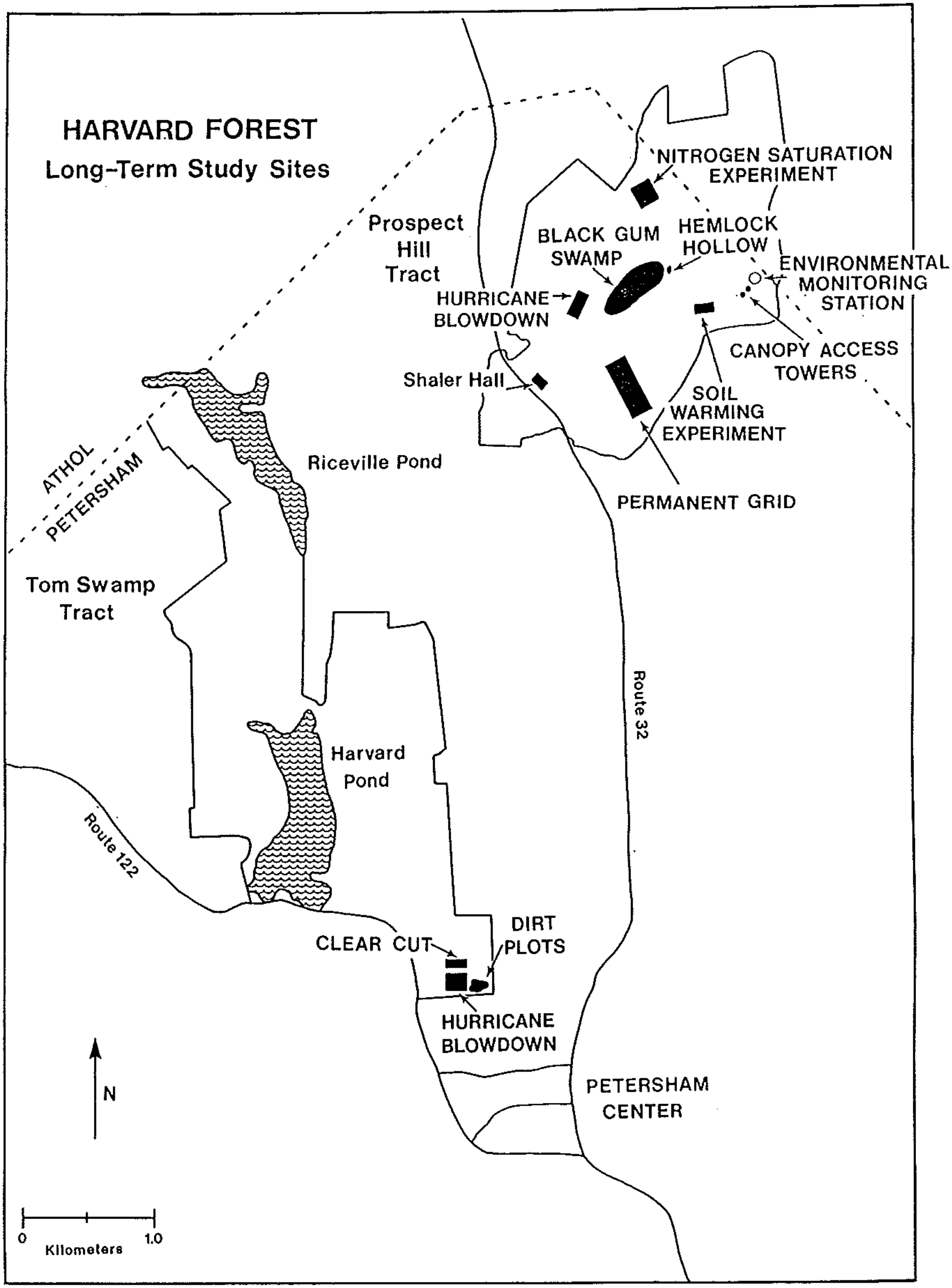


Fig. 2. Major study sites at the Harvard Forest in the north central part of Petersham, Massachusetts.

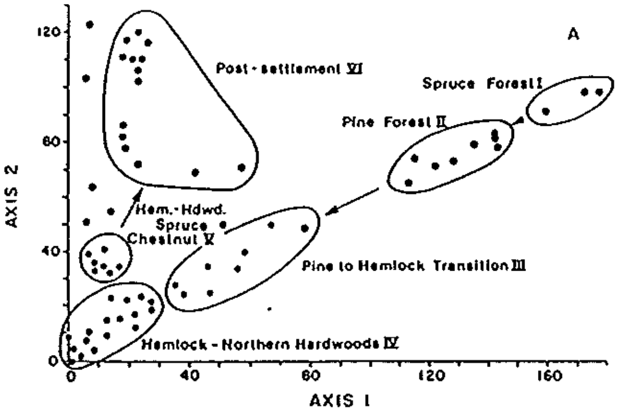


Fig. 3a. The post-glacial history of the vegetation of the hemlock stand in the center of the Prospect Hill Tract as depicted through Detrended Correspondence Analysis of the pollen data. Progressive change in vegetation from 10,000 to 5000 B.P. resulted in the eventual formation of a hemlock-northern hardwood forest. Climate change and the arrival of chestnut resulted in slight changes ca. 3000 B.P. The diagram indicates that the vegetation composition has changed rather continuously during the Holocene and that the major change in the last 5000 years was induced by broad-scale land-use activity by European settlers. From Foster and Zebryk (1993).

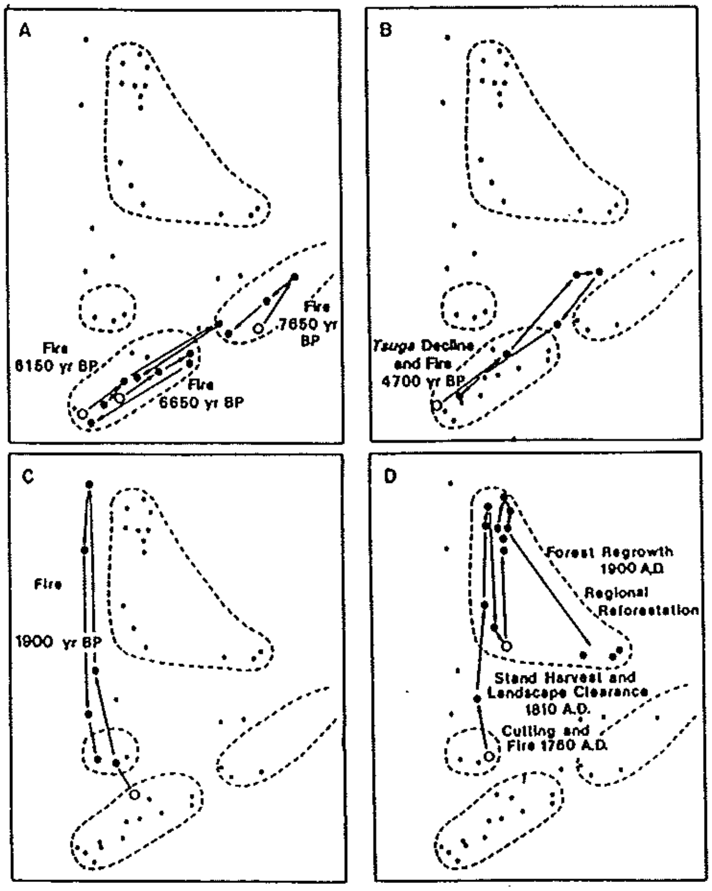


Fig. 3b. Detail of the DCA diagram above depicting the considerable short-term dynamics of the vegetation in relationship to disturbances, including fire, pathogens, and land-use. The vegetation dynamics associated with each disturbance are indicated by arrows that connect temporally contiguous pollen samples. Sample movements reflect changes in vegetation composition following disturbance. In each case, except following recent land-use activity, the vegetation returns to approximately its pre-disturbance composition following a period of 500-1000 years. From Foster and Zebryk (1993).

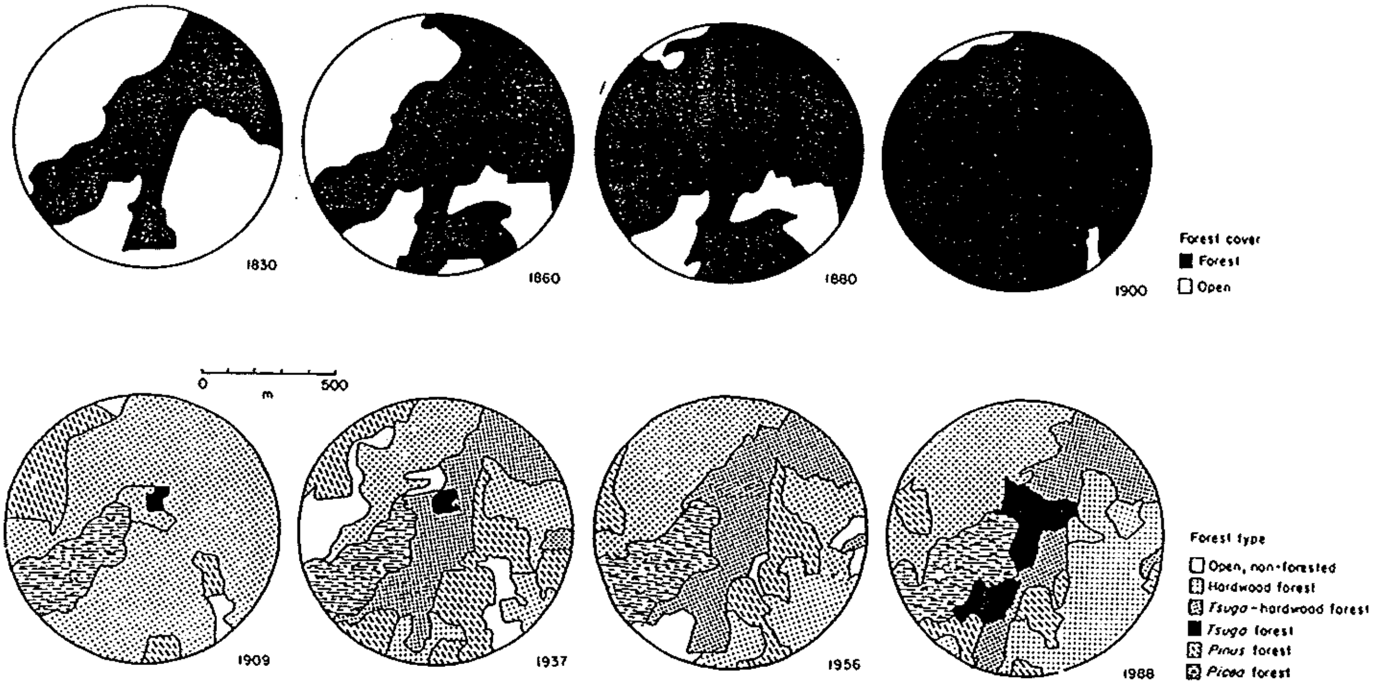


Fig. 4a. Forest cover and type changes on the central part of the Prospect Hill tract from the height of agricultural clearing (1830 A.D.) to the present. During the mid 19th C, open land was either pasture or tilled fields, and forests included swamp areas and coppice woodlots that were repeatedly cut for firewood. Abandonment of agricultural land led to a progressive increase in forest cover through the early 20th C. Forest dynamics during the present century has involved the growth of sprout hardwoods and early successional stands of gray birch and red maple, the demise of chestnut in 1913, and a progressive increase in hemlock as the forests have aged. From Foster *et al.* 1992.

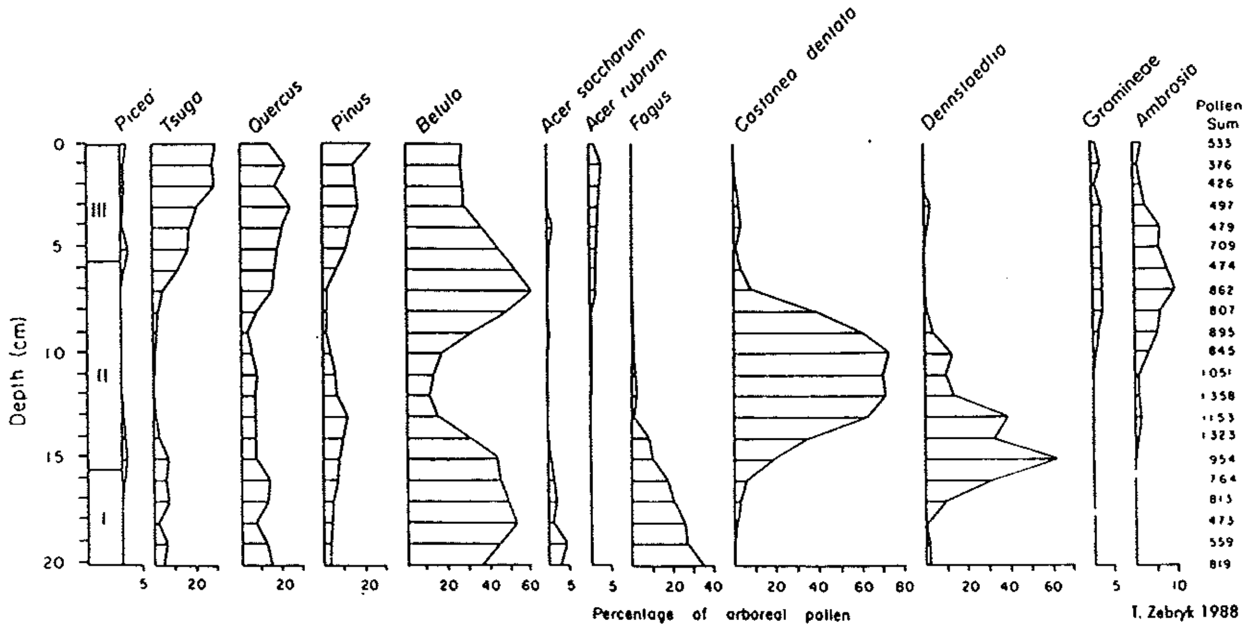


Fig. 4b. Pollen diagram depicting the major compositional changes since the 17th C of a hemlock stand located in the center of the Prospect Hill tract (the center of the 500-m radius figure above). Repeated cutting starting in the mid 18th C, resulted in a dramatic change in composition and an increase in chestnut (Castanea) through the early 20th C. The modern forest of hemlock, pine, oak, birch and red maple is unlike any that has occupied the site during the past 400 years. From Foster *et al.* (1992).

Table 1a. Major experiments and projects in Harvard Forest LTER I and their relevance to important types of disturbance in the region.

DISTURBANCE TYPE:	Physical	Land-Use	Atmospheric Deposition	Climate Change
Retrospective Studies				
Paleoecology	*	*		*
Historical Ecology	*	*		
Hurricane Reconstruction	*			
Forest Structure and Process				
Forest Carbon Flux		*	*	*
Canopy Photosynthesis				*
Soil Organic Matter Dynamics	*			
Vegetation and Soil Surveys	*	*	*	
Experiments				
Nitrogen Saturation			*	
Soil Warming				*
Hurricane Simulation	*			
Modeling and Synthesis				
Experimental Remote Sensing		*	*	
PnET - carbon, water, N model			*	*
Northeastern U.S. GIS		*	*	*

Table 1b. Major experiments and projects in Harvard Forest LTER I and their relation to the five core LTER study areas.

LTER CORE AREA:	Primary Production	Population Dynamics	Organic Matter	Nutrient Cycling	Disturbance
Retrospective Studies					
Paleoecology	*	*	*		*
Historical Ecology	*	*			*
Hurricane Reconstruction		*			*
Forest Structure and Process					
Forest Carbon Flux	*		*	*	*
Canopy Photosynthesis	*		*	*	*
Soil Org. Matter Dynamics	*		*	*	*
Veg. and Soil Surveys	*	*	*	*	*
Experiments					
Nitrogen Saturation	*		*	*	*
Soil Warming		*	*	*	
Hurricane Simulation	*	*	*	*	*
Modeling and Synthesis					
Exper. Remote Sensing	*	*	*	*	*
PnET - C,H_2O, N Model	*		*	*	*
Northeastern U.S. GIS		*	*	*	*

conditions and regional gradients in wind speed and direction; (2) a topographic exposure model (EXPOS) that uses output from the HURRECON model and a digital elevation map to predict landscape-level exposure to wind; and (3) damage assessments from aerial photographs, archival records, and field measurements. This approach was tested in studies of two important hurricanes: the 1938 New England Hurricane and Hurricane Hugo in Puerto Rico (1989), storms of comparable magnitude in regions that differ greatly in climate, vegetation, and physiography. Model predictions were found to agree with actual damage patterns on spatial scales ranging from < 1 km to > 500 km (Fig. 5). Results from modeling of the 1938 Hurricane are being applied to studies of forest ecosystem carbon flux, vegetation dynamics, and cross-site comparisons. This approach is currently being used to determine regional gradients of hurricane disturbance and to assess interactions with other disturbances such as land-use (Boose *et al.* 1994, Foster and Boose 1994).

A.2. Forest Structure and Process

The evaluation of ecosystem response to disturbance requires accurate measurement of baseline conditions and significant ecosystem functions. Our investigations of forest structure and process have focused on fundamental ecosystem processes that are influenced by human and natural disturbances.

A.2.a. *Whole Forest CO_2 Flux* - The Environmental Measurement Station (EMS) was established to help define the influence of midlatitude forests on net ecosystem exchange (NEE) of CO_2, O_3, NO_y (total nitrogen oxides), isoprene, and other hydrocarbons as well as heat and momentum. The tower is instrumented to measure NEE by eddy correlation at an altitude of 30 m (6 m above the canopy). The focus of research has been to determine net carbon (C) storage for periods ranging from 1 hour to 3 years, to define the biological and physical factors that regulate net storage, and to study the fixed nitrogen cycle by measuring fluxes across the atmosphere-forest interface.

Net C uptake (1990-1991) was 3.2 Mg C ha^{-1} yr^{-1}, and gross production and ecosystem respiration were 11.1 and 7.9 Mg C ha^{-1} yr^{-1}, respectively (Fig. 6; Wofsy *et al.* 1993). The accumulation rate, higher than that typically assumed for similar forests in global carbon studies, reflects forest recovery from hurricanes and human land-use. Carbon storage is largest southwest of the tower in forests on former agricultural land and smallest to the northwest where the forest was used as a woodlot and never cleared. Analyses also indicate significant interannual differences in net C uptake due to variations in summer temperature and cloudiness. Comparison with results from canopy photosynthesis, forest dynamics, and land-use studies, as well as hurricane and ecosystem modeling, are enabling us to interpret the mechanisms of short- and long-term ecosystem exchange.

A.2.b. *Canopy Photosynthesis* - Canopy photosynthetic rates vary considerably due to species differences and vertical gradients of light, CO_2, and relative humidity. To evaluate this variation and to scale these measurements forest-wide, we have measured diurnal and seasonal courses of photosynthesis in the canopies of four species (utilizing two 25-m towers) and sampled leaf nitrogen, chlorophyll content, and specific weight in order to relate gas exchange to leaf biochemistry and physiology. Leaf-level data have been coupled with estimates of soil and stem respiration rates, scaled up, and compared to eddy correlation NEE estimates. Diurnal and seasonal patterns of canopy assimilation, estimated from leaf-level gas exchange, correspond

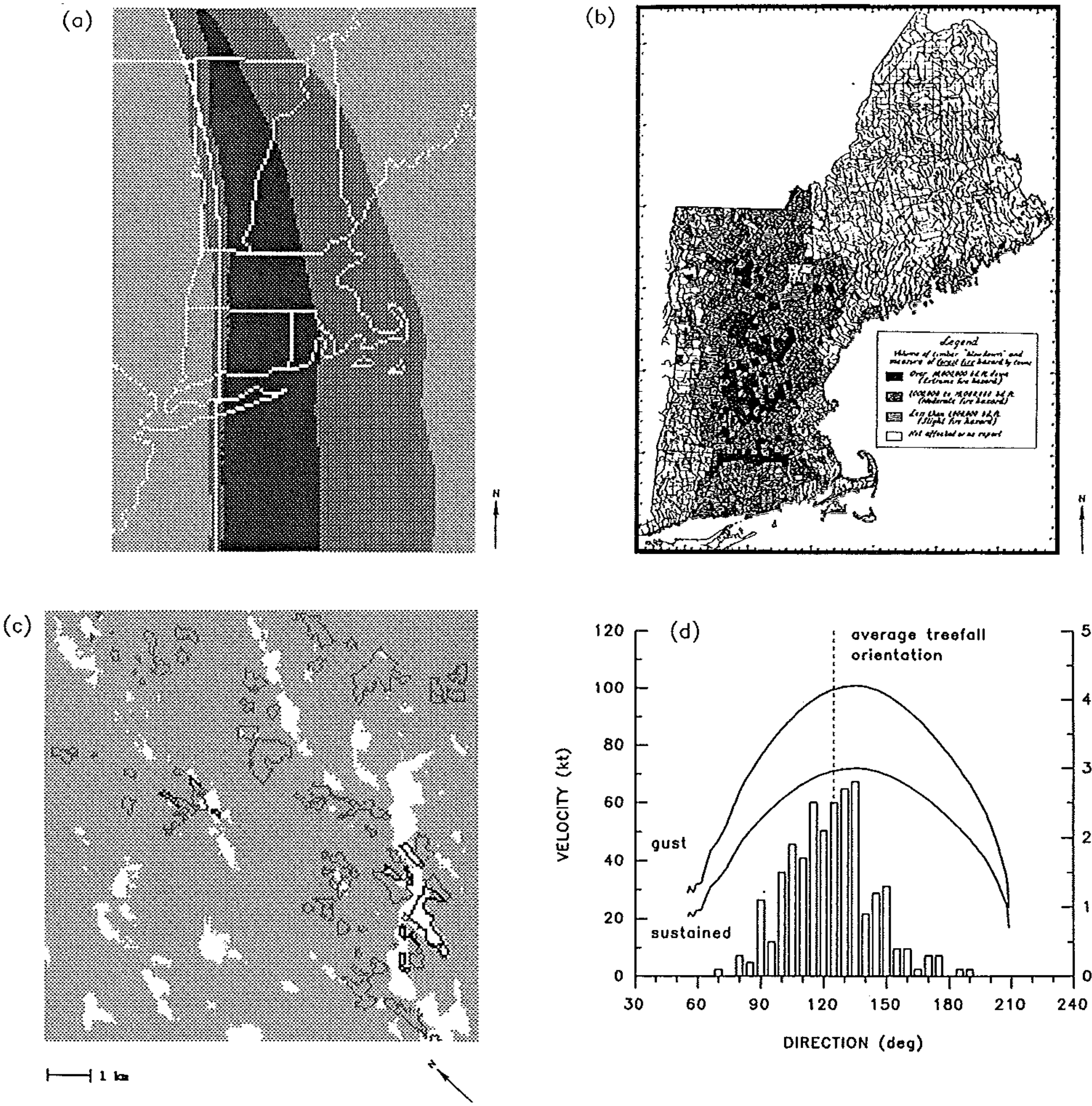


Fig. 5. Reconstruction of the 1938 Hurricane. (a) Regional prediction of peak wind gust velocity across New England using the HURRECON model. Light grey = 20-59 kt, medium grey = 60-79 kt, dark grey = 80-129 kt (1 kt = 0.514 m/s). (b) Volume of timber blown down on a town by town basis (1000 bd. ft. = 2.36 m^3; NETSA 1943), showing good agreement between predicted wind speed and actual forest damage. (c) Landscape-level exposure to peak winds across the town of Petersham using the EXPOS model (white = protected, grey = exposed), and actual damage to mature white pine stands. In general undamaged stands (black outline) were located in protected areas, while destroyed stands (grey outline) were located in exposed areas. (d) Site-level predicted wind conditions at the Harvard Forest using the HURRECON model (lines), and actual treefall orientation (bars; Rowlands 1941). There was good agreement between the predicted peak wind direction and the average treefall orientation. The analysis suggested that most trees fell during the approach of the storm (wind direction closer to east). From Boose *et al*. (1994).

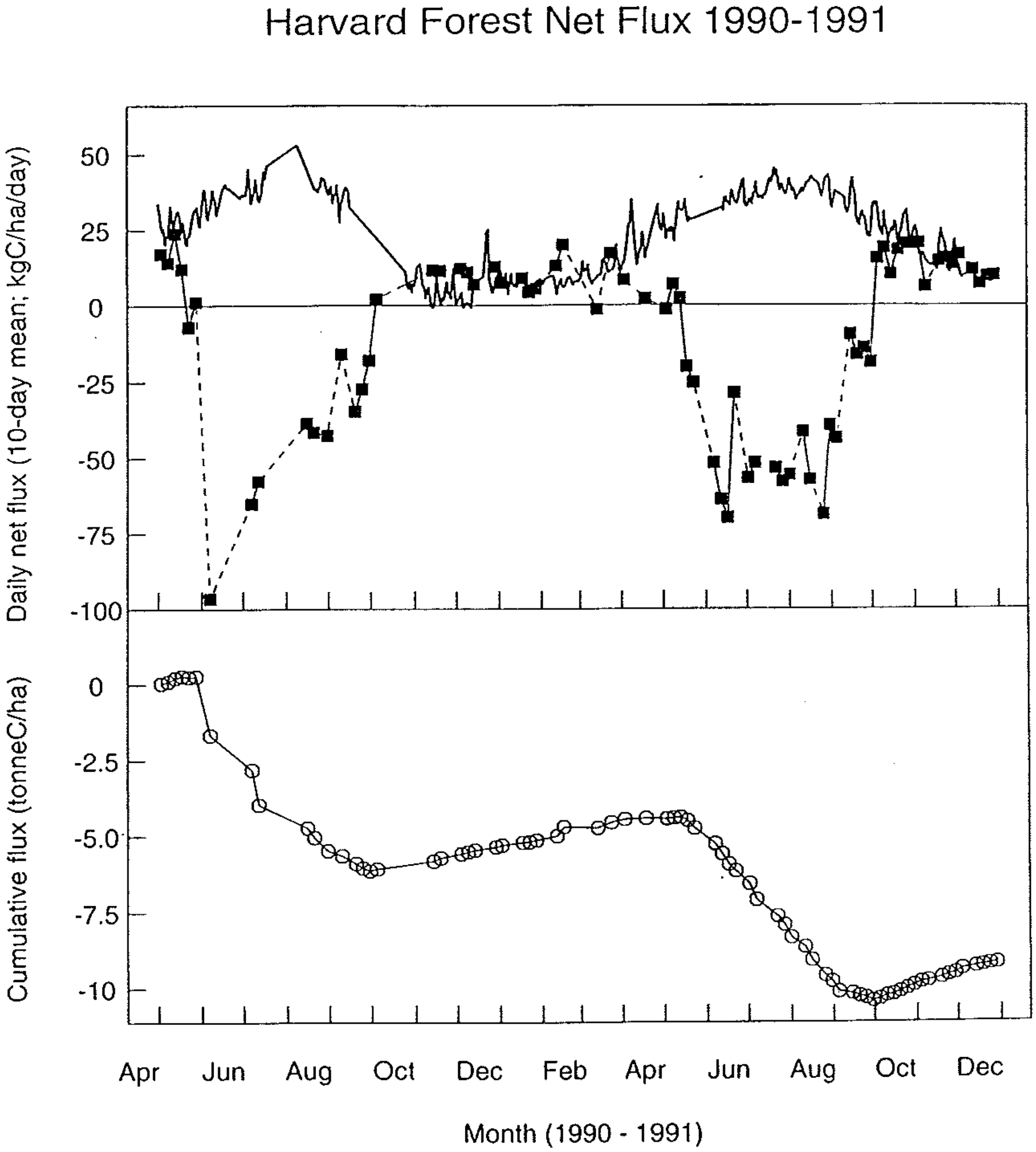


Fig. 6. (Top) Net ecosystem exchange (NEE) of CO_2 (averaged over 10-day periods ■) from April 1990 to December 1991. Broken lines indicate inadequate data for a 10-day interval. Daily values for ecosystem respiration are shown in the upper curve. (Bottom) Cumulative net CO_2 exchange, arbitrarily starting at zero on 1 April 1990.

closely with NEE estimates, suggesting that both methods provide reliable estimates of net photosynthetic uptake. Together with studies of soil organic matter dynamics these estimates of C assimilation are greatly refining our efforts to model ecosystem production and C dynamics across many spatial scales.

A.2.c. *Soil Organic Matter Dynamics* - Biological and physical controls on soil organic matter storage are being investigated by manipulating above- and belowground litter inputs to soils in a mixed hardwood stand. Treatments include 2x litter, no litter, no roots (trenched), no roots-no litter, and OA-less (one time replacement of organic and A horizons with B horizon soil). The OA-less treatment was implemented to track soil recovery after impoverishment. These treatments are implemented on a 1-ha area and are referred to as the long-term DIRT (Detritus Input and Removal Treatments) experiment. We have routinely measured key processes (soil respiration and nutrient leaching), surveyed site resources, and characterized baseline soil properties. Potentially mineralizable C and N (long-term laboratory incubations) and depth profiles for ^{13}C and ^{15}N contents were determined for all soils collected at the start of the study. Field-based soil respiration measurements have shown differences among treatments and permitted partitioning of total flux among root respiration and decomposition of root- and leaf-derived soil organic matter (Fig. 7). We are collaborating with other LTER sites to establish similar experiments along climatic and edaphic gradients in North America.

A.2.d. *Vegetation, Soils and Land-use* - The influence of past disturbances and variation in physical site conditions on modern vegetation composition and structure was investigated in an intensive survey of 269 plots (400 m^2) that were first sampled in 1937. Re-sampling after 55 years allowed us to assess the relative change in importance of historical factors with increasing time since agricultural abandonment. Modern forest composition and structure are strongly controlled by disturbance (prior land-use and hurricanes) and soil drainage (Foster 1992, 1993; Whitney and Foster 1988). Differential species response to historical disturbances is in part explained by variation in life history characteristics associated with reproduction and dispersal.

Ongoing studies to determine the influence of past land-use on modern soil characteristics are comparing N mineralization, organic matter quality and quantity, and cation distribution on plowed, pastured, and permanent woodlot sites. Data from this study are being incorporated into investigations of forest ecosystem C flux and soil organic matter dynamics. In addition, we have determined N and lignin content of the forest canopy at a 20-m scale using an aircraft-mounted AVIRIS (Advanced Visible Infrared Imaging Spectrometer) sensor. AVIRIS data have been used with the model PnET (see Modeling and Regionalization - Section A.4) to predict net ecosystem production (NEP; Fig. 8) and field-checked against vegetation data.

A.3. Experimental Manipulations

Experimental manipulations provide an evaluation of ecosystem dynamics and critical processes under controlled or replicated conditions. In our LTER research they enable the investigation of infrequent, slow, or anticipated disturbance processes using similar measurements and technologies.

A.3.a. *Nitrogen Saturation* - Chronic atmospheric N deposition represents a

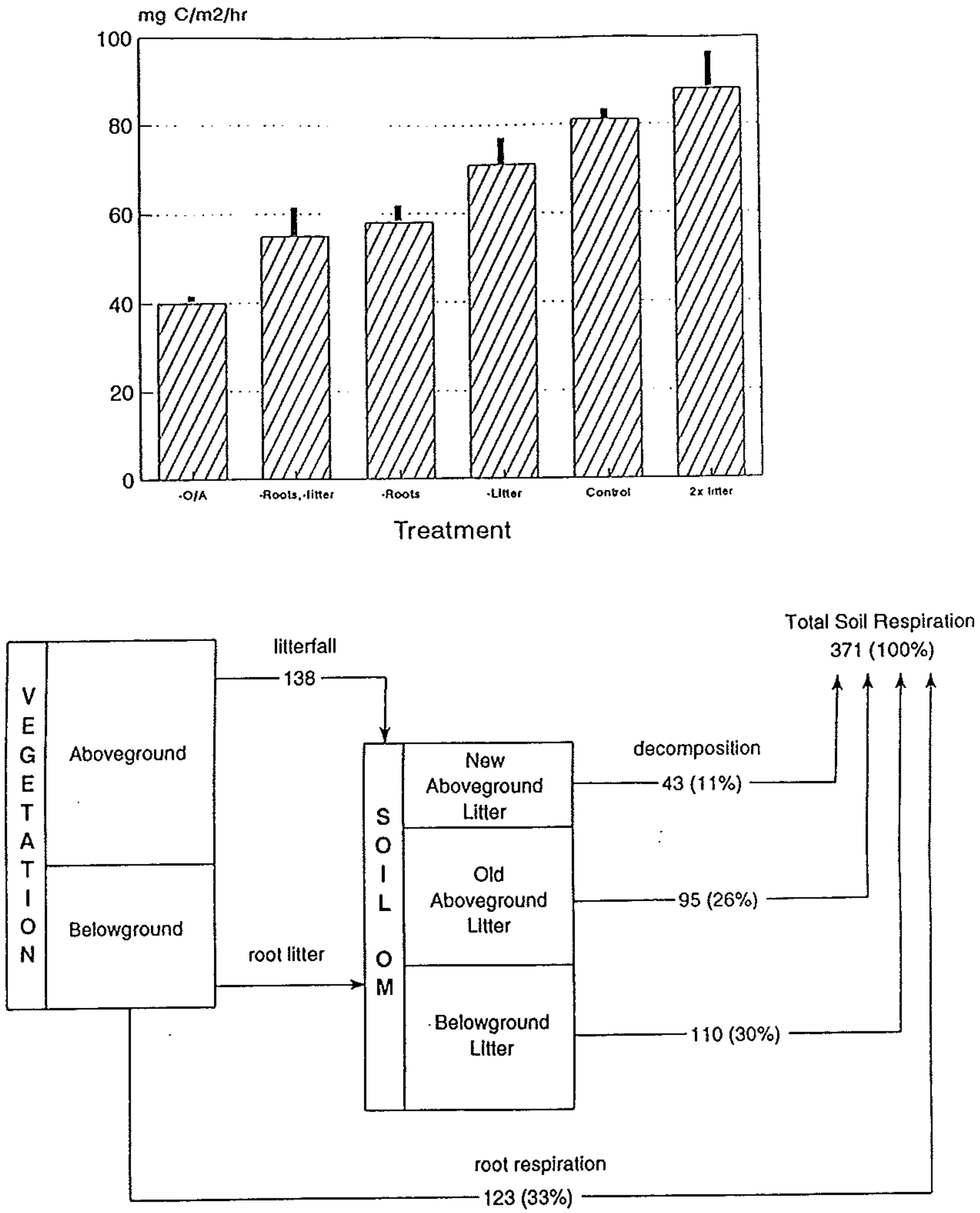


Fig. 7. (Top) Mean soil CO_2 flux (+SE) from the DIRT plots during the 1991 study period (-O/A:July-August, all other plots: June-August). (Bottom) Soil respiration budget for the DIRT study site. Numbers are flux rates (g C m^{-2} yr^{-1}) and percentages (in parentheses) of total soil respiration for each component. From Bowden et al. 1993b.

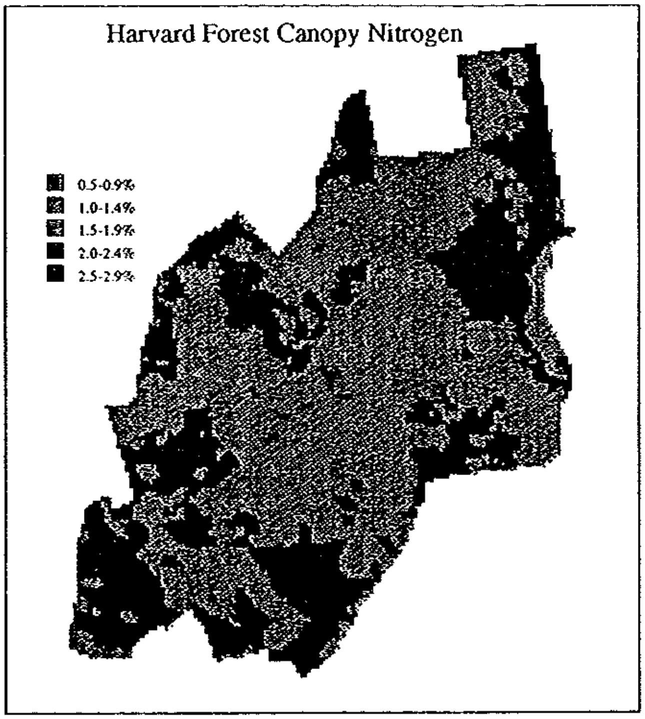


Figure 8a . Distribution of mean foliar canopy nitrogen for the Prospect Hill tract, Harvard Forest. Values derived from AVIRIS data using 20 field calibration sites. Standard error is ± 0.16% N. Values of 1.4% and below represent conifer plantations and a large spruce dominated wetland in the center of the tract.

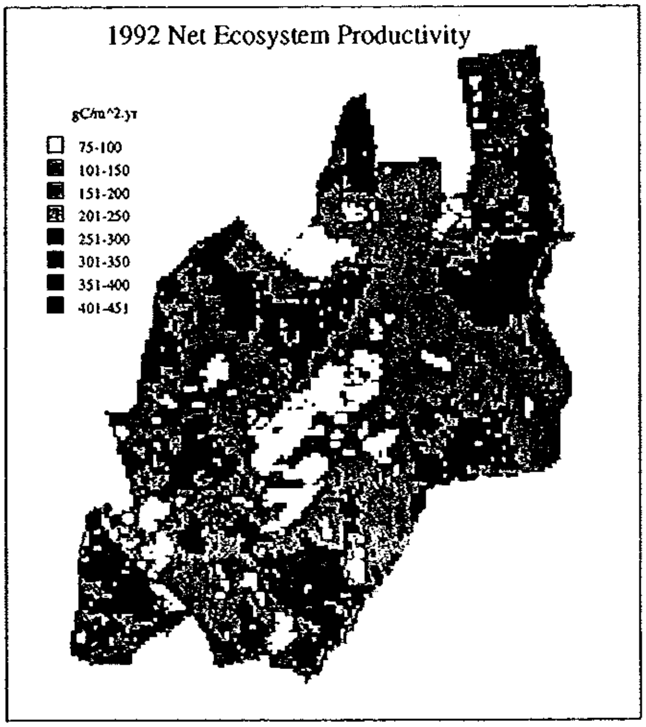


Figure 8b . Estimated net ecosystem production for the Prospect Hill tract, Harvard Forest. Values calculated by PnET model using foliar nitrogen values derived from AVIRIS data.

recent disturbance to New England forests. The long-term response of N-limited forests to this novel disturbance was investigated on two stands (red pine and mixed hardwood) given fertilizer N applications (50 kg ha^{-1} yr^{-1} and 150 kg N ha^{-1} yr^{-1}) for the last six years (Aber *et al.* 1989, Aber 1992). The fertilization levels are one and three times the current atmospheric N deposition in central Europe. We hypothesized rapid increases in foliar N and NPP, a gradual increase in N mineralization and nitrification, and, subsequently, increases in N_2O efflux and nitrate leaching. Measured field processes include net N mineralization, net nitrification, N leaching, litter fall, aboveground NPP, fine-root turnover, foliar chemistry, and soil fluxes of CH_4, N_2O, and CO_2. In 1991 and 1992 we added ^{15}N-labeled ammonium and nitrate separately to half of each control and low N plot to follow the movements of added N into soil and vegetation.

Major findings are: (1) N additions reduced forest-floor CH_4 consumption by 50% (Fig. 9; Steudler *et al.* 1989); (2) approximately 100% of added N was retained by the stands over the first 3 years, with most in soil organic matter; and (3) net N mineralization increased, apparently due to mineralization of previously immobilized fertilizer N (Table 2). The results have stimulated interest in the role of N deposition in the global methane cycle, and have led to new studies on DOC and DON and the effects of N additions on litter decomposition and N immobilization.

A.3.b. *Soil Warming* - Models of climate change predict a global mean temperature increase of 3°C during the next century (Houghton *et al.* 1992). The soil warming experiment assesses forest response to warming with an emphasis on soil processes (decomposition, trace gas fluxes) that could alter ecosystem function, atmospheric chemistry, and global climate. Treatments are: (1) soil temperature raised 5°C above ambient with heated cables; (2) soils with cables but no heating (disturbance control); and (3) control plots. Fluxes of soil gases (CO_2, CH_4 and N_2O) and N availability have been measured monthly since initiation of the project in 1991 (Peterjohn *et al.* 1993).

During the first year, heating doubled CO_2 efflux and N mineralization; during the second year the N mineralization increase was sustained, but CO_2 efflux was raised only about 10% (Fig. 10). In both years soil warming increased methane oxidation 27-32% but had no effect on N_2O efflux, presumably because there is no nitrification. The difference in timing for the response of C and N mineralization to soil warming may reflect increased decomposition of two soil organic matter pools: (1) a small, active pool that has high C:N ratio and is readily depleted by warming and (2) a large, slower pool that has a lower C:N ratio, thus releasing less CO_2 per unit of material processed.

A.3.c. *Hurricane Simulation* - Despite considerable data on the physical impact of hurricanes little is known about biogeochemical, microenvironmental, and population-level impacts or the specific responses of plants to physical damage and altered environment. Two experimental blowdowns were designed to simulate the physical effects of hurricanes. Trees in a mature forest were randomly selected according to the species and size classes damaged in the 1938 Hurricane and were pulled down using a winch (Fig. 11). Measurements include: mapping of trees and microtopography, damage, establishment, growth, vegetative reproduction, soil fluxes of CH_4, N_2O, and CO_2, microenvironment (light, temperature, humidity, wind speed, soil temperature, soil moisture),and seedling growth and physiology (Table 3).

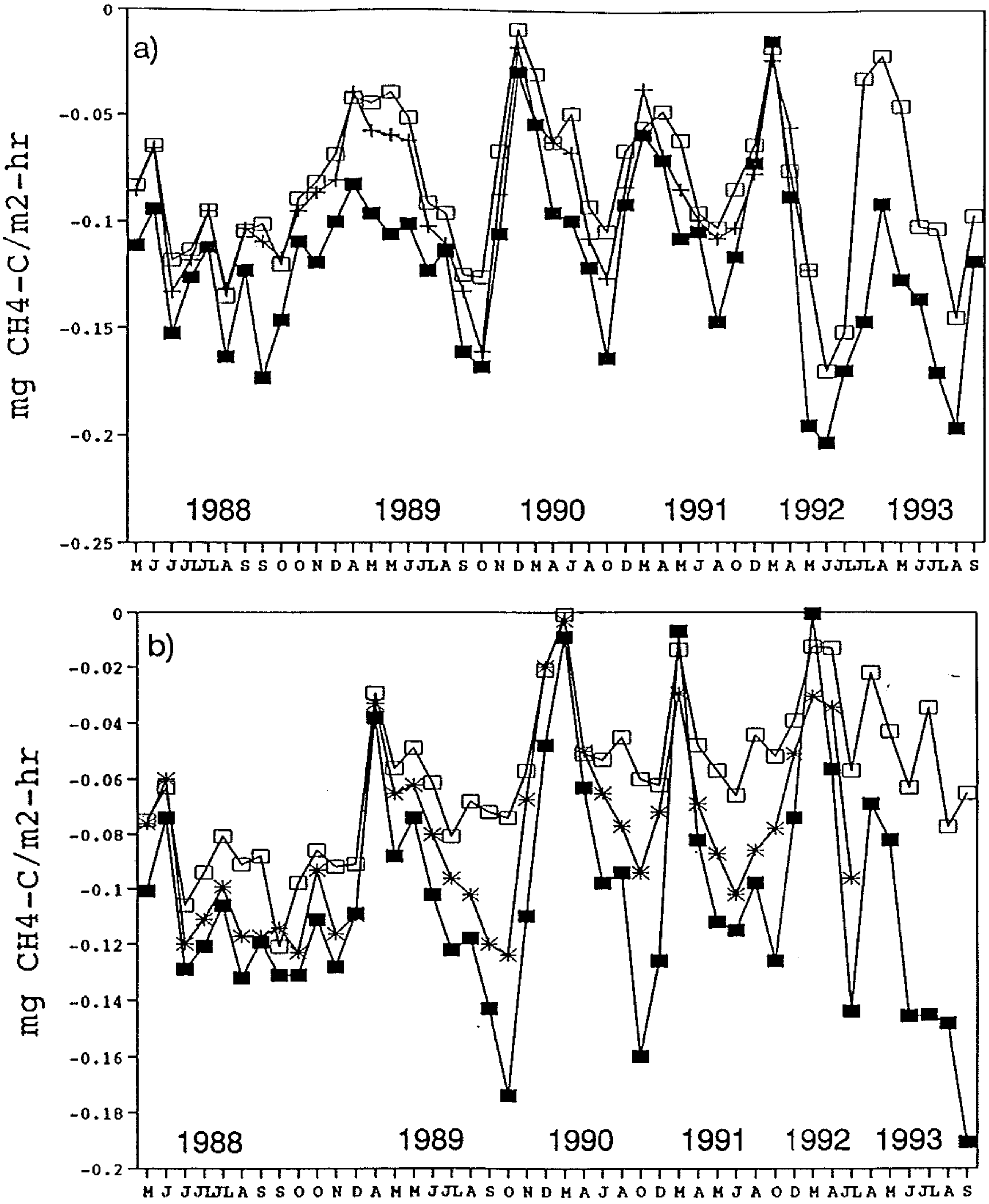


Fig. 9. Methane consumption by soils in a mixed hardwood (a) and red pine (b) stand in control (—■—), 50 kg N/ha-yr (—✳—) and 150 kg N/ha-yr (—⊟—) treatments.

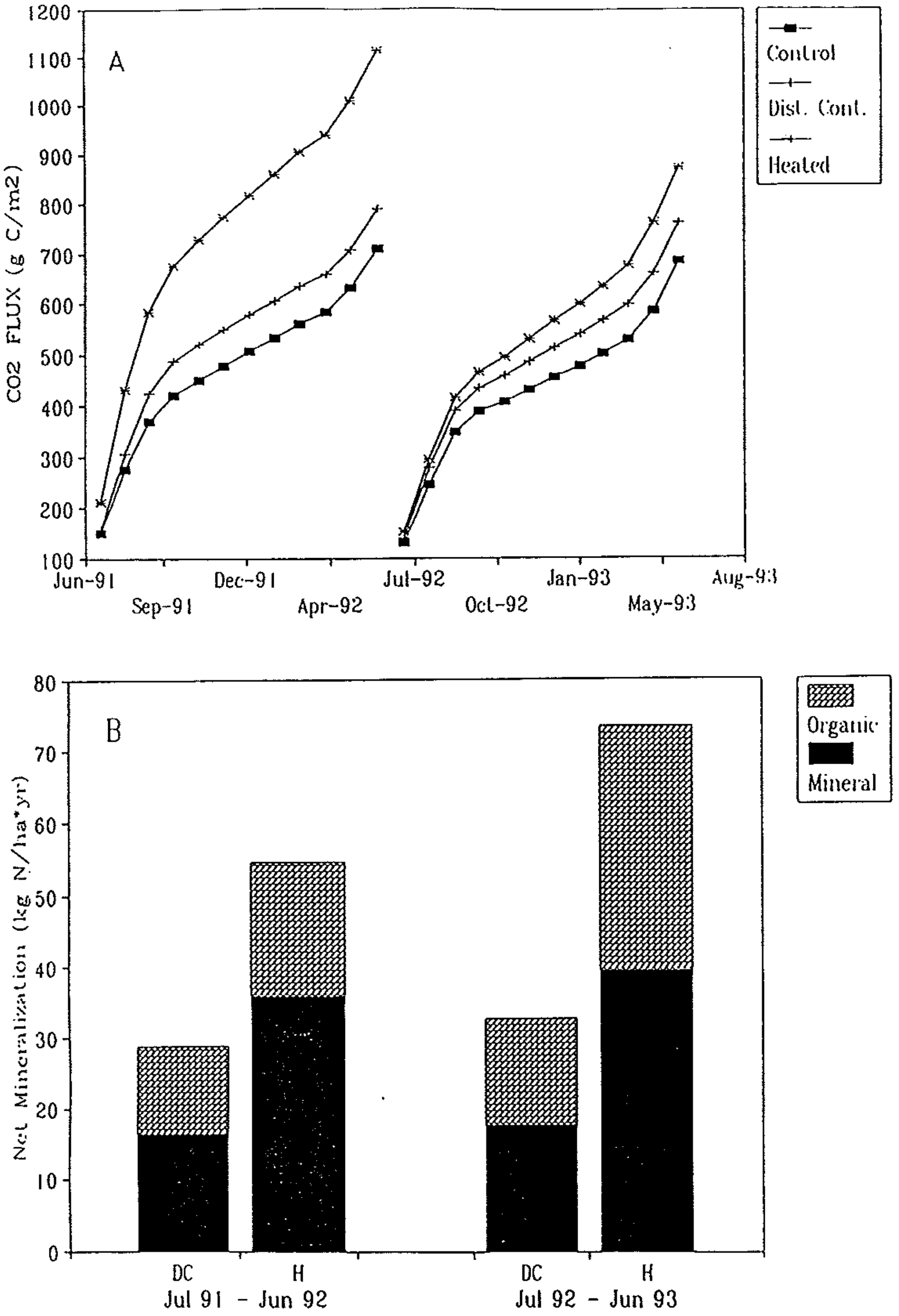


Fig. 10. A. Cumulative CO_2–C flux from the soil warming plots by treatment for 2 years. B. Total net nitrogen mineralization for two treatments (heated and disturbance control) for two years. Data are presented for both the organic horizon and upper 10 cm of the mineral soils.

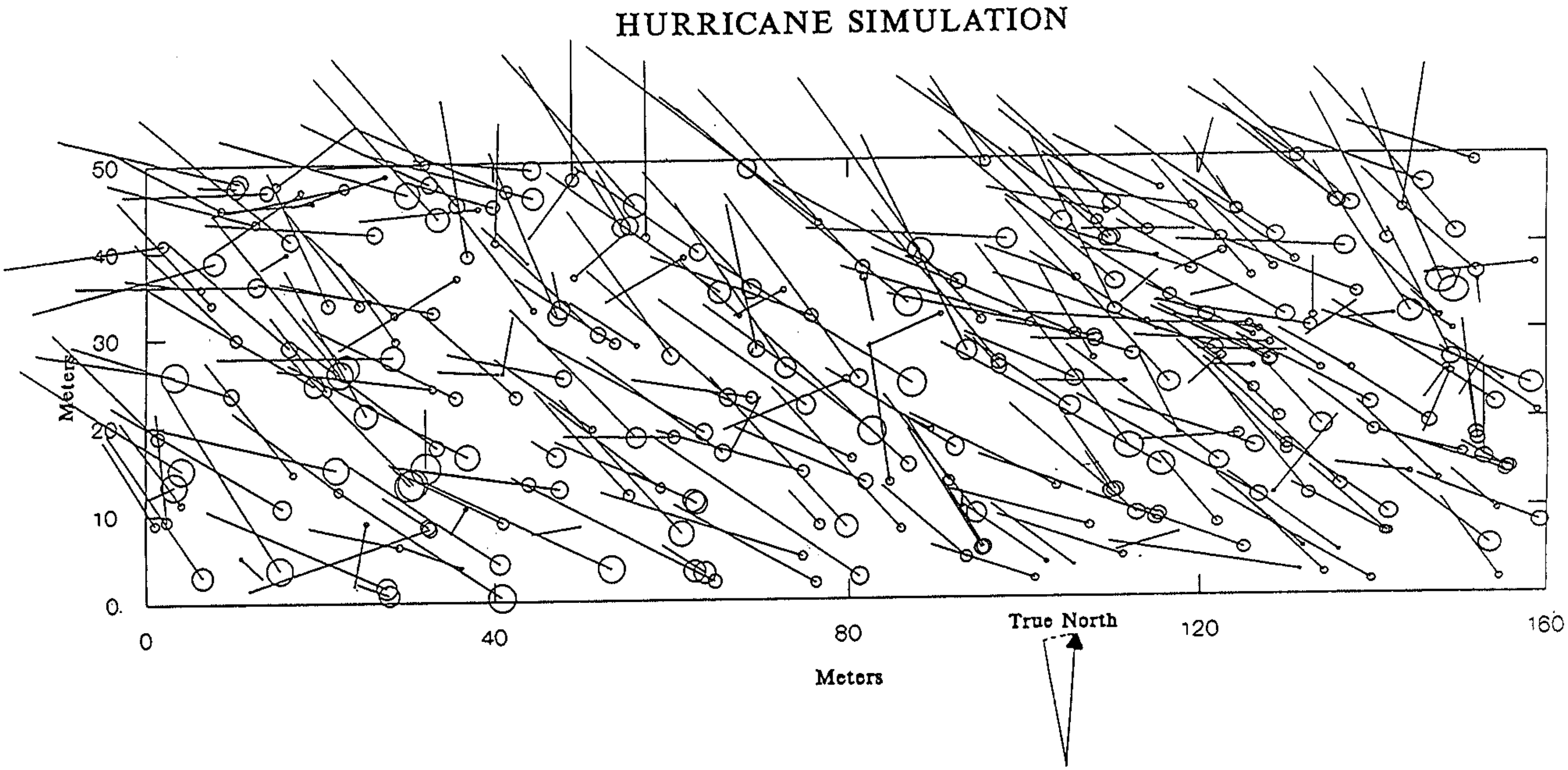


Fig. 11. Map of the long-term hurricane simulation site (0.8 ha) showing orientation of uprooted trees, width of uproot mounds (diameter of circles), and length of boles (line length). Uprooting accounted for 50% of the damage resulting from the pulldown. More than 60% of the damaged trees (including bent, snapped and leaning stems) were indirectly damaged when trees fell on other trees or were uprooted with a large mound. Range of orientations closely parallel the orientations of stems uprooted in the 1938 hurricane (Foster 1988). Trees were located prior to the manipulation using a triangulation technique and mapped in a Geographic Information System. Understory and regeneration plot centers (see Table 3) are located in transects running 85.5 degrees true east at 12.5, 27.5, and 42.5 meters from the southern edge of the grid.

Table 2. Inputs, losses, retention and estimated distribution of added nitrogen over the first three years of nitrogen additions (all values in $g.m^{-2}.yr^{-1}$, from Aber *et al.* 1993b).

	STAND					
		PINE			HARDWOOD	
Treatment	Control	Low N	High N	Control	Low N	High N
N inputs						
atmos. deposition[1]	0.8	0.8	0.8	0.8	0.8	0.8
fertilization	0	13.8	41.3	0	13.8	41.3
Total	0.8	14.6	42.1	0.8	14.6	42.1
N losses						
gaseous	<.1	<.1	<.1	<.1	<.1	<.1
leaching[2]	<.1	<.1	2.2	<.1	<.1	<.1
Total	<.1	<.1	2.2	<.1	<.1	<.1
N retention						
(% of N inputs)	100	100	95	100	100	100
Distribution						
Change in extract. N	0	0.6	1.3	0	0.4	1.0
Woody Biomass	0.8	0.8	0.8	1.1	1.3	1.6
Foliage	0	2.6	3.2	0	0.1	0.9
Fine Roots[3]	-	-	-	-	-	-
Soil Organic Matter	0	10.5	34.5	-0.3	12.7	38.5
(% of total addition)	67	75	83	54	89	92
(by difference)						

[1] Estimated sum of wet plus dry deposition of nitrogen (NADP regional data and Ollinger *et al.* 1993).

[2] Leaching losses estimated as lysimeter concentrations times volume of water leaching below the rooting zone as calculated by a monthly water balance/ photosynthesis/ transpiration model (Aber *et al.* 1993a).

[3] We have assumed that total N in fine roots will not increase substantially due to fertilization. Increases in concentration which might occur would be offset by decreasing biomass.

Table 3. Measurements in simulated hurricanes (and controls) in LTER I (past) and LTER II (proposed).

MEASURMENT LTER I	LTER I	LTER II
Entire Population		
Tree diameter	X	X
Tree leafout/mortality	X	X
Tree sprouting	X	X
Mound/pit dimensions	X	
Tree fall orientation	X	
Sampled in 10 m^2 plots		
Shrub cover/height	X	X
Sapling density/height	X	X
Sapling diameter	X	X
Sprout density/height	X	X
Sprout diameter	X	X
Woody debris/microtopography	X	
Sapling physiology		X
Sampled in 1 m^2 plots		
Seedling growth, survival	X	X
Understory vegetation	X	X
Woody debris cover	X	
Substrate	X	X
Understory light levels	X	
Understory temperature	X	
Sampled in microsite plots (pit, rootplate, mound, mound-top, under fern, in open, intact understory)		
Vegetation cover/composition	X	X
Seedling growth, survival	X	X
Substrate	X	X
Overhanging cover	X	X
Microsite light levels	X	
Microsite temperature	X	
Soil Moisture, N content	X	
Seedling physiology	X	X
Treatment-level sampling		
Seed bank composition	X	
Seed input	X	
Leaf litter quality	X	
Air, deep soil, litter temperature	X	X
Light	X	X
Soil moisture	X	X
Trace gas fluxes (CH4, CO2, NOx)	X	X
N mineralization	X	X
Woody debris	X	X
Soil disturbance	X	
Photographs at permanent stations	X	X
Leaf Area Index		X

The experimental blowdowns have reshaped our interpretation of temperate forest response to disturbance (Foster and Boose 1994). We have established that: (1) the technique provides a close simulation of natural windthrow in terms of type and quantity of damage to trees and soils; (2) recovery of vegetation, microenvironment, and ecosystem processes is remarkably fast, primarily as a result of high survivorship and resprouting of damaged trees and rapid growth of understory plants (Fig. 12); (3) biogeochemical responses were minimal and rapidly resumed pre-disturbance levels (CO_2 and CH_4 emissions were not significantly different than the controls, N_2O emissions were reduced 78% for one year by the blowdown, and net N mineralization was not affected (Bowden *et al.* 1993a)); and (4) microenvironmental heterogeneity provided a wide array of resource levels (e.g., light quantity and quality, N availability, soil moisture, and CO_2 concentrations; Carlton 1993).

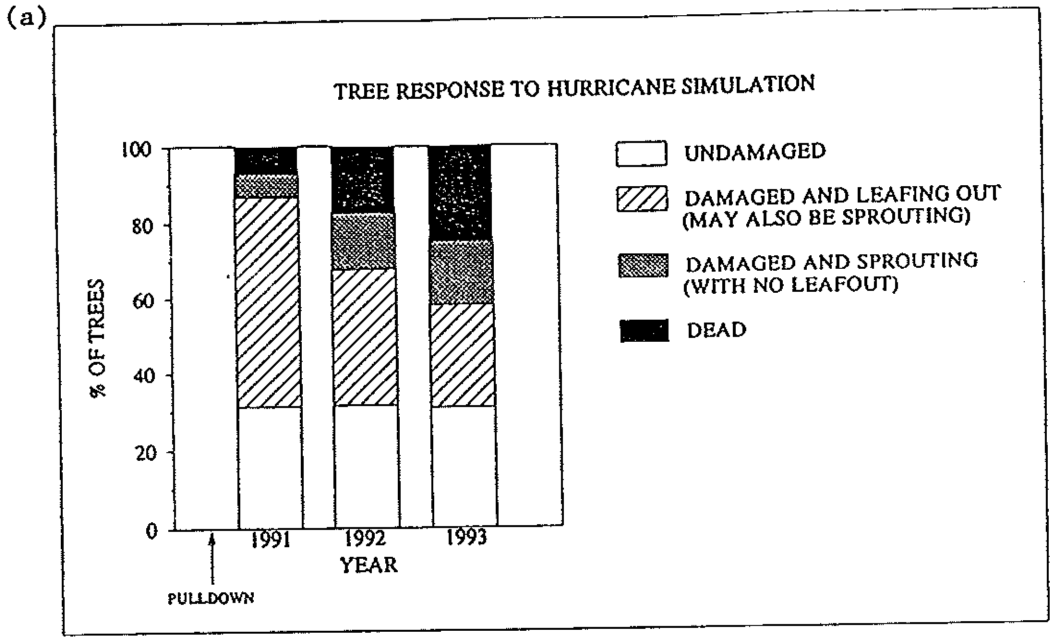
A.4. Modeling and Regionalization

Our unique data set on short-term (daily-to-annual) C balances at soil, leaf, stem, stand, and whole canopy scales enabled us to parameterize and validate a simple model of C and water balances (PnET). We use PnET to appraise the accuracy and consistency of results obtained from very different types of measurements. PnET has also been applied using as input the fine-scale GIS overlay (20-m scale) of canopy N concentration generated by AVIRIS. From this effort, we have been able to produce maps of NEP, which are currently being compared with eddy correlation data for validation.

Site studies provide a strong base for regional extrapolations of the effects of physical and chemical climate change on forest ecosystems. One effort, funded by EPA and the U.S. Forest Service, focuses on linking PnET to a GIS of the northeastern U.S. (Aber *et al.* 1993a; Fig. 13). Regional variation in physical climate and wet and dry element deposition are summarized in a series of multiple linear regression equations to provide the climatic drivers needed to run the regional PnET model (Ollinger *et al.* 1993, 1994). The model has been validated against data on carbon (NPP, NEP by eddy correlation), water (stream flow), and nitrogen (tissue concentrations, stream water concentrations) for both the Harvard Forest and Hubbard Brook LTER sites. Initial predictions focus on the effects of climate change on water yield, forest production, and net C storage. The long-term data available through these two LTER sites is absolutely critical for validation of model predictions.

A.5. Comparative Cross-site Studies

In order to evaluate the applicability of our LTER results to other regions, Harvard Forest has been involved actively in numerous intersite activities including: (1) the intersite litter decomposition experiment (LIDET); (2) modeling and landscape-level analysis to compare natural and human land-use disturbances at Luquillo, Andrews, and Harvard Forest; (3) comparison of trace gas fluxes following Hurricane Hugo at Luquillo and the hurricane simulation at Harvard Forest; and (4) application of the PnET model to both Hubbard Brook and Harvard Forest. Harvard Forest LTER personnel have also hosted LTER workshops to promote intersite work on litter decomposition (which led to the LIDET experiment), soil warming, remote sensing, and soil organic matter storage (DIRT).



(b) LEAFOUT FREQUENCY FOR DAMAGED TREES FOLLOWING HURRICANE SIMULATION

(c) BASAL SPROUT FREQUENCY FOR DAMAGED TREES FOLLOWING HURRICANE SIMULATION

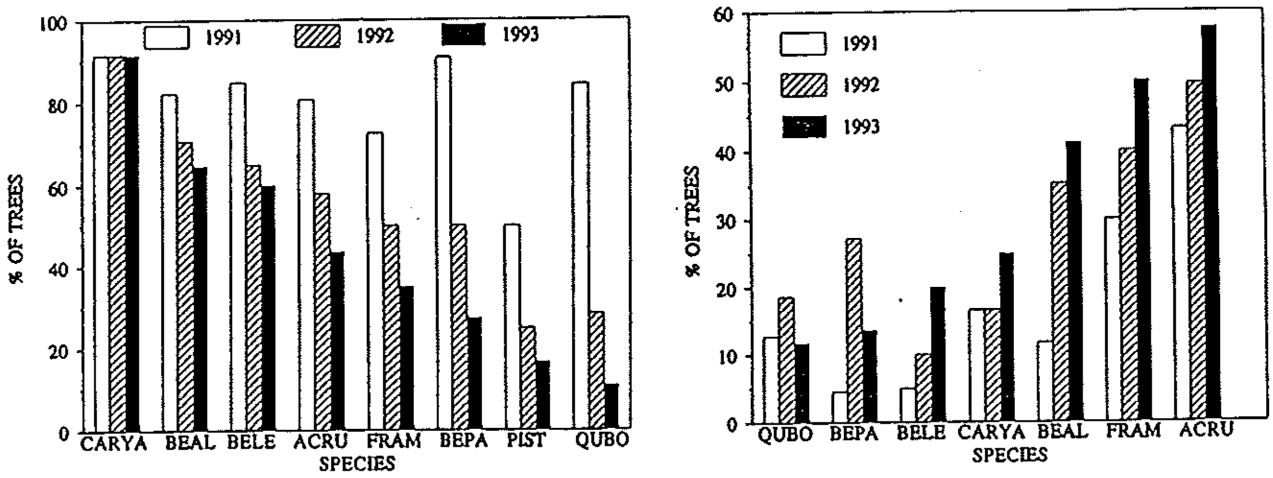


Fig. 12. Survival and response of trees following simulated hurricane. Initial survival and prolific sprouting of damaged trees may explain why C and N losses did not increase after catastrophic wind disturbance (Bowden et al., 1993). (a) Fate of 736 live trees in the 0.8 ha red oak-red maple forest after simulated hurricane. In 1991 >90% of the pulled or otherwise damaged trees were still alive (leafing out, sprouting, or both). During the next two years, many of the damaged trees died (no sprouting or leafing out), but a small fraction (16.44% in 1993) persisted through sprouting alone. (b) Leafing out of damaged trees (502 trees) showing differences among species in patterns of survival over time. Species acronyms are the first two letters of the genus name and the first two letters of the specific epithet. **CARYA** designates *Carya ovata* and *Carya glabra*. *Betula papyrifera* (**BEPA**) and *Quercus borealis* (**QUBO**) show the greatest mortality after the first growing season. (c) Percent of damaged stems (502 trees) that developed basal sprouts following experimental blowdown. Frequency of basal sprouting increased slightly for most species during the three-year period following the pulldown, but sprouting frequency of **BEPA** and **QUBO** decreased by the third growing season, a year after the drastic decline in leafout for these species. Preliminary analysis using logistic regression indicated that sprouting and leafout responses varied significantly by damage type, prior condition, and diameter. From Lezberg and Foster (1994).

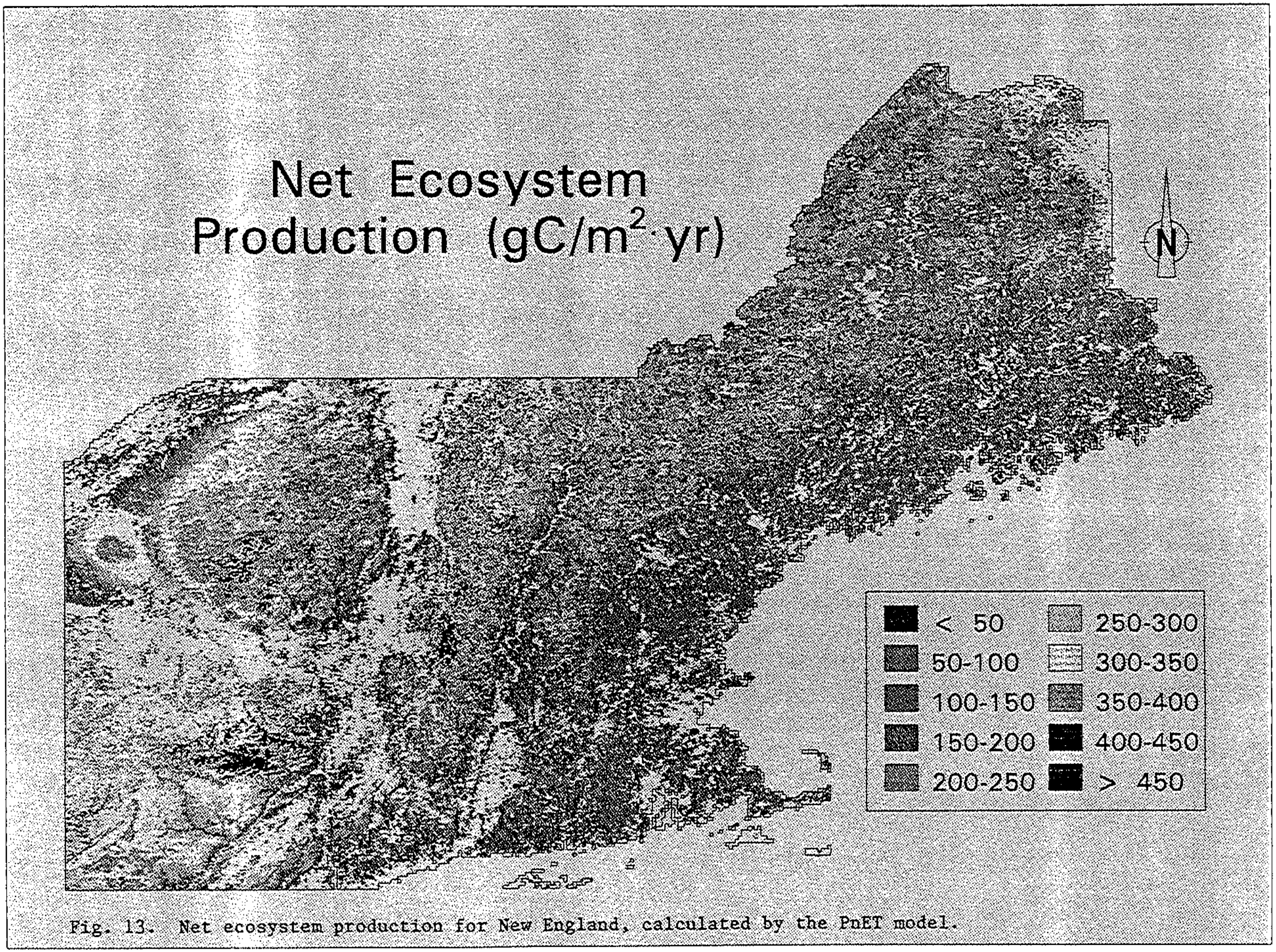


Fig. 13. Net ecosystem production for New England, calculated by the PnET model.

Table 4. Journal distribution of Harvard Forest LTER publications

Canadian Journal of Forest Research	10
Ecology	7
Journal of Ecology	6
Oecologia	5
Ecological Applications	4
Trends in Ecology and Evolution	4
Canadian Journal of Botany	3
Biogeochemistry	2
Journal of Geophysical Research	2
Nature	2
New Phytologist	2
Ambio	1
American Naturalist	1
Annual Review of Ecology and Systematics	1
BioScience	1
Botanical Review	1
Ecological Modelling	1
Ecological Monographs	1
Forest Ecology and Management	1
IAWA Bulletin	1
International Journal of Remote Sensing	1
Journal of Atmospheric Chemistry	1
Journal of Forestry	1
Journal of Soil Science Society of America	1
Plant and Soil	1
Science	1
Scientific American	1
Trees, Structure and Function	1
Books **	3
Book Chapters	12
Theses	11
Gray Literature	3
Total	93

** Whitney, G. 1993. *From Coastal Wilderness to Fruited Plain: an Ecological History of Northeastern United States*. Cambridge University Press.

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B. PROPOSED RESEARCH

The central theme of Harvard Forest LTER I was the comparative analysis of important disturbances to temperate forests, particularly wind disturbance and human-induced atmospheric deposition and climate change. Major experiments and long-term measurements were developed in order to: (1) document important ecosystem characteristics and processes and compare results obtained through different approaches or contrasting techniques; (2) evaluate the effects of human and natural disturbances on these ecosystem characteristics and processes; (3) develop a broad retrospective context for our long-term studies; (4) relate results from empirical, site-based investigations to broader spatial scales through modeling; and (5) evaluate the general applicability of our findings through extensive cross-site and network-wide studies.

Two major results emerge that unify our studies and direct the integration of our future research:

(1) We conclude that the legacy of past human land-use affects most aspects of modern ecosystem structure and process and greatly determines ecosystem response to modern disturbance and experimental manipulation. For example, the type of 19th Century land-use (i.e., whether tillage, pasture, or woodlot) and the timing of abandonment from agricultural use, appear to strongly influence: (i) the composition and structure of forests; (ii) the magnitude and spatial distribution of carbon (C) assimilation across the landscape; and (iii) the susceptibility and response of stands to hurricane damage. Based on this conclusion, our future work will incorporate a detailed knowledge of human disturbance and cultural history into our experiments, measurements, and modeling activities.

(2) We conclude that a comprehensive understanding of ecological processes and their application to current management concerns is obtained only through a thorough analysis of mechanisms, patterns, and responses across a range of spatial and temporal scales. Our initial results from studies of C assimilation highlight this conclusion. Analysis of leaf-level photosynthesis provides an understanding of the mechanistic basis for C assimilation and its relationship to leaf chemistry, CO_2 concentrations, and microenvironmental conditions and also provides one estimate (through scaling) of stand-level production. Comparison of this estimate with eddy correlation measurements of C flux and NEE at the stand level and with estimates based on simple C and water balance models of ecosystem productivity (PnET) enables us to evaluate and refine our understanding of the underlying controls and mechanisms. In turn, this understanding may be scaled up to the landscape and regional levels through modeling, coupled with remote sensing (AVIRIS) and GIS. Based on this conclusion our future work will integrate mechanistic studies (e.g., of physiology, population processes, and ecosystem processes) with observational measurements and broad-scale assessment and modeling. This approach will rely on our understanding of fundamental mechanisms to relate site-based observation to broad scale processes.

In LTER II we will integrate our projects through a common focus (i.e., the interdisciplinary analysis of human land-use legacies on ecosystem process and structure) and across scales. In terms of research structure we propose to continue our keystone long-term experiments and to initiate new retrospective, ecosystem, and modeling studies to ascertain the mechanisms by which human disturbances influence ecosystem function and structure. We will extend this research across four well-defined scales: the site, landscape, subregion, and region (Fig. 14). We will also begin to assess mechanisms by which ecosystem-level processes (e.g., wind disturbance, land-use) influence patterns of plant and animal distribution across the landscape (e.g., Fig. 15).

Specific objectives of the Harvard Forest LTER II include:

I. Strengthen the temporal and spatial context for the research through retrospective studies, field and remotely-sensed observations, and modeling. Contrast the pre-European dynamics and responses of forest ecosystems to disturbance with historical and modern responses to recent land-use, environmental change, and natural disturbance.

II. Evaluate mechanisms by which plant and animal populations respond to disturbance and environmental factors and utilize this information to interpret patterns of distribution at broader scales.

III. Experimentally assess human-induced alteration of ecosystem functioning, with particular emphasis on C and N. Extend past studies of chemical (e.g., N saturation) and climatic impacts (e.g., soil warming) to include physical impacts from land-use.

IV. Evaluate controls (land-use legacies, climate, vegetation, soils) on carbon exchange at the whole-stand level and biological and physical controls on soil organic matter storage.

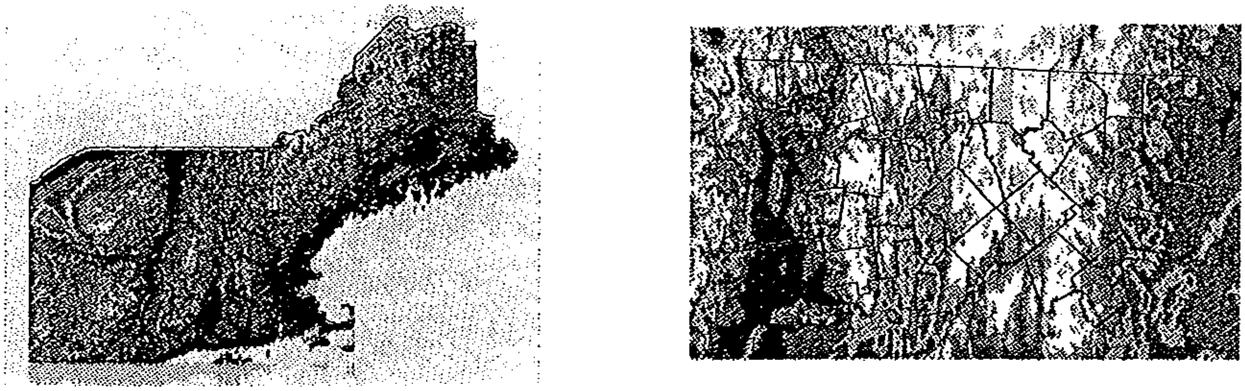
V. Synthesize I, II, III, and IV through the development of regional models that incorporate the results of empirical investigations.

B.1. Retrospective Studies

B.1.a. *Long-term Hurricane Disturbance Regimes*

Using the approach described in Section A.1.b we will reconstruct the meteorological and ecological characteristics of all hurricanes that have had a significant impact on New England forests over the last 400 years. Analysis of recent hurricanes (20th Century), where good meteorological and forest damage data are available, will enable us to test and refine our models and investigate the interaction of meteorological, physiographic, biotic, and historical factors in determining forest damage. Analysis of historical hurricanes (1600-1900) will provide a framework for generating estimates of long-term hurricane frequency and intensity (e.g., average return time for winds of a given velocity and direction). These estimates will be used to evaluate landscape-level disturbance regimes at Harvard Forest and regional disturbance gradients across New England. A parallel study will be conducted for the Luquillo LTER and the island of Puerto Rico in order to compare tropical and temperate hurricane disturbance regimes. The regional information generated by these studies will be directly applicable to other research sites (e.g., Hubbard Brook, Institute of Ecosystem Studies, LMER sites, Guanica Forest in Puerto Rico).

On a continental scale (~5000 km), there are significant meteorological differences between hurricanes in temperate and tropical latitudes. Tropical



(a) New England

(b) North Central Massachusetts

(c) Petersham township

(d) Prospect Hill tract

Scale	REGION	SUBREGION	LANDSCAPE	SITE
Primary study area	New England	N.C. Mass.	Petersham	Prospect Hill
Approximate size	1000 km	100 km	10 km	1 km
Elevation range	0-1870 m	30-610 m	190-420 m	280-425 m
Paleoecological				
Lake pollen	*	*	*	
Hollow & soil pollen				*
Historical				
Proprietors records		*	*	*
Vegetation maps		*	*	*
Decadal census data		*	*	
Deeds & histories				*
Hurricane reconstruction				
HURRECON model	*	*	*	*
EXPOS model		*	*	
Resource assessment				
Vegetation surveys		*	*	*
Soil surveys				*
Landsat TM	*	*	*	*
AVIRIS				*
EMS tower				*
Population dynamics				
Plant		*	*	*
Lepidoptera		*	*	*
Modeling & regionalization				
Climate model	*	*	*	
PnET model	*			*
CENTURY model				*
Experimental manipulations				*

FIG. 14. Spatial scales of prior and proposed research. Maps show elevation of primary study areas at each scale. See Appendix 5 for more details.

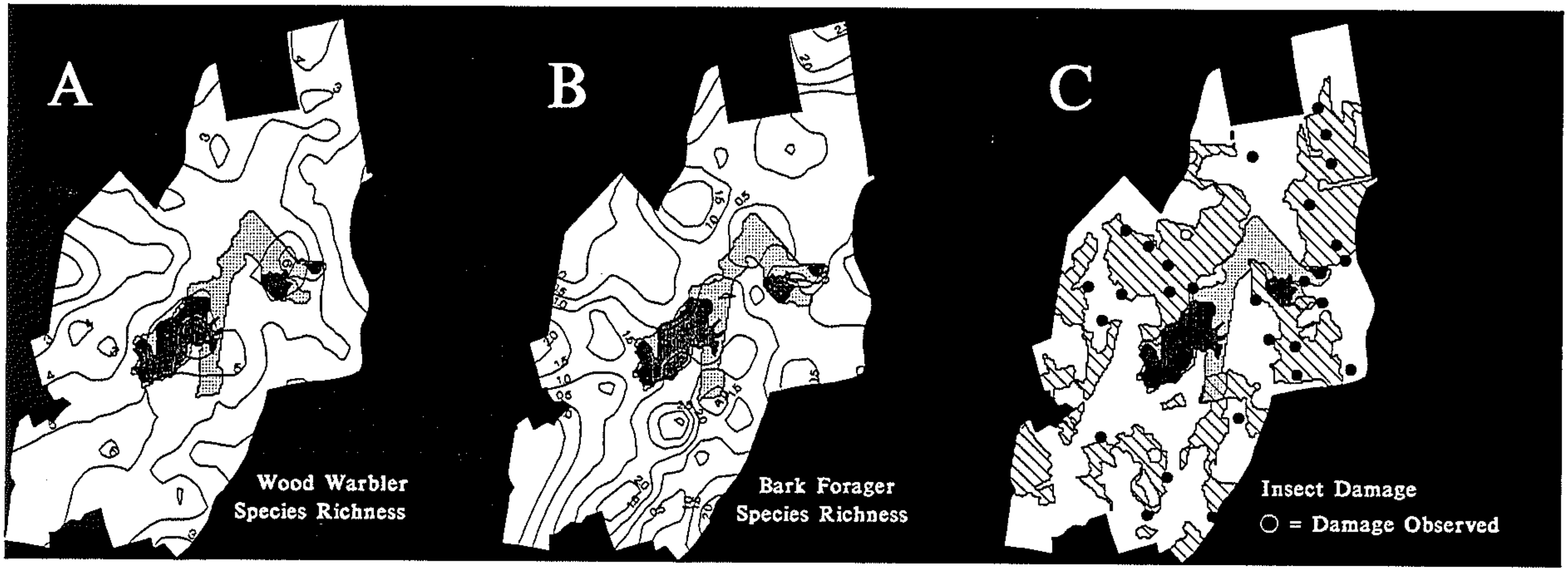


Fig. 15. Examples of animal studies recently initiated on the Prospect Hill tract of Harvard Forest to evaluate effects of disturbance and other environmental factors on populations. Maps show a central area of primary forest, historically maintained as woodlot (light stipple) and patches of forested wetland (darker stipple). Animal populations were surveyed on a grid system across the entire site. (A) Contour map showing variation in species richness of wood warblers, a guild of foliage-gleaning forest birds. (B) Species richness of bark-foraging birds. (C) Point observations of insect damage to tree foliage. Patchy distributions of animal populations and differing associations with land use and habitat are apparent. For example, maximum warbler diversity is centered on the forested wetlands, but bark forager diversity is not. Patches of insect damage (C) occur in deciduous stands of low to moderate basal area (crosshatched). Additional data layers, such as maps (Fig. 8a) of canopy nitrogen levels (that may indicate patches of high-quality forage for insect herbivores), will provide causal links to ecosystem-level processes that may drive observed patterns of animal distribution. Statistical analyses (e.g., path analysis) will separate the direct and indirect effects of land use history, current habitat, and other factors on animal populations in this system, and long-term data collection will permit assessment of temporal effects.

forests in hurricane-prone areas are often subject to more frequent, more intense, and longer-lasting hurricane disturbance than corresponding temperate forests. We will document these differences as they exist for New England and Puerto Rico.

On a regional scale (~1000 km), there are significant gradients of long-term hurricane frequency and intensity caused by the pattern of historical storm tracks and the weakening of hurricanes over land and especially over mountains. These gradients contribute to broad-scale differences in forest disturbance regimes. We will quantify these historical gradients across New England (southeast to northwest) and across Puerto Rico (east to west).

On a subregional (~100 km) to landscape (~10 km) scale, spatial patterns of forest damage are controlled by meteorological, physiographic, biotic, and historical factors. The combination of historical storm tracks and the location of coastlines and mountain ranges may limit the probable directions of the most damaging winds. In hilly or mountainous areas, limited wind directions combined with local topography may create local variation in long-term susceptibility to hurricane winds, possibly causing broad-scale differences in forest composition and structure. We will identify the probable range of catastrophic wind directions at each site (preliminary work: Harvard Forest = southeast quadrant, Luquillo = north quadrant) and evaluate spatial patterns of long-term hurricane susceptibility for each site. Results of this work will help to complete our knowledge of the disturbance history of the north central Massachusetts subregion (Fig. 16) and complement ongoing paleoecological, historical, community, and population studies.

The project will yield general computer models that may be utilized to study the effects of topography on wind direction and the relation of forest damage to wind speed and duration; to reconstruct historical hurricanes in other regions; and to explore future hurricane impacts on particular forests under different global change scenarios. In addition we will develop measures of hurricanes that reflect their ecological impact on forests (e.g., peak wind gust speed or total energy of sustained winds above a given velocity); such measures will facilitate comparisons of different storms. As our understanding of wind damage to forests improves, the models will be extended to predict forest damage as a function of storm meteorology, topographic exposure, and stand composition and structure, permitting us to model the effects of past land-use on hurricane damage and to scale up the results from the hurricane simulation experiment.

Funding for this project in LTER I was derived from the Harvard Forest and Luquillo LTER grants and the Harvard Forest endowment. Additional support is currently pending from the Ecosystem Studies program at NSF.

B.1.b. *Human Impacts and Broad-scale Forest Dynamics*

Disturbance studies have concentrated primarily on forest and landscape response to short-term, pulse-type disturbances including fire, windthrow, and logging. Few studies have addressed broad-scale and long-term processes such as regional deforestation and agriculture. Such research is critical due to the past and current pervasiveness of land-use in such contrasting environments as eastern North America, northwestern Europe, and Mesoamerica (Berglund 1991, Turner *et al.* 1990, Di Martino 1993, Butzer 1992).

Fig. 16. Predicted topographic exposure across the North Central Massachusetts subregion to east, southeast, and south winds using the EXPOS model. Black = protected from all 3 directions, intermediate greys = exposed to 1 or 2 directions, lightest grey = exposed to 3 directions. The spatial distribution of predicted protected areas varies considerably across this subregion, as a function of the underlying topography. The proposed reconstruction of historical hurricanes with the HURRECON model will identify the range of directions for catastrophic hurricane winds and the historical gradient of maximum wind speed across the subregion. Preliminary work suggests that peak hurricane winds come from the southeast quadrant, while hurricane frequency and intensity decrease slightly across the subregion from southeast to northwest. Results of this work will help to complete our knowledge of the disturbance history of the subregion.

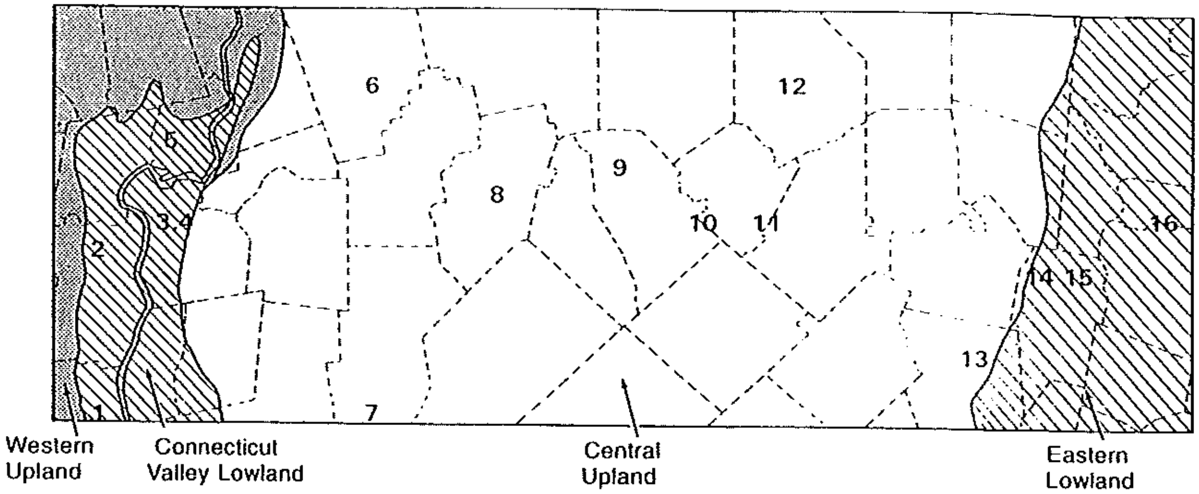
In LTER I we documented at a site scale that land-use activity (forest clearance, agriculture, reforestation) transformed the landscape and generated enduring legacies in forest structure and composition (Foster 1992, Foster *et al.* 1992), soil characteristics (Motzkin *et al.*), C dynamics (Wofsy *et al.* 1993), and forest susceptibility to hurricane damage (Foster and Boose 1992). In LTER II we will increase the spatial and temporal scope of the research by addressing a series of fundamental questions concerning broad-scale and long-term human impacts: (1) How does the institution of a novel disturbance regime of land-use alter vegetation organization in relation to natural environmental conditions and disturbance processes? (2) At what rate do species assemblages reorganize as the intensity of disturbance changes? (3) Following broad-scale decline in intensity of disturbance does the vegetation reorganize according to prevailing environmental conditions, and does it revert towards its former composition?

These questions will be answered with an integrated analysis of the natural vegetation, disturbance regime, land-use history, and vegetation dynamics of central New England using paleoecological, historical, physical, and environmental data. The study will provide a critical background for related LTER studies on C dynamics, and population, community, and ecosystem response to disturbance. It will have broad application beyond the HF LTER due to similarities between the land-use history of New England and large parts of eastern North America, western Europe, and some tropical regions.

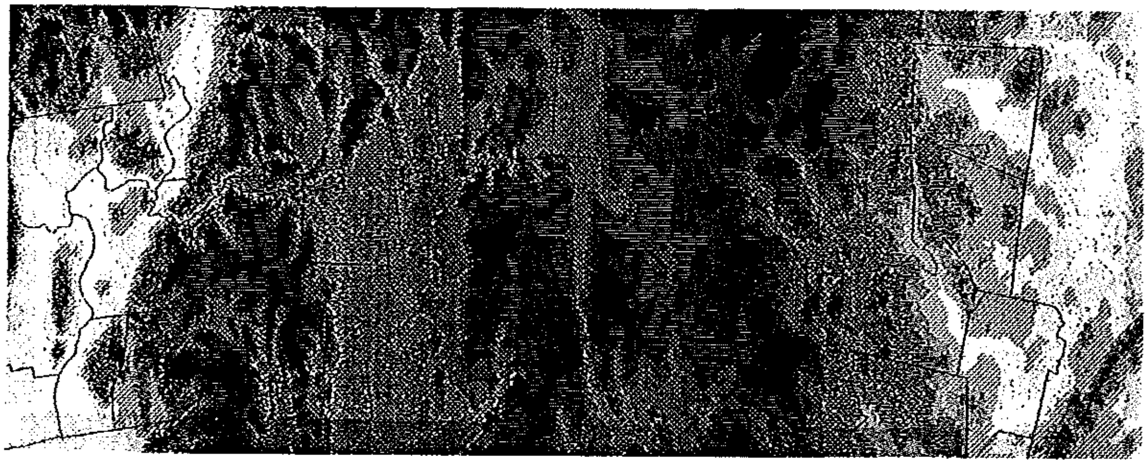
We will examine the last 2000 years of landscape history of central New England as a natural experiment. The north central Massachusetts study area (3150 km^2) includes distinct environmental and cultural gradients (Fig. 17; Appendix 5). The 2000-year period includes gradual climatic and cultural change followed by the European period of intense human activity (Mulholland 1988, Foster 1993). In the European period the landscape was deforested, intensively farmed, abandoned, and then reforested naturally (Fig. 18). In order to address our major questions we will establish a spatially and temporally resolved history of vegetation and fire for the pre-settlement period, document the 300-year history of European cultural activity and associated changes in forest cover, composition, and pattern, and evaluate the role of disturbance versus climate in controlling the vegetation.

Four major data sources will be utilized: (1) fine-resolution pollen analysis of a network of 16 sites will provide decadal information on sub-regional forest composition and dynamics. Pollen data will be analyzed at three spatial scales: (i) landscape, i.e., the area sensed by individual pollen sites (~10 km radius; Jackson 1993), (ii) subregion, i.e., the vegetation pattern sensed at our 16 sites collectively, and (iii) region, i.e., within New England, using established pollen data bases and our new data (E. Grimm pers. comm., Russell *et al.* 1993); (2) cultural information will include archaeological data on Indian activities and historical data on European land-use. The intensity and type of land-use will be quantified on a decadal basis for each township to provide high spatial and temporal resolution; (3) historical vegetation data and maps (1650 to 1985 A.D.; e.g., Fig. 19) will provide spatially and taxonomically accurate information and an independent check of the paleoecological record; and (4) environmental data on climate, soils, geology, and physiography will enable us to establish the relationship between these factors and vegetation and to examine the extent to which cultural and environmental gradients covary.

a. STUDY LAKES AND PHYSIOGRAPHIC AREAS



b. ELEVATION



c. MEAN ANNUAL TEMPERATURE

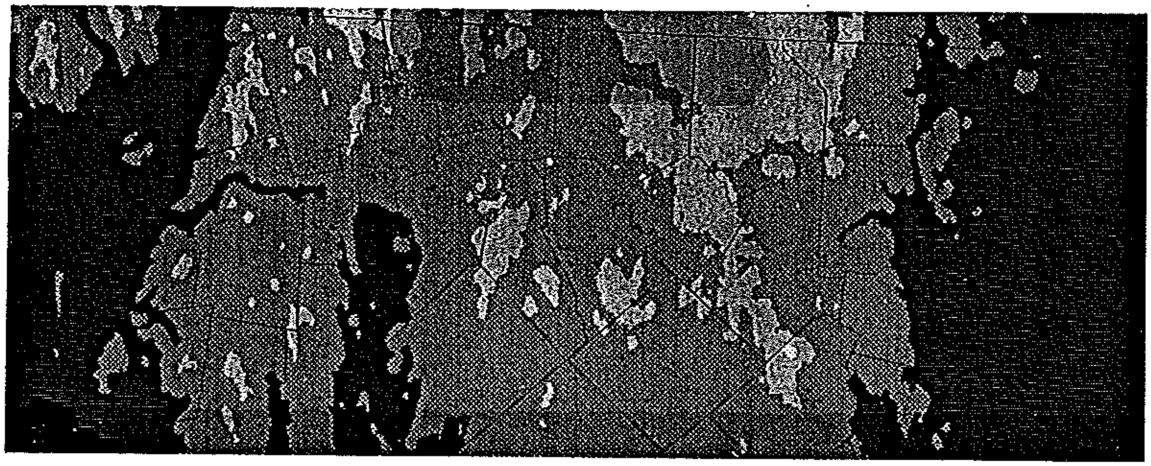


Fig 17. Physical and climatic features of the north central Massachusetts subregion: (a) study lakes (1-16) form a transect across the major physiographic areas; (b) elevation in 25 m classes ranging from < 50 m (white) to > 375 m (black). Digital elevation model (resolution ~ 80 m) is part of an extensive GIS data base of the subregion; and (c) predicted mean annual temperature in 1°C classes ranging from 5-6°C (white) to 9-10°C (black). Values derived from climate model of Ollinger *et al.* (in press) which generates monthly minimum and maximum temperature and precipitation estimates. The subregion is 35 x 90 km.

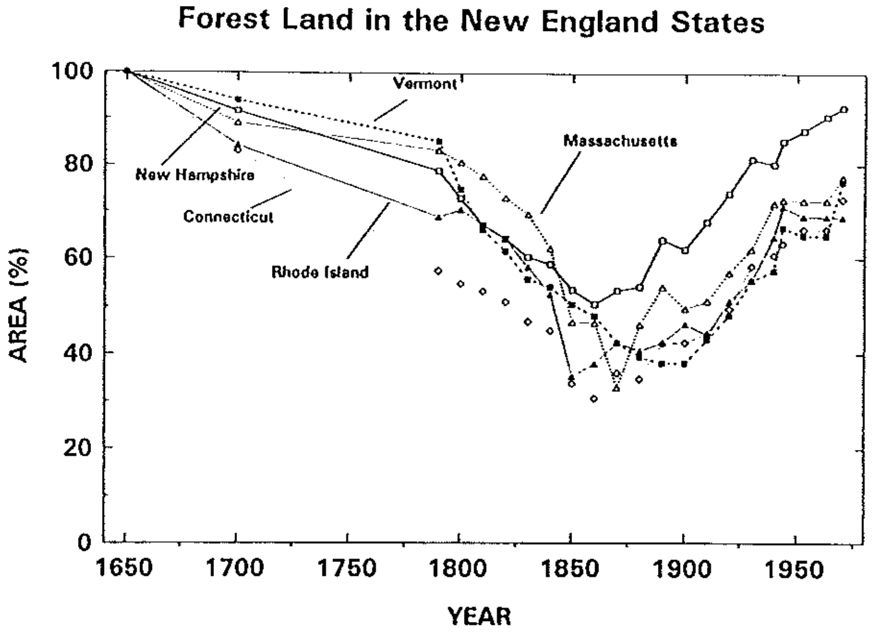


Fig. 18a. Historical changes in forest cover for the New England states excluding Maine. Forest clearance and agricultural activity peaked in the mid to late 19th C and shows a consistent trend across the region. Natural regeneration has led to a major increase in forest during the 20th C. From Foster (1992).

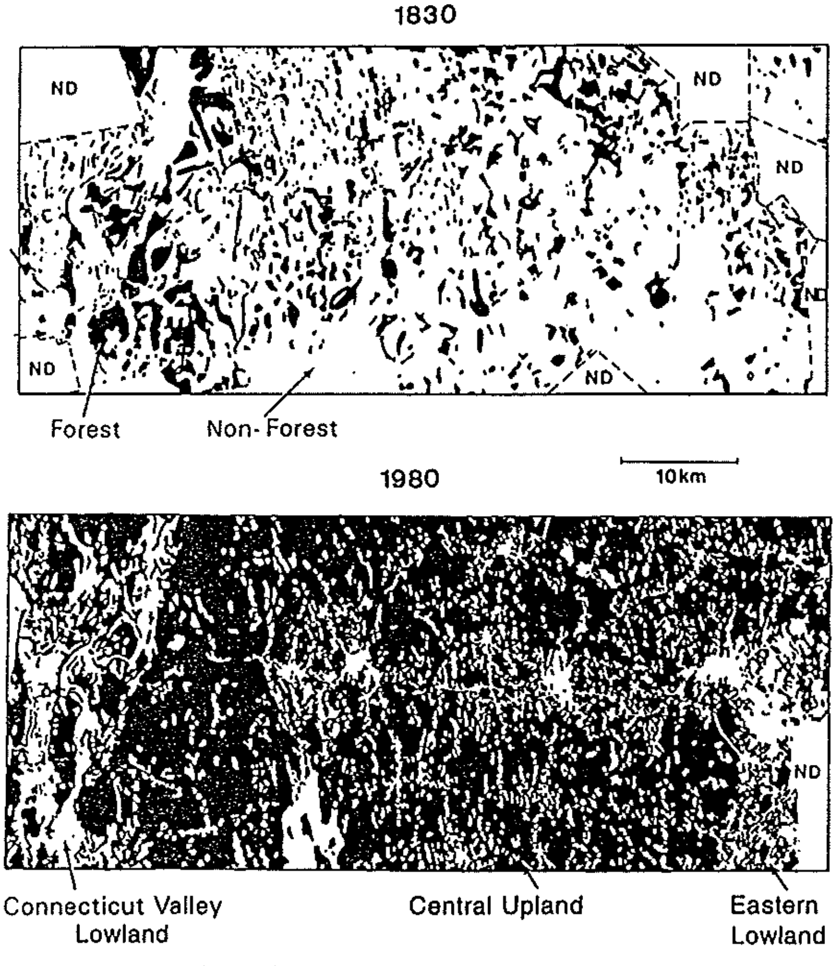


Fig. 18b. Distribution of forest cover in north central Massachusetts at the approximate height of agricultural activity (1830) and at the present (1980). Broad-scale variation in forest pattern varies with cultural activity across physiographic and environmental gradients. ND indicates not yet digitized. From Foster (1993).

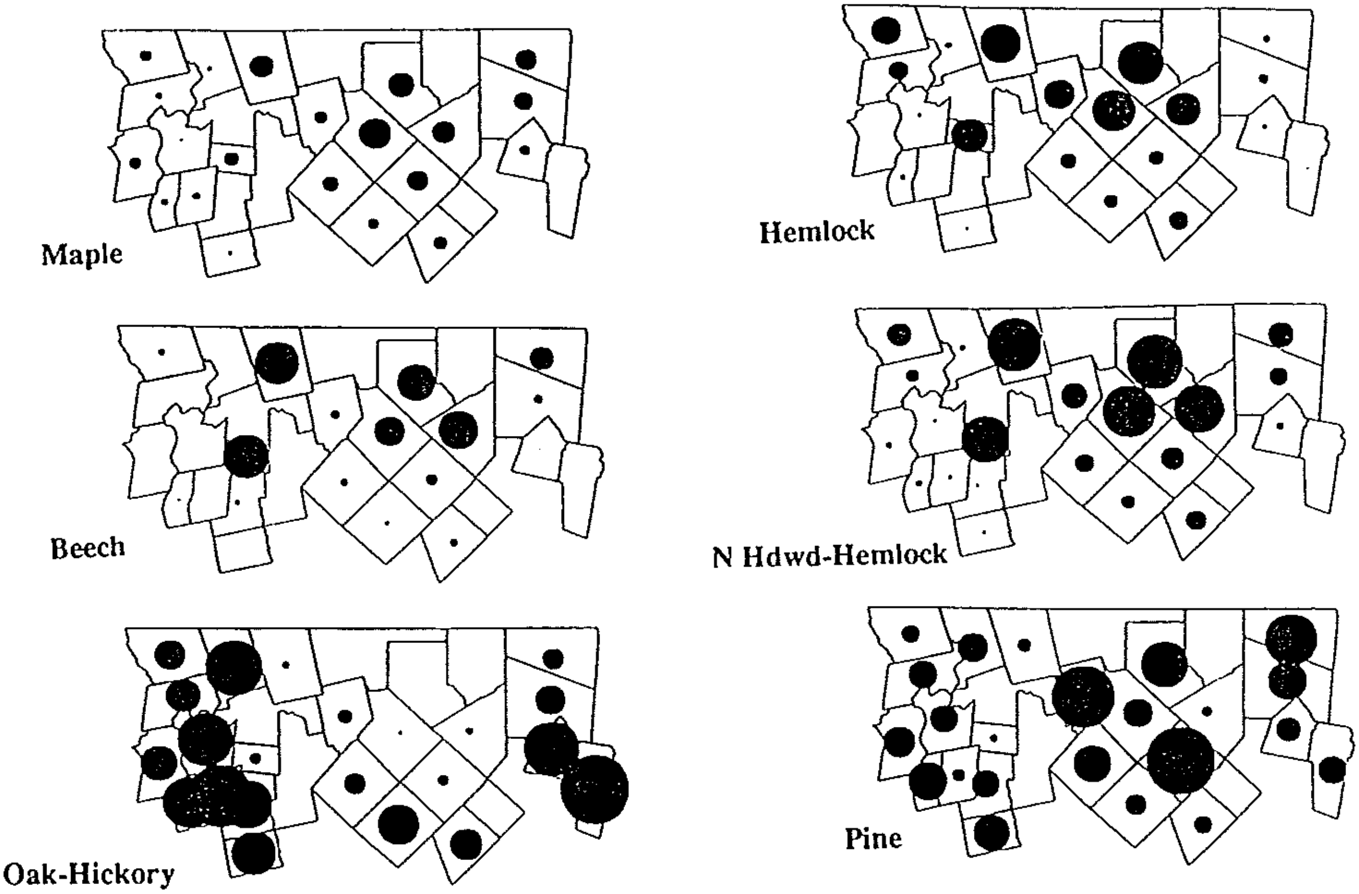


Fig. 19. Proprietor's Data (18th C.) for selected tree species and species assemblages in the study area. Relative abundance for species occurrence in each township is proportional to the size of the dot and ranges from 1% (smallest) to 40% (largest). A pronounced gradient is evident from low elevations in the west and east where oak and hickory are abundant to the Central Upland where northern hardwoods and hemlock predominate.

We expect that European land-use will result in novel pollen assemblages and increased rates of vegetation change. At broad-scales, land-use effects will overwhelm environmental gradients and generate convergence in forest composition. Subtle new gradients in forest composition will result, reflecting the interaction among regional variation in land-use, climate, and physiography. These expectations will be assessed by multivariate analysis and analysis of rates of change of pollen data at the sites individually and collectively, and during different historical periods. The results will be compared to land-use indices and environmental data to quantify their importance in determining vegetation gradients.

In addition to addressing the major questions posed above the study will provide new information on the: (1) character of the pre-settlement forest, in terms of composition, spatial variation and short- and long-term dynamics; (2) geographical pattern of pre-settlement fire and evidence for pre-European Indian activity; and (3) changes in environmental factors that have occurred during the European period.

Additional funding for retrospective studies in LTER I was derived from NSF, Mellon Foundation, and Harvard Forest. In LTER II outside and endowment funds will be utilized to supplement the proposed research. A proposal to support a portion of this work was recently submitted to NSF (Appendix 3).

B.2. Forest Structure and Process

B.2.a. *Regional Vegetation Pattern and Composition*

Site and landscape-scale studies in LTER I documented that land-use, natural disturbance, and physical environmental factors together explain local plant distribution and forest composition and structure (Whitney 1991, Gerhardt 1993, Foster 1992, Whitney and Foster 1988). These studies suggest that the imprint of human activity on community characteristics persists for more than 100 years and that an evaluation of the distribution, type, intensity, and timing of land-use is critical for the understanding of modern forests. In LTER II we seek to determine whether the land-use/vegetation relationships observed at the site and landscape-scale are also evident at a subregional scale, where there are stronger environmental gradients. Results from this effort will be well integrated with retrospective studies, will place the site-based studies of population mechanisms and ecosystem processes in a broader context, and will be relevant to other regions due to similarities in agricultural and forestry practices.

Major questions concerning the effects of human activity on the broad pattern of species and forest distribution include: (1) do environmental factors, including climate, physiography, and soils override the local effects of human activity? and (2) does the variation in land-use activities (i.e., type, intensity, and duration of activity) create new species assemblages and gradients in vegetation distribution?

The study area is north central Massachusetts, for which extensive retrospective and environmental data provide background on the temporal and spatial patterns of vegetation and land-use activity (see Section B.1.b). Sampling is stratified on a township basis. This sampling scheme enables us to use township-based cultural and vegetation data for analysis as well as variables that vary continuously across the area (e.g., soils, climate). In each township approximately ten 400-m^2 plots were randomly and quantitatively sampled for all vascular plant species. Environmental variables measured include slope, aspect, landscape position, soils, 1938 Hurricane damage, and intensity of recent land-use and disturbance. Land-use data include information on agricultural history from the 1830 land-use maps (i.e., designation as a primary or secondary woodland), and township data on agricultural, industrial, and residential activity from our State Census database (1760 - 1990 A.D.).

Vegetation data will be analyzed on a township (i.e., landscape) and subregional basis to relate the results to environmental and historical data and to compare the vegetation and the pollen data. Analysis of environmental and land-use relationships to vegetation will be assessed using Spearman rank and Pearson product-moment correlation coefficients calculated between the axes scores of Detrended Correspondence Analysis (DCA) (ter Braak 1990) and environmental and land-use variables. Comparison with historical vegetation data will include state-wide surveys in 1905, 1917, 1938, 1955, and 1972, early settlement data (proprietor's records) from the 17th and 18th C, and pollen results from the transect of 16 sites across the subregion.

Past studies of vegetation relationships to land-use have been supported by the Mellon Foundation, NSF, and Harvard Forest. Partial support will also be derived from LTER in the future.

B.2.b. *Population Processes and Landscape Patterns*

Deforestation and agriculture in north central Massachusetts during the 18th and 19th Centuries destroyed or disrupted populations of forest species, but subsequent reforestation in the 19th and 20th Centuries has led to a period of population expansion for these species. Vegetation studies conducted during LTER I at the site and landscape scale have provided a wealth of presence-absence and abundance data that show significant relationships between the distribution of forest species and past land-use (Whitney and Foster 1988, Foster 1992, Gerhardt 1993). These results indicate that the current pattern of species distribution observed in the north central Massachusetts subregion results from differences in species' abilities to respond to the changes in land-use activity over this period. These differences relate to differences in life history traits of species that affect both colonization and persistence in a landscape that is temporally and spatially dynamic.

For LTER II we are initiating population studies that will focus on impacts of the physical disturbance of plowing on the distribution of understory plants. Plowing destroys plant clones and alters the balance between vegetative and sexual reproduction as modes of population persistence and expansion for plant species. We will also examine the direct and indirect impact of this type of land-use on the butterfly herbivores of these species to determine how the effect of land-use cascades through higher trophic levels. Many butterfly species are weak fliers, are poor dispersers, and have a high degree of host plant specificity. Butterfly populations will therefore depend not only on the abundance of their host plants, but also on the spatial distribution of host plants in the landscape.

We have selected a group of ericaceous species (*Gaylussacia baccata*, *Vaccinium angustifolium*, *V. vaccillans*, and *Gaultheria procumbens*) and their butterfly herbivores (e.g., *Incisalia henrica* and *I. augustus*) for intensive field and experimental studies. The plant species show substantially different distribution patterns with respect to past land-use (Fig. 20), but share similar life history characteristics. The butterfly herbivores of these species feed on a variety of ericaceous plants, but vary geographically and by habitat in their choice of host plants (Opler and Krizek 1984).

Comparative and experimental studies of the plant species will measure fecundity, seed germination, seedling survivorship, and rate of vegetative spread. These traits have been selected on the basis of our analysis of existing data (Table 5) as well as results from the literature (e.g., Whitford 1949, Sobey and Barkhouse 1977, Havercamp and Whitney 1983, Eriksson 1989).

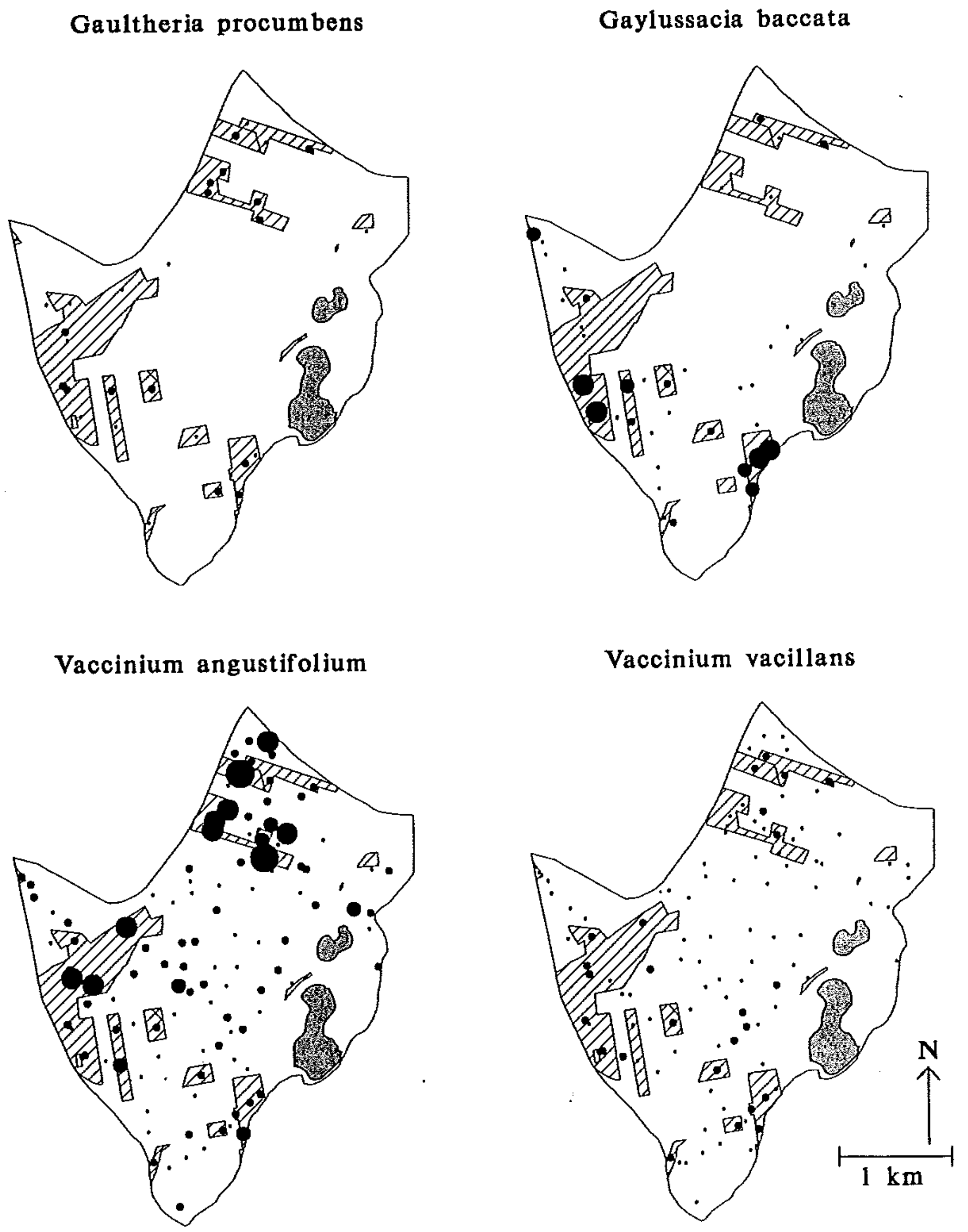
Landscape and regional studies will determine whether butterfly and host plant distribution are decoupled because of processes acting at different scales. For example, the distribution of a butterfly species at a site may depend on the presence of host plants. At a landscape scale, distribution of the butterfly species will depend on its ability to colonize and persist in available habitats. We will also use data produced by the Massachusetts Audubon Society's Butterfly Atlas Project to generate a preliminary causal model describing influences of land-use history and current vegetation on butterfly species diversity and distribution patterns. The model will be tested with path analysis (Retherford and Choe 1993, Israels 1987) to estimate direct and indirect effects of land-use and current vegetation.

This work addresses the problem of how populations persist in a spatially and temporally dynamic landscape that is heavily modified by human activity. Results from these studies will help us determine characteristics of species that enhance their ability to colonize and persist in this landscape. Our data indicate that some species ("good colonizers") move freely in this landscape while others ("poor colonizers") do not. We wish to determine what proportion of suitable habitat is necessary for maintaining populations of poor colonizers in a landscape that is fragmented and spatially complex.

Nutrient differences in soil may also be related to past land-use activity (either causally or by correlation). Soil nutrient differences affect plant nutrient uptake, potentially altering resource allocation to sexual reproduction and the competitive relationships among plants (Tilman 1988). In turn, caterpillar growth rates are influenced by the quality of their food supply. Nutrient supply rates will affect plant quality and either increase or decrease caterpillar growth rates. Rate of caterpillar growth may affect rates of parasitism and predation, which further influence butterfly population dynamics (Loader and Damman 1991).

The interaction between soil nutrient levels, host plant quality, and caterpillar growth will be determined by field studies of variation in leaf nitrogen (N) concentration and greenhouse experiments that manipulate herbivore and N levels in a factorial design. Response variables will be both plant and caterpillar growth rates. Nitrogen levels will be chosen that correspond to observed N levels in the field.

Results from our herbivore-nitrogen experiment will link with the soil warming experiment. This disturbance, by raising N-mineralization rates, also should affect population dynamics and patterns of species distribution. The


Gaultheria procumbens

Gaylussacia baccata

Vaccinium angustifolium

Vaccinium vacillans

Fig. 20. Species distribution in relationship to land-use history. The distribution and abundance of four ericaceous species in a Harvard Forest study are shown in relationship to major land-use activities, including: plowed (white) and unplowed (diagonal lines). Relative abundance is indicated by the size of the dark circles. Two prominent lakes are shown in gray shading along the eastern edge of the area.

Table 5. Percent frequency of occurrence of life history traits for rare and common species (occurring in <5% and >30% of plots respectively) on the Prospect Hill tract. Distribution of traits by abundance are significant at the table-wide level, P<0.05. Traits examined that were not significantly different at the table-wide level included seed size, dominant pollination mode, shoot morphology, maximum height, root and shoot modifications (i.e. rhizomes, stolons), and phenology. Fruits were classed as unassisted if there was no obvious dispersal vector (i.e. capsule, follicle, nut); secondary animal dispersal was not considered.

	Percent freqency of occurrence				
REPRODUCTIVE CHARACTERS	Common	Rare	Chi Square	df	P
Fruit and spore dispersal					
ingested	57	27	15.1	3	<0.003
wind	25	12			
unassisted	18	60			
attached externally	0	1			
Vegetative dispersal					
high lateral spread	64	27	12.68	2	<0.01
absent	21	29			
little or no lateral spread	14	44			
Seeds/fruit					
4-20	68	24	14.22	2	<0.003
1-3	27	64			
numerous, minute	5	11			
Fruit type					
berry	29	8	27.6	10	<0.003
spore	21	4			
capsule	14	23			
drupe	14	14			
achene	11	28			
pome	7	0			
follicule	4	3			
aril	0	4			
caryopsis	0	8			
nut	0	5			
schizocarp	0	3			
VEGETATIVE CHARACTER					
Growth form					
perennial herb	46	39	14.31	4	<0.01
woody, shrub, or understory tree	29	24			
fern or clubmoss	21	4			
graminoids	3	26			
annual/biennial	0	7			
OTHER					
Principle habitat					
open	100	58	16.85	1	<0.003
woods	0	42			

effect of experimentally manipulated levels of N on plant quality and caterpillar growth will be used to predict the impact of host plant quality on butterfly population dynamics. These predictions will be linked with canopy N estimates (AVIRIS) and surveys of insect damage to facilitate prediction of the location of future insect outbreaks.

Additional funding for population studies has come from the Harvard Forest Research Experience for Undergraduates Program (NSF) and Harvard Forest Endowment. These funding sources will continue during LTER II. In addition, we will seek outside funding in support of our population studies.

B.2.c. *Whole Forest CO_2 Flux*

During Harvard Forest LTER I, we have demonstrated the wealth of information that can be derived from accurate, long-term, CO_2 flux measurements. Certain climate fluctuations (cloudiness, summer temperatures, winter snow cover) have had major impact on forest ecosystem processes, while others often considered more important (soil moisture, water vapor deficit) have had only slight influence on rates of canopy photosynthesis. Recent results indicate that past disturbances (land-use and hurricanes) affect the spatial pattern of C flux across the Harvard Forest as well as long-term temporal trends in C assimilation. In LTER II we would like to identify more clearly the temporal and spatial patterns of ecosystem fluxes and relate these to environmental and vegetational factors and disturbance processes. We therefore propose to: (1) extend the continuous flux measurements; (2) enhance strongly the analytical and modeling efforts linked to the EMS data; (3) expand collaborative investigations of ecophysiology, soil processes, disturbance history, and vegetation distribution to investigate the factors underlying the large differences in net C uptake for different stands around the EMS; and (4) analyze the uptake mechanisms for atmospheric nitrogen oxides, in order to elucidate the ecological impacts of pollution-derived fixed nitrogen.

The following questions will be addressed in this work: (1) to what extent do variations in C uptake rates reflect the legacies of different land-use activities and natural disturbances? This question is essential for understanding the potential for C uptake by forests. If the system responds primarily to soil conditions, climate, and nutrient inputs, assessments may rely on current observed states of ecosystems. If the system responds significantly to disturbance over time-scales of decades or centuries, then observations must define these effects to interpret current rates of C storage (Fig. 21); (2) what are the key biological and environmental indices regulating net C uptake? The large data sets acquired in the proposed experiments will enable us to disaggregate the influence of various factors, including soil moisture, vapor pressure deficits, leaf N content, soil C content and turnover rates. Resolution of this question requires continued measurement of key parameters; (3) how does the forest respond to climate change on seasonal, annual, and interannual time-scales (including temperature, rainfall, snow cover, pollution inputs)? We have already obtained information on system response for several growing seasons, however a larger data base is clearly needed given possible non-linear interactions among environmental forcing factors.

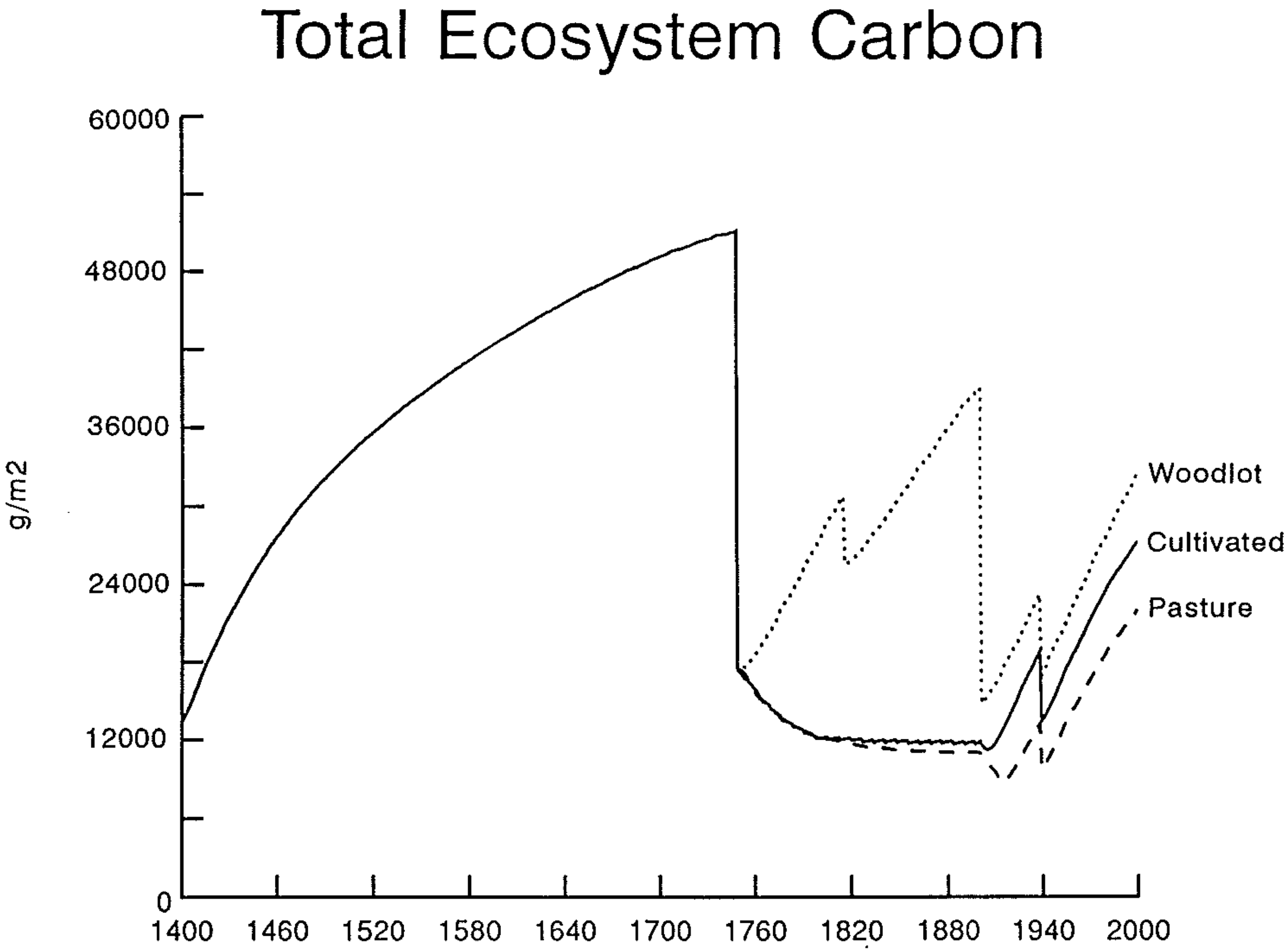


Fig. 21. Estimated total ecosystem carbon at the Harvard Forest using the CENTURY model (Parton *et al.* 1988). Three generalized land-use sequences were modeled: continous forest (woodlot), forest-pasture-forest (pasture), and forest-cultivated-forest (cultivated). In all three sequences the forest was allowed to grow undisturbed for 350 years followed by a clearcut in 1748. Subsequent disturbances included the 1815 Hurricane (woodlot only), a 1900 clearcut (woodlot only), and the 1938 Hurricane. In the pasture sequence, pasture was maintained from 1750 to 1900. In the cultivated sequence, fertilizer was applied at low rates (3 g N m^{-2} yr^{-1}) from 1750 to 1800 and at higher rates from 1800 to 1900 (18 g N m^{-2} yr^{-1}), using historical values. Pasture and cultivated fields were abandoned to forest in 1900. CENTURY predicted that the present day carbon storage rates for all three land-use sequences were approximately the same (roughly 200 g m^{-2} yr^{-1}). This work will be applied to the entire Prospect Hill tract using GIS and detailed historical records in the Harvard Forest Archives.

In LTER II we will continue to derive the bulk of our funds from various agencies (DOE, NASA, NSF) with LTER support for equipment replacement, long-term measurement and data analysis.

B.2.d. *Canopy Photosynthesis*

Carbon accumulation in the forest varies considerably between years due to variation in precipitation, temperature, and other environmental factors. Events such as masting in oak species or the outbreak of gypsy moth or other pest species may also have an effect on the physiology of particular tree species and on the ecosystem as a whole. We will continue to measure the annual fluctuations of leaf-level CO_2 exchange to investigate how variable patterns of environmental factors influence ecosystem-level C accumulation. We will also relate patterns of year-to-year variation in CO_2 exchange with the annual net ecosystem C uptake as measured by the eddy correlation system.

In the future we plan to use a "cherry picker" to gain access to many more trees and additional species. We will expand the number of species sampled and contrast the physiology, biochemistry and C accumulation of species across the successional gradient. These studies will improve our ability to scale from the leaf level to the level of stands comprised of numerous species. It will also help to interpret the differences in C accumulation rates sensed at the EMS and related to differences in stand successional age and land-use history.

Additionally, we will look at patterns of CO_2 heterogeneity within the forest since variability in CO_2 concentrations near the forest floor may have substantial effects on photosynthesis and growth, particularly for seedlings and saplings. We will quantify spatial and temporal patterns of CO_2 concentrations in the stands where leaf-level photosynthesis of mature trees is being measured. We will also characterize temporal patterns of CO_2 heterogeneity in gaps and in undisturbed forest sites. For these measurements, we will use a fully-automated sampling system designed for rapid simultaneous sampling of CO_2 in the field (see C.11).

LTER funds will continue to support personnel and equipment needs of this project, in addition to funds from NSF (non-LTER) and DOE.

B.2.e. *Soil Organic Matter Dynamics*

The long-term litter manipulation (DIRT) plots established at the Harvard Forest in 1990 and 1991 offer a simple, experimental means of answering fundamental questions on the source of soil organic matter (SOM), the relative contributions of root respiration and decomposition of various detrital pools to soil respiration, the contributions of leaf litter and root litter to different kinetic SOM fractions (active, slow, passive), origins of physical fractions (particulate, colloidal, and dissolved), and the recovery of SOM after soil impoverishment. During the last three years we used LTER support to install the plots, to sustain field treatments (See Section A.2.c. - no litter, double litter, no roots, no roots and no litter, and O/A-less.) and to conduct long-term (> 1 yr) laboratory incubations to determine potentially mineralizable C and N in soils collected in the first year of the study. In addition, we instrumented the plots with soil solution samplers (lysimeters), soil temperature probes (thermocouple arrays), and moisture (TDR) probes; mapped tree boles and topography; and made intensive measurements of key field processes (soil respiration and nutrient leaching) with support from DOE.

We propose to: (1) continue manipulating litter inputs to soils in the plots; (2) make periodic measurements of soil respiration and soil solution chemistry in the field; and (3) link changes in SOM quality (C and N dynamics) to treatments by conducting laboratory incubations of soil samples collected in treatment years 4 (1994) and 8 (1998). In particular, the kinetics of C, N and P released from the laboratory incubations will be used to evaluate the importance of younger (< 10 yrs old) and older SOM to element cycling and to estimate the relative amounts of C and N in active and stable SOM pools.

The suite of field measurements (soil moisture, soil temperature, lysimetry, soil respiration) conducted during the first funding cycle of our LTER activities will be continued during the next grant period. The frequency of sampling may be adjusted, however, as we allocate more of our LTER resources to conducting laboratory incubations (below) of samples collected at critical intervals following the start of our experiment. Soil respiration, soil moisture, and soil temperature are currently measured weekly from May through October and twice-monthly to monthly during the winter months. Tension lysimeters (60-cm depth) and zero tension lysimeters (below the O horizons) are sampled weekly from April to November, depending on soil moisture conditions. We expect to limit the frequent soil respiration measures to every other year of the next six year cycle.

Microbial respiration and net N mineralization in forest floor (Oe+Oa) and mineral soil (0-15 cm) samples collected from the plots in 1994 and 1998 will be measured using year-long laboratory incubations in microlysimeters (*sensu* Nadelhoffer 1990). Inorganic N will be leached from samples at the ends of weeks 1, 2, and 4 and monthly thereafter. Respiration will be measured using periodic short-term (5-hr) measurements of CO_2 production. Product accumulation curves for respired CO_2-C and mineralized N will be constructed for each microlysimeter. We will fit resulting data to single- and double-exponential models to determine whether the SOM is best described by one or two kinetic pools. Results from the 1994 and 1998 incubations will be compared with those from the 1991 incubation, representing near-baseline conditions. We expect that the sizes and activities (rate constants) of mineralizable C and N pools in soils within each site will be influenced by manipulating the amount and source of detrital inputs and that treatment effects will increase with time. Results of these incubations will be used for testing and revising (if needed) components of biogeochemical models (e.g., MBL-GEM - Rastetter *et al.* 1991) that simulate SOM dynamics.

We will seek support from sources other than LTER to conduct more detailed studies of finer-scale processes. For example, we will seek outside support to measure gross N mineralization, nitrification, and immobilization by the ^{15}N isotope dilution method (Davidson *et al.* 1991), and microbial biomass C (Vance *et al.* 1987) and N (Brookes *et al.* 1985) pools in forest floor and soil samples collected for our Year 4 and Year 8 laboratory incubations (see above). Gross N fluxes in soils collected from our treated plots may prove to be sensitive indicators of any changes in SOM quality that result from chronic manipulations of root and litter inputs to soils in our plots. Additionally, comparison of gross N transformation rates with the microbial biomass-N pool and CO_2 released during incubations should provide useful information on soil N turnover rates and the associated microbial demand for C (Davidson *et al.* 1991).

Light fraction (LF) SOM and microbial biomass pools can respond rapidly to changes in litter inputs and often constitute significant amounts of active SOM (Ladd *et al.* 1981, Powlson *et al.* 1987, Christensen 1992). Because of their importance to energy and nutrient flow, these components will be measured on subsamples of soils collected for the 1994 and 1998 incubations. Light fraction will be collected from mineral soil (0-15 cm) by density fractionation with sodium polytungstate (1.6 Mg m^{-3}) and will be analyzed for C and N content and N mineralization potential (7-day anaerobic incubation). Microbial biomass (C and N) will be determined using fumigation-incubation procedures (see above). Carbon and N contents of the microbial fraction and LF material will be determined on a Carlo Erba CN Analyzer.

We will continue encouraging outside investigators to use the plots. For example, W. McDowell (University of New Hampshire) and colleagues are now using our plots to identify the relative influences of leaf litter and roots on dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) dynamics. Also, E. Sundquist (USGS, Woods Hole) has instrumented the plots with gas tubes to identify diurnal patterns and depth profiles of CO_2 production by roots and heterotrophs. We look forward to additional non-destructive uses of our plots by others as the treatments proceed. We emphasize that we view our set of field manipulations as a long-term experiment providing a resource to researchers through the year 2000 (the final year of our current request) at minimum and considerably longer if possible.

B.3. Experimental Manipulations

B.3.a. *Hurricane Simulation*

The hurricane simulation provides a unique opportunity to compare population and ecosystem response to hurricanes and other disturbance processes and to integrate this work with retrospective and landscape studies. We propose to put the detailed site work of LTER I (see Table 3) into a broader context by: (1) comparing site-based response parameters (e.g., tree sprouting, seed bank contribution, life history characteristics of species colonizing and surviving, trace gas fluxes) to responses found at other hurricane sites (Luquillo, South Carolina, Florida) and to the 1938 Hurricane; and (2) comparing temperate forest responses and environmental changes following simulated hurricanes with responses to natural and created gaps, winter storm damage, and forest cutting.

As one of the core LTER experiments, continuation of the hurricane experiments is a major priority of LTER II. Future studies are motivated by the need to: (1) document the full extent of forest development and recovery following wind disturbance through continuity in measurements of population dynamics and ecosystem processes (see Table 3); (2) link our measurements of ecosystem response (trace gas fluxes, mineralization rates) with observations of biomass distribution and population dynamics by taking spatially explicit measurements of leaf area index, biomass distribution, environmental variables, and soil processes; and (3) investigate mechanisms underlying plant response to wind disturbance at the individual plant and population level.

To better understand the growth and photosynthetic response of woody plants to hurricane disturbance, we will use non-destructive dimensional measurements to estimate carbon gain and allocation patterns in seedlings, residual saplings, and sprouts. Preliminary gas exchange measurements indicate that saplings and sprouts in the blowdown achieve higher net photosynthesis rates than those in the forest understory. Therefore, we propose continuing gas exchange measurements to resolve these differences. Correlation analysis will be used to examine relationships between growth patterns and rates of photosynthesis.

To explain the mechanisms underlying patterns of vegetative recovery we will focus attention on factors influencing the dynamics and composition of seedling and sapling banks in pre-disturbance forests. This effort will include comparative study of stand seedling bank composition as well as experimental investigation of factors, such as the dominant fern understory, that potentially shape the character of the seedling bank. We propose that the fern understory, through its modification of resource levels, may act as a seedling filter which plays a critical role in determining the abundance, size structure, and species composition of the seedling and sapling bank. The fern understory has already been demonstrated to modify resources critical to seedling performance in the hurricane experiment (Carlton 1993). With information from the proposed study, the relative role of the fern filter in pre- and post-disturbance communities can be compared.

Analysis of understory response to simulated hurricane will focus on defining life-history traits that characterize species colonizing, surviving, and thriving in wind-created microsites. We ask what traits characterize successful species in hurricane disturbed sites and if salvage operations altered the presence and abundance of these characteristics during post-hurricane recovery. Suites of species and traits that are new, absent, and abundant following the hurricane simulations will be compared with those found in stands blown down in 1938, at two different scales: (1) the Harvard Forest; and (2) the north central Massachusetts subregion. These life history and broad-scale approaches to hurricane recovery will be closely linked with parallel investigations of plot and population response to land-use (sections B.2.a. and B.2.b.)

B.3.b. *Nitrogen Saturation*

We will continue the chronic N addition experiment for the next six years, maintaining existing measurements, some at lower frequency, and adding new measurements suggested by results to date. Major questions posed by these results are: (1) what are the major mechanisms accounting for nearly complete N retention in all sites? and (2) will all treated sites show the same sequence of responses to continued N additions, with the timing and amplitude of response determined by initial degree of N limitation and level of N addition?

(1) Mechanisms for N retention -- While direct immobilization through microbial growth is one possible mechanism, large amounts of labile C would be required, beyond those being metabolized in the control stands. In essence we would be hypothesizing the continuous existence of a large pool of labile C in control forest soils at the Harvard Forest, which would contradict the generally accepted concept that microbial activity in soils is C rather than N limited (e.g., Flanagan and Van Cleve 1983, Foster *et al.* 1980, Bååth *et al.* 1981). An alternative hypothesis is that abiotic reactions between ammonium (and perhaps nitrate) and soil organic matter provide a pathway for N immobilization that is not dependent on the availability of labile C (e.g., Axelsson and Berg 1988, also see reviews by Johnson 1992 and Nommik and

Vahtras 1982). As abiotic reactions may occur with solid phase organics or with dissolved forms (DOC), and DOC represents an important component of mobile, labile soil C, the dynamics of this fraction of soil organic matter are of particular importance.

We propose an integrated set of experiments to determine the response of soil CO_2 flux to N additions, the potential for abiotic immobilization, and the generation and movement of DOC in soils within the chronic N plots. All experiments have been initiated with current LTER support, but will require continued funding to complete. Part of this work has been accepted for support by the USDA Competitive Grants Program. The components of this study are: (i) Measurement of DOC and DON flux below the forest floor and below the rooting zone in both pine and hardwood chronic N stands. Forest floor fluxes are measured by zero-tension lysimeters put in place in 1992; rooting zone measurements are acquired by adding DOC and DON analyses to samples taken from existing porous cup tension lysimeters. Forest floor samples are collected continuously and on an event basis. (ii) Measurement of DOC and DON flux from decomposing leaf litter as affected by additions of nitrate and ammonium. This is a laboratory study with all major species of litter on the Harvard Forest plots and factorial applications of N in amounts equivalent to those being added in the field. We hypothesize that increased N loading will increase DON flux through abiotic immobilization of mineral N by low C:N DOC. We further hypothesize that added N will not increase CO_2 flux nor reduce DOC leaching. (iii) Continuous measurement of CO_2 flux from control and high N addition soils, as well as former control soils undergoing a first year of high N additions. In this experiment we will test whether additions of N lead to increases in CO_2 flux which are compatible with traditional microbial immobilization through biomass growth. CO_2 fluxes are measured over daily intervals using the soda-lime technique, which we have validated against more difficult and time consuming gas chromatography methods (Raich *et al.* 1990). (iv) Measurement of abiotic N immobilization potential in chronic N soils. This experiment will use sterilized soils from the chronic N plots to which ^{15}N has been added. We are currently testing different methods of soil sterilization to determine the effect of each on mineral N release. Sterilized soils will be treated with different concentrations and forms of ^{15}N and the rate of immobilization (if any) will be determined.

(2) Response sequences accompanying continued N additions -- Initial measurements of N cycling rate, nitrification, and foliar N concentrations all suggest that the hardwood stand was more strongly N limited at the beginning of the study than was the pine stand (Aber *et al.* 1993). The high N pine stand has shown the largest response in both nitrification and N leaching losses. The high N hardwood plot has begun to show occasional losses of nitrate. We hypothesize that all stands will show steady increases in N mineralization, nitrification, foliar N concentration and N losses (see initial hypotheses, Aber *et al.* 1989).

Nitrogen additions will continue to be made in six equal applications between May and October. The same three treatments will continue: Control, 50 and 150 kg N ha^{-1} yr^{-1}. We will also continue to collect suction lysimeter samples (60 cm depth) at 2-4 week intervals throughout the year except when the ground is frozen. Green foliar samples will be collected annually, and tree growth measurements will be made every three years as has been done to date. We will reduce the frequency of annual N mineralization measurements from every year to once every three years. This change is driven by the need to preserve the site for long-term measurement, to reduce costs, and because N mineralization rates are changing slowly over time.

B.3.c. *Soil Warming*

The soil warming plots, established with funding from EPA, DOE, and the LTER, provide an experimental means of exploring process-level responses of soils to chronic warming. During the first three years of the experiment we have observed changes in fluxes of CO_2, CH_4, and N_2O from the soil, changes in net N mineralization, and some preliminary indications of changes in net nitrification. We also made baseline measurements of soil C stocks, soil C quality, and the ^{13}C and ^{15}N contents of soil organic matter. In 1994, with DOE funds, we will create a set of new plots to determine the relative contributions of microbial respiration and root respiration to CO_2 efflux in heated plots. This will involve establishing 12 new plots - 3 that have cables and are heated; 3 that have cables but are not heated; 3 that are trenched, have cables and are heated; and 3 that are trenched, have cables and are unheated. We have successfully used trenching to address the question of the relative contribution of microbes and roots to soil CO_2 flux in the litter manipulation (DIRT) study (Bowden *et al.* 1993).

With LTER funds we propose to measure long-term changes in the soil fluxes of CO_2, CH_4, and N_2O in the 18 plots established in the original study and the 12 new plots described above. We will also measure (quarterly) long-term soil N dynamics, looking for changes in rates of net mineralization, net nitrification, and the amount of N stored in microbial biomass. We will use standard methods for all of these measures (Steudler *et al.* 1989; Bowden *et al.* 1990; Pastor *et al.* 1984).

Once every two years we will measure soil organic matter stocks and quality in all treatments. We will use the lignocellulose index (Melillo *et al.* 1989) and possibly the cellulase activity index (Linkins *et al.* 1990a, b) to explore changes in soil organic matter quality as a function of soil heating.

B.4. **Integration and Regionalization**

The use of field results to develop and parameterize site- to regional-scale models is an ongoing integrative process within the Harvard Forest LTER. Examples of such work to date include the following:

1. A large suite of soil respiration measurements from the chronic N and soil warming plots has been used to parameterize a regional-scale soil respiration model, which has been extended to temperate forests globally (Kicklighter *et al.* 1994). This same soil respiration model has been incorporated into two simple models of forest carbon balance (PnET and TEM); results have been applied to the Harvard Forest (Fig. 8) and the northeastern U.S. (Fig. 13; Aber *et al.* 1994).

2. Data on rates of photosynthesis at the canopy level have been used to parameterize a model of short-term (hours to days) C flux; predicted C flux has been compared with that measured by the EMS. Tower data also have been used to validate C balances (monthly time step) predicted by PnET.

3. ^{15}N redistributions on the N Saturation plots following the termination of ^{15}N additions to these plots (see sections A.3.a and B.3.c.) are being used to test and improve forest biogeochemical models such as MBL-GEM (Rastetter *et al.* 1991) and PnET (see above). Our isotopic labelling experiments on the N Saturation plots have created unique and highly unbalanced ^{15}N distributions on the plots. Nadelhoffer is seeking additional support (NSF Ecosystems) to continue sampling N isotopic contents of soil pools and plant tissues through time and to compare simulated ^{15}N redistributions with measured ^{15}N redistributions through time to test these and other models. Resultant improvements of models will increase our confidence in model-based predictions of C and N cycling and will contribute to our ability to extrapolate model results to larger regions.

4. Archival records of both land management practices and land-use change have been used with the CENTURY model (Parton *et al.* 1988) to examine the chronology of net C storage at the Harvard Forest since European settlement (Fig. 21).

5. Archival records of forest damage and recent field measurements of blowdown sites from the 1938 Hurricane have been used to test and refine the HURRECON and EXPOS models from the site to the regional scale. A current project is examining variation in treefall orientation from this hurricane across the north central Massachusetts subregion.

We propose to continue and extend these synthetic activities. We believe that integration between sub-projects and the continued cross-checking of results by different measurements is critical to our continued success. Existence of several comparative data sets collected with different methods increases the accuracy of modeling results and the opportunities for model validation. Future modeling work will include the following:

1. At the site scale, we propose to continue the development of models of C and water balance driven by spatially-explicit maps of foliar N and lignin concentration now becoming available through analyses of AVIRIS data. Results can be validated against results from the EMS tower both for average fluxes for the entire forest, and for directional fluxes which can be compared with mapped predictions.

2. We will seek outside funding to continue our work with CENTURY, examining the chronology of C storage at Harvard Forest. Thus far, we have used CENTURY to examine C storage for generalized Harvard Forest land-use sequences (forest-tillage-forest, forest-pasture-forest, continuous forest). During LTER II we plan to utilize the extensive spatially- and temporally-detailed records in the Harvard Forest Archives as input data for CENTURY simulations. We will address whether current C storage rates differ for different land-use histories (tillage, pasturage, or woodlot). Predictions for present or recent C storage will be compared with those from PnET and with C flux measurements at the EMS.

3. At the regional scale we propose to continue to work with PIs from the Hubbard Brook LTER site (Driscoll, Lovett, and Federer) to improve the accuracy of our regional climate/atmospheric deposition model (Ollinger *et al.* 1993), including ozone deposition and the full suite of critical nutrient outputs (macronutrients, hydrogen, and aluminum).

4. A second regional modeling approach will be to use our General Ecosystem Model (MBL-GEM, Rastetter *et al.* 1991) to investigate C and N dynamics in temperate forests (funded by NSF). GEM has been applied to a comparative historical analysis of the patterns of C sequestration in temperate, tropical, and boreal forests (McKane and Rastetter 1991). We propose to use GEM to simulate the effects of changes in climate and land-use on the storage of C and N in temperate deciduous and coniferous forests of the northeastern United States. We will also compare the GEM simulations to the modeling results from PnET.

5. The HURRECON and EXPOS models will be used to reconstruct long-term hurricane disturbance regimes on a series of spatial scales (see section B.1.a for details).

C. Relevance of Activities to LTER goals

C.1. Long-term Experiments

The development of a series of well-conceived integrated experiments has been a critical part of our LTER I research program. The experiments have been rewarding both for their scientific application and as a device for focusing collaborative activities among our diverse group of scientists. The long-term nature of the experiments has enabled us to follow processes and observe results that would not be feasible under the usual 2-3 year NSF grant. Changes in many processes we are studying (e.g., N saturation, soil organic matter dynamics) are inherently slow and require long-term observation. Others, such as ecosystem response to soil warming, exhibit major changes over time that might lead to false conclusions under short-term observation.

A central emphasis of LTER II will be the continuation or elaboration of our long-term experiments either through repeated treatment (e.g., N saturation experiment) or through long-term measurements of a one-time manipulation (e.g., simulated hurricane). It is clearly neither possible nor desirable to maintain the original sampling intensity for all experiments. Therefore, most measurements will undergo change in frequency or type. For example, in the simulated hurricane trace-gas analysis revealed essentially no difference between the treatment and control. Consequently, in LTER II we will shift from monthly summer efflux measurements to sampling in the third and sixth year. In contrast, regrowth of the vegetation is an important ongoing process that warrants long-term inventory. We will follow this on permanent plots throughout the course of the next 20 years at a minimum.

Two changes have occurred in our original plan of long-term experiments. In LTER I we had intended to: (1) establish overstory deadening plots to simulate mortality by insects or pathogens and (2) repeat our hurricane simulation every 5-6 years. Outbreaks of a native pathogen (Eastern Hemlock Looper) convinced us to substitute for item (1) a series of permanent plots in hemlock-dominated forests in which we maintain long-term measurements of vegetation, soil processes, and trace gas fluxes in anticipation of overstory mortality. The plots were established early in LTER I and studied intensively (Foster *et al.* 1992). We will continue to evaluate the effects of this natural outbreak as a long-term experiment. For the hurricane simulation, results from LTER I convinced us that an alternate plan to repeating the manipulation would be more relevant scientifically. Our new plan contains two elements: (1) to follow recovery in detail on the existing blowdown and (2) to develop a second experiment that combines hurricane blowdown and salvage logging in order to compare their relative impact and interaction in terms of forest ecosystem recovery. We are working to develop the additional funding to implement this much larger experiment.

C.2. Long-term Data Sets

The following long-term data sets are maintained by the Harvard Forest LTER project. Research results derived from these data sets are summarized above. Spatially-explicit data sets have been incorporated into the GIS.

a. Climate data. Minimum and maximum temperature (since 1936) and 24-hour precipitation (since 1913) are measured daily.

b. Forest inventory. Vegetation of the Harvard Forest (1200 ha) is quantitatively sampled every 10-30 years in stands mapped from aerial photos.

c. Vegetation and Soil survey. In 1992 permanent plots were established in the location of the 1937 inventory plots. Vegetation was sampled for all vascular species. Three soil pits in each stand were used to sample basic physical and chemical properties.

d. Aerial photographs. The Harvard Forest archives aerial photographs (1:4000 to 1:40000 scale) of research sites at 5-15 year intervals (since 1937).

e. Post hurricane vegetation response. Regeneration following the 1938 Hurricane is measured in permanent plots at Harvard Forest (14 plots, since 1938) and Pisgah Forest in southern NH (14 plots, since 1984). Measurements include tree species, dbh, canopy position, and estimates of ground cover.

f. Mapped tree plots. Three stands are sampled every 5-15 years: 4-ha mixed hardwood stand (since 1962), 0.7-ha hemlock stand (since 1990), and 2-ha mixed hardwood stand (since 1990). Standing trees (dbh > 5 cm) are mapped and species type, dbh, canopy class, and condition are recorded.

g. Chronic nitrogen addition. Nitrogen is added as ammonium nitrate at rates of 0, 50, and 150 kg ha^{-1} yr^{-1} in oak-maple and red pine stands. Measurements include: net mineralization, net nitrification, litter decomposition, tree growth, foliar chemistry, litter chemistry, soil solution nitrate, ammonium, DOC and DON, and CH_4, CO_2, and N_2O fluxes (since 1988).

h. Environmental Measurement Station. Continuous measurements of eddy correlation flux for CO_2, H_2O, O_3, and nitrogen oxides are made, along with ambient concentrations of these species. Momentum and heat fluxes and associated intensive quantities are measured continuously. Wet deposition is measured using a fractionating collector. Continuous data are obtained for CO, NO and NO_2 concentrations. Incident PAR and net radiation are measured, along with soil temperature at several sites, continuously. The data set defines hourly, daily, seasonal, and annual net exchanges of key quantities between the forest and the atmosphere and provides information on the environmental factors that help to regulate these exchanges (since 1989).

i. Hurricane simulation. Trees were pulled down to simulate a hurricane blowdown in a 0.8-ha mixed hardwood stand (1990). An adjacent 0.6-ha mixed hardwood stand serves as a control plot. Vegetation was mapped and measured before and after the pulldown, and changes in microtopography were recorded. A deer exclosure encloses half of the blowdown and control. Measurements include micrometeorology (PAR, air and soil temperature), vegetation regeneration (trees and all understory species), litter chemistry, and trace gas fluxes of N_2O, CO_2, and CH_4 (since 1990).

j. DIRT plots. Long-term litter manipulation plots (3 x 3 m each) were established in 1990, and receive the following treatments annually: 2x-foliar litter, no foliar litter, no roots, no roots-no litter, and O-A-less. Measurements include soil respiration, soil solution chemistry, soil moisture, potentially mineralizable N and C, and ^{15}N and ^{13}C profiles by soil depth (since 1990).

k. Prospect Hill clearcut regeneration. A red pine plantation with hardwood understory was clearcut in 1990. Fifty permanent plots (25 within deer exclosure) are resampled annually for species, height class, origin, and evidence of browsing (since 1990).

l. Prospect Hill phenology. Annually 3-5 individuals each of 33 woody plant species are observed to record leaf and flower development (since 1990).

m. Soil warming. In 1991 heating cables were installed in 12 of 18 6 x 6 plots; of these 6 plots are heated to 5°C above ambient soil temperature. Measurements include soil moisture, net mineralization, net nitrification, and trace gas fluxes of CO_2, N_2O, and CH_4 (since 1991).

n. Birds and insects. The long-term abundances and spatial distributions of birds are sampled and related to variations in forest habitat structure, composition, and history. Populations are quantified by point counts and overlay of species distribution maps via GIS onto maps of forest vegetation (Fig. 15). Insect outbreaks are mapped and related to the distribution and abundance of bird populations. These baseline data will be used to design intensive autecological studies. Results will be related to modeling and broad-scale analyses of bird populations and forest landscape change.

o. Decomposition of coarse woody debris. The role of logs and branches in the organic matter and nutrient budgets of temperate forests is examined through: determination of the maximum rate of loss of biomass for red pine and red maple, the effects of diameter on rates of loss, and the net flux of N and phosphorus during decomposition. Branches and 1 m sections of boles were placed in red pine or mixed hardwood forest after determination of initial densities and nutrient composition. Periodic harvesting and analysis of a subset of materials is undertaken regularly.

In addition, the Harvard Forest Archives contains: (1) nearly 500 maps of topography, soils, land-use and disturbance history, forest stands (at 10-15 year intervals since 1907), experiments, permanent plots, and study locations for the Harvard Forest; (2) 85 years of unpublished studies, including raw data, notes, and manuscripts; (3) more than 3000 photographs of forest stands since 1922; and (4) computer databases for the map collection, published and unpublished studies, and 22,000 volume Harvard Forest Library.

C.3. Research on Five Core Areas Common to LTER Sites

A major goal of the Harvard Forest LTER is to develop coherent data sets that allow for the analysis of long-term ecosystem dynamics and facilitate comparison with other LTER sites. These data sets address the five core areas of the LTER Program.

Pattern and Control of Primary Production -- Included in this category are direct measurements of NEE (e.g., the EMS) and leaf-level and whole tree C accumulation, measurements of aboveground production (e.g., long-term permanent plots, litterfall and woody increment), and indirect measurements of belowground production in many manipulation and control plots (e.g., N saturation, soil warming, DIRT). Our unique data sets on C dynamics across many spatial scales have enabled us to model forest production using PnET at a site and regional scale.

Spatial and Temporal Distribution of Populations -- Long-term measurement of forest dynamics has been a focus of Harvard Forest research and has been expanded in LTER I to include all vascular species in permanent plots and birds and insects at permanent points. Quantitative studies also include tree age-structure analyses, seedling growth, architecture and age-structure analysis in disturbance experiments and assessment of seed rain, buried seed pools, and tree growth, mortality, establishment, and sprouting in the hurricane simulation. GIS analysis of individual and population distributions have been a central part of the site-based studies.

Organic Matter Dynamics -- Plant litter and soil organic matter are measured on a routine basis on all experimental sites at Harvard Forest. Several techniques including stable isotope ratios of C and N are used to detect changes in these materials. Trace gas analysis of soil fluxes of radiatively important gases contribute to the understanding of decomposition and soil respiration. The DIRT study is addressing soil organic matter dynamics (DIRT), whereas decomposition processes are being evaluated through intersite studies (LIDET) and analysis of dynamics of coarse woody material. Paleoecological studies provide data on organic matter accumulation in lake sediments, peats, and organic soil horizons.

Nutrient Cycles -- A major focus of our research involves following changes in nutrient pools in plant biomass and the dynamics of inorganic and organic nutrient pools in the soil. Biosphere-atmosphere exchanges of nutrients are studied through nutrient inputs in precipitation and particulate material and nutrient losses in solution and gaseous form.

Pattern and Frequency of Disturbance -- Disturbance is a central theme of the Harvard Forest LTER and is addressed through field experiments, modeling, retrospective studies, and long-term measurements. The hurricane simulation is designed to increase our understanding of the consequences of natural disturbance. The N saturation experiment, the soil warming experiment, and the Environmental Measurement Station are designed to study how human influences affect ecosystem structure and function. The paleoecological work and soil/vegetation survey allow a clearer picture of past rates of change and the current implications of land-use practices. LTER II will explore these implications in a comprehensive and integrated framework.

C.4. Synthesis and Modeling

Several synthesis and modeling projects are described above (Sections A4 and B4). These include the development of models of forest ecosystem function and for the reconstruction of hurricane impacts. Both of these models work within a GIS and are used to make regional predictions. Currently there are four spatial scales at which GIS work is pursued (see Fig. 14). The hurricane model is applied at all four scales. The forest ecosystem model (PnET) has been used at both the site scale (20 m pixels) and at the regional scale (1 km pixels). At the 20 m scale, unique data on canopy chemistry have been derived using NASA's AVIRIS, an airborne, experimental, high spectral resolution instrument. At the 1 km scale, a model of regional physical and chemical climate has been developed to drive the model.

These sub-projects demonstrate the applicability of results from the Harvard Forest LTER to current significant environmental problems. We are contributing to the understanding and prediction of current C and trace gas balances in temperate zone forests and the probable responses of these systems to climate change and atmospheric deposition, all within the historical context of these changes. We are also contributing to the measurement of spatial patterns of critical ecosystem processes and the development of new remote sensing technologies.

C.5. Data Management

Emery Boose was the LTER computer and data manager from 1989 to 1992 and was responsible for all research and administrative data management activities, computer system design and installation, software development, and staff training. During the first phase of LTER our computer system expanded greatly through supplemental LTER funding. Expansion of computing facilities and increasing reliance of Harvard Forest staff on computer resources warranted the hiring of a site data manager (Dr. Richard Lent) in 1992. Dr. Lent is a wildlife ecologist with extensive experience in data management, study design, statistical analysis, and GIS. His duties include all aspects of data management for LTER activities and consultation with the scientific staff on data management issues, study design, and statistical analysis.

The Harvard Forest computer system is currently based on 66 and 33 Mhz 486 IBM-PC microcomputers. Major software applications (GIS, remote sensing, database management system) comply with the LTER minimum standard installation (MSI; see Foster and Boose 1991). For example, our GIS and remote sensing software provide raster and vector file compatibility with Arc/Info and Erdas; our database management system, dBASE-IV, supports structured query language. We will expand upon this core system with addition of a workstation-based local area network (LAN) and direct Internet connectivity. Cabling for the LAN will be installed during winter-spring 1994, with hardware and software acquisition to follow.

LTER data are stored on multiple media, currently floppy disk and Bernoulli cartridges (300 Mb capacity per cartridge with data compression). With acquisition of a workstation-based LAN, and upgrading of our 66 Mhz 486 PC's with optical disk and tape drives, additional high-capacity storage options will be available. Redundant backup of data files onto different media guards against failure of any one storage device and permits several options for retrieval of a given data set.

This approach provides varied functionality for storage, retrieval, and use of LTER data. Hard disk copies are used for active versions of data files and for high-speed direct access to the data sets by scientists. Tape backup is slower but inexpensive and will allow individual researchers to maintain high-volume backups of their data. Optical disks will be our primary long-term storage medium because of their longer shelf life compared to magnetic media. Bernoulli cartridges serve a dual role, both as high speed direct access storage and as backup media. They are well suited for handling files such as satellite images, which are large and require fast disk access for processing. The large (1000 Mb range) hard drives of the LAN file server will provide another medium for data archiving and also will provide on-line Internet access to LTER data.

Data received from an investigator are loaded onto a high-capacity storage device (e.g., hard disk drive or Bernoulli cartridge). Data compression techniques are used to archive large files, e.g., GIS and remote sensing images. Electronic copies of the data and accompanying documentation files are stored in a fireproof vault. These copies are made to floppy disk and/or tape cartridge, depending on the size of the file. Media are inspected and re-written periodically to ensure their continuing readability. Paper copies of field data sheets are kept on file in the archives and/or with the original investigator. These procedures ensure that LTER data will be stable and available to future researchers.

As we continue to upgrade our computer facilities, the workstation's large capacity disk will become the on-line repository for LTER data files. This machine will provide Internet access to data using software such as a Gopher server. Data files will follow a standard ASCII archival and data exchange format (e.g., Gorentz 1992). The LAN server's hard drive will be backed up at least weekly onto tape or optical disk. Multiple copies of these media will be stored in the Harvard Forest archives and at an off-site location. Individual researchers also maintain their own backup copies. Thus at least four copies of a given data file will be maintained in geographically separate locations.

Harvard Forest follows standard procedures for data quality assurance (e.g., Stafford *et al*. 1986). An investigator usually develops a study design in consultation with the Data Manager and/or a statistician. This process might include variable selection, sampling methods, statistical analyses, and design of field data forms and computer databases. The investigator provides the Data Manager with documentation for each data file produced. These metadata are entered into our data catalog and include the project title, core area, list of investigators, funding source, study sites, start and ending dates, a keyword list, abstract, methods, storage media, file format, and file structure (e.g., variable names and codes, missing data codes, and a description of each field with measurement units). Names of the actual data files and any supplemental documentation files stored with the data are also listed, along with the storage location and device on which the data reside. This device will usually be a hard drive or optical disk on our LAN but may also be an offline floppy disk, tape, Bernoulli cartridge, or optical disk. The user can then retrieve the actual data and more detailed documentation. This provides a link between the data catalog and the archived data sets for subsequent retrieval.

Data entry and validation are the responsibility of the individual researchers, using software of their choice. We currently use dBASE IV and Lotus for data entry at Harvard Forest. Both programs are exportable to ASCII format for easy transfer to other applications and LTER sites and for on-line retrieval and Internet access (see Gorentz 1992). After data collection in the field or laboratory, data entry is done by a technician or research assistant (unless the data have been collected electronically, e.g., by an automatic data logger). After initial data entry, a second person checks the computerized data against the original field forms. Entry errors are flagged and corrected. Any other apparent errors (e.g., possible equipment malfunction) are checked by the investigator. As an additional level of error checking, summary statistics and diagnostic graphics are computed for each variable, which help to detect outliers and suspect values. Any errors thus detected are corrected by the investigator, who makes the final decision as to the validity of suspect data. The resulting validated data set is then submitted to the Data Manager for archiving. Paper copies of the original field data sheets are filed for future reference.

Requests for LTER data are routed through the Data Manager, who refers the request to the original investigator if necessary. Harvard Forest follows in large part the standard LTER data management policy (Anon. 1990). This policy recognizes the need to provide the scientific community with LTER data sets in a timely manner, while at the same time protecting the interests of the investigators who collected the data. Four categories of data are recognized. The first, published data and metadata, are freely accessible to anyone without review. The second category, collective site data, usually routine measurements such as weather observations, are available for scientific purposes one year after the data are generated. The one year period allows sufficient time for the raw data to be validated, documented, and archived before it is made available. Third, original measurements by individual researchers are available for specific scientific purposes two years after the data are generated. Such data can be released earlier with permission of the researcher. The final data type is unusual long-term data collected by individual researchers. Such data can be withheld for longer periods if deemed necessary (with justification) by the investigator. Data in this category might include, for example, wildlife or plant population data, which often require collection for multiple years before any valid results can be inferred. All data sharing is done with the request that the original researchers receive due acknowledgement, including coauthorship where appropriate, and that the Harvard Forest library receive copies of any publications that make use of LTER data.

Any person with a valid scientific use for LTER data may make a request. Examples of use of LTER data by outside researchers include

Date	Data	Purpose
Jun 1991	Climate data (daily)	CO_2 models
Aug 1991	Climate, productivity	Climate study
Oct 1991	Description of soil warming	Inventory
Feb 1992	New England hurricane tracks	Disturbance study
Mar 1993	Climate data (daily)	Thesis project
Jul 1993	Climate data (daily, monthly)	Thesis project
Jul 1993	GIS layers (forest types)	Wildlife gap analysis

C.6. Intersite Activities

Scientists from the Harvard Forest LTER site have been very active in planning and participating in intersite studies. Jerry Melillo and Knute Nadelhoffer organized the NSF-sponsored workshop in 1989 that led to the development of the ongoing Long-term Intersite Decomposition Experiment Team (LIDET) project to study the controls of plant litter decay. John Aber, Jerry Melillo, and Knute Nadelhoffer are now participating in this long-term project, and the Harvard Forest is one of the twenty-seven sites at which the full range of litter materials is being decomposed.

Jerry Melillo and Paul Steudler are participating in the organization of a U.S. trace gas network that has the following six objectives: (1) to promote the comparability of trace gas flux measurements among sites; (2) to promote measurements in a diversity of ecosystem types; (3) to facilitate data synthesis; (4) to coordinate and foster interactions between measurement groups and modeling groups; (5) to provide ready means for testing and comparing gas flux models; and (6) to establish a long-term data archive for trace gas flux and associated data. The terrestrial LTER sites will serve as the core sites in the research network. The Harvard Forest LTER will play an important role in addressing scaling issues because we are using both small chamber and eddy correlation techniques to measure trace gas fluxes. Steve Wofsy's EMS will be featured in the Harvard Forest's contribution to network activities.

Knute Nadelhoffer is coordinating the development of an intersite study of the controls on soil organic matter storage in forest and grassland ecosystems. The study, as currently conceived, will include six LTER sites (Andrews, Bonanza Creek, Central Plains, Cedar Creek, Harvard Forest and Konza Prairie) and the La Selva site in Costa Rica. The overall goals of the study are to: (1) quantify the relative contributions of above- and belowground detritus to organic matter and nutrient storage in forest and grassland soils; (2) evaluate the roles of above- and belowground detritus in controlling soil biological activity and the dynamics of active and stabilized soil organic matter pools; and (3) improve models of soil organic matter and nutrient dynamics using information on plant-microbe-soil interactions, climate, vegetation, and soil physical/chemical attributes. Rich Boone and Knute Nadelhoffer have already established a proof-of-concept study at the Harvard Forest to provide preliminary data in support of the full multi-site proposal.

Our research team is also cooperating with Dennis Ojima, Bill Pulliam, and Bill Parton at Colorado State University in their application of the CENTURY model to LTER sites. Rich Boone and Emery Boose hosted a CENTURY workshop at the Harvard Forest in 1993, and are currently using CENTURY to explore the consequences of Harvard Forest land-use history on soil organic C stocks, soil respiration, and N mineralization.

Emery Boose and David Foster have worked closely with Bob Waide and colleagues from the Luquillo LTER site on the hurricane modeling project. The contrasts between Harvard Forest and Luquillo in terms of climate, vegetation, and physiography have provided an ideal setting to develop and test the HURRECON and EXPOS models. Future work on long-term hurricane disturbance regimes will continue to treat these two sites in parallel.

John Aber hosted a workshop at the University of New Hampshire to discuss the potential of remote sensing to contribute to on-site and inter-site research within the LTER network. The 25 attendees represented 15 LTER sites and the network office, with scientists from NASA and Rutgers University also present. Several recommendations resulted from the workshop, including the first outline of the network's policy on group purchase of remote sensing images. Letters were also generated presenting the group's strong support for both continued LANDSAT operation and the development of HIRIS, NASA's high spectral and spatial resolution instrument for the Earth Observing System.

The northeastern regional GIS and modeling effort involves PIs from the Hubbard Brook LTER site (Driscoll and Federer); data are exchanged between sites for model development and validation.

Two members of the Harvard Forest LTER participate in the GIS Working Group, David Foster (Chairman) and Emery Boose. Together they have convened meetings at the Harvard Forest and in Estes Park for representatives from across the LTER Network. The GIS Working Group has concentrated on defining appropriate technology for the Network (Minimum Site Installation) and identified common areas of research across the network. Foster and Boose co-authored a recent assessment of the rapid development of GIS in the LTER program and provided NSF with recommendations for future activity.

C.7. Related Research Projects

The well-characterized stands at the Harvard Forest have been utilized by a NASA-funded project to test advanced remote sensing technologies. The Accelerated Canopy Chemistry Program has supported detailed sampling of N, lignin, cellulose, and water contents of entire forest canopies over 30 m x 30 m to 50 m x 50 m plots throughout the forest. This sampling provides ground truth for application of the aircraft-mounted AVIRIS sensor, which acquires data at 20 m spatial resolution and 10 nm spectral resolution (400-2500 nm spectral range). From this data base, we have demonstrated that N and lignin concentrations of canopies can be determined within a scene, and that the resulting images of N concentrations can be used both to estimate the net C balance spatially over the Harvard Forest and to improve the mapping of species distribution by the fine scale delineation of species within physiognomic groups (e.g., separation of pine, hemlock, and spruce).

Experiments using ^{15}N tracers at ecosystem scales have been conducted at both Harvard Forest (Section A.3.a.) and the Bear Brooks Watershed in eastern Maine with support from the NSF Ecosystems Studies Program. We are collaborating closely with investigators conducting similar experiments now under way at six NITREX sites in Europe. Data that we have acquired at Harvard Forest and Maine, together with forthcoming data from the European forest ^{15}N tracer experiments, will provide a large data set on N transfers in a range of forest ecosystems that should allow for testing and modifying ecosystem simulation models.

Examination of the mechanisms regulating N retention on the chronic N plots, particularly the incorporation of most of the added N into soil organic matter, recently has been initiated with support from USDA. We are examining the significance of abiotic N immobilization, the relationships between biotic N immobilization and DOC concentrations, partitioning of immobilized ^{15}N among different organic matter fractions (microbial biomass, acid-soluble organic matter, and acid-insoluble organic matter), and C versus N limitations on soil microflora. Findings from this work should explain why the chronic N plots have such a large N storage capacity and should aid modeling efforts to examine the responses of northeastern temperate forests to atmospheric N deposition.

The Harvard Forest is the main focus of the DOE Northeast Regional Center of the National Institute for Global Environmental Change (NIGEC). The NIGEC program was initiated shortly after inception of the Harvard Forest LTER; the originators decided to make studies at the Harvard LTER the main focus, leveraging from the conceptual thinking that underlay the LTER at this site. The NIGEC program supports the EMS, the soil warming experiment, glasshouse and canopy photosynthesis measurements, the DIRT study, and modeling programs, for a total of about $800,000 annually. NIGEC has emphasized long-term studies with relevance to global issues, such as C storage in terrestrial ecosystems and fundamental questions that apply to scaling-up of local measurements. There has been enormous synergy between NIGEC and LTER, reflecting the interactive and cross-disciplinary activities; the level of coordination and collaboration between research groups has been enhanced by the strategic nature of the NIGEC program.

C.8. Dissemination of Information

Harvard Forest is in an advantageous position to communicate the results of its research activity to a wide audience through the activities of the Fisher Museum. Dr. John O'Keefe, a forest ecologist, serves as Fisher Museum Coordinator. A major aspect of his position involves disseminating an overview of current research to the broad academic community and the public.

Requests for general research information or interpretive programs are handled by the Museum Coordinator. Several long-term experiments have been incorporated into the Museum's interpretive nature trails. In 1991 Dr. O'Keefe produced a sixteen-minute, multi-image, slide/tape program describing the Harvard Forest LTER program and placing it within the context of research across the LTER Network. In 1992 an NSF grant funded conversion of this program to videotape for widespread distribution.

Scientific posters describing LTER research are displayed in the Museum after their use at meetings, reprints are available in the Museum shop, and research results are incorporated into permanent exhibits. Annually approximately 5,000 visitors (university and professional groups, secondary schools, general public) learn about our LTER activities through the Museum and several thousand see the slide show and are given interpretive tours.

Each winter Harvard Forest hosts an LTER Symposium attended by over one hundred scientists and graduate students. The symposium presents an opportunity for all scientists (within and outside the LTER) to review the research at the Harvard Forest and provides exposure for the LTER research program to the regional scientific community. Abstracts from the symposium are published and provide an excellent summary of current research.

C.9. Archives and Inventories

Inventories of the Harvard Forest biota include periodic surveys of vegetation since 1937 and recent surveys of birds and insects. Vegetation inventories (See Long-term data sets above) include: sampling of the 1200-ha area on a 10-30 year interval; a survey in 1937 and 1992 of vascular species on 269 permanent plots in the Prospect Hill Tract; periodic sampling of permanent plots to evaluate change following the 1938 Hurricane; and mapping every 5-15 years of three stands. In LTER I we sampled trees on all major study sites (e.g., N saturation plots, soil warming, EMS) and mapped trees on the hurricane simulation (control and treatment) and DIRT plots. Since 1990, phenology has been recorded for over 30 species of woody vascular plants.

Soils on the Harvard Forest were surveyed and mapped (1:4800 scale) by the Soil Conservation Service in 1944; the maps have been digitized, and original reports are available in the Harvard Forest Archives. In 1992-1993, as part of the Prospect Hill vegetation survey, soils were surveyed and samples collected at 172 locations to provide information on nutrient stocks and availability, and evidence of prior land-use. At each location, soil profiles were described and soils were collected from the forest floor and mineral soil (0-15 cm). Organic matter content, C and N content, pH, texture (mineral soil only), and bulk density are being determined for all samples. Samples will be stored in the Harvard Forest Sample Archive.

An archive (24 ft x 40 ft) for soil and plant samples is under construction as part of a 1993 NSF award to create a Nutrient Analysis Laboratory at the Harvard Forest. The archive is modeled after the JARS facility maintained by the U.S. Forest Service at Hubbard Brook and will have 7-ft high storage shelves, a large garage door, and a small heated area (ca. 13 ft x 20 ft). We will use the archiving and retrieval system developed at Hubbard Brook, with all samples marked with a bar code and electronically catalogued. The facility will provide storage for more than 32,000 samples in standard containers (4" x 2.5" ht). Other archives maintained for Harvard Forest samples include an herbarium and insect collections.

C.10. Leadership, Management, and Organization

The LTER program is administered at the Harvard Forest, location of many of the co-investigators, the Forest Manager, the Fisher Museum, and the financial office. As principal investigator and Director, D. Foster is responsible for project administration, coordination of Science Team meetings, and site representation in the LTER Coordinating Committee. The Science Team consists of the co-investigators, who all focus a large percentage of their research on the LTER and related projects at the Harvard Forest. The Science Team meets bi-monthly and is responsible for policy decisions (e.g., on data sharing), developing new research directions, formulating inter-site collaborations, and representing the LTER in the scientific community.

Results from the HF LTER are reviewed yearly at the Harvard Forest LTER Symposium. This forum for talks by LTER scientists is used to review progress and new directions. The symposium is widely advertised to scientists and students throughout the northeastern U.S. Symposium abstracts are published and distributed to all LTER and LMER sites, to NSF program directors, and to ecologists nation-wide. Thus, the meeting provides critical oversight for HF LTER program development and advertises opportunities for collaboration.

Administratively, the Harvard Forest is a department in the Faculty of Arts and Sciences of Harvard University. The Harvard Forest administers the Masters Program in Forestry and faculty at the Forest offer courses through the Department of Organismic and Evolutionary Biology, which awards the PhD degree. Forest management is undertaken by a Woods Crew directed by the Forest Manager. The Coordinator of the Fisher Museum oversees many of our education and outreach programs. Funding for the operation and staff of the Harvard Forest is derived from endowments, whereas research activities are supported with grants (see Appendix 1).

C.11. New Projects and Technologies

AVIRIS - The use of high spectral resolution remote sensing and NASA's AVIRIS instrument has been described in Section C.7. This is a new and still experimental extension of remote sensing which essentially puts the capabilities of full laboratory spectrometers into space. The instrument, designed to fly on the ER-2 aircraft, has roughly a 10 nm spectral resolution from 400-2500 nm and a 20 m spatial resolution. NASA has funded the Accelerated Canopy Chemistry Program to determine the potential of this technology to provide extensive appraisals of forest ecosystem function by measurement of the N, lignin, and cellulose concentrations of whole forest canopies. The Harvard Forest has been the most intensively examined of the four major research sites included in the program.

Environmental Measurement Tower - Technological innovation has been a principal feature of the EMS since its inception. We extended eddy correlation flux measurement from periods of a few days to many years, by developing computer-controlled, automatically calibrated instrument arrays along with integrated "smart" software to reduce vast amounts of data (eddy correlation channels (8) are recorded at 4 Hz continuously), introduce calibration factors, and flag data with potential problems as indicated by variations in calibration response and poor correspondence with correlates. Programs have been developed to determine the magnitude of systematic errors, such as the flux "lost" during stratified periods, using the large data base to compare when the forest should have been invariant, while factors introducing systematic errors changed.

We intend to extend our development of continuous autonomous measurement capability to soil respiration measurements. A soil flux chamber that can be used for continuous measurements is currently being tested, featuring a top that automatically closes for a brief period when needed and a null-point method for detection of CO_2 fluxes (like a large leaf chamber), designed to avoid artifacts associated with elevated (or depressed) CO_2 concentrations in the chamber. Arrays of such chambers will be linked to the eddy correlation flux system to help disaggregate observations of net ecosystem exchange, as observed from 30 m altitude.

During the next LTER period we will enter a new phase where hand-built electronic components will be replaced by units available commercially. We will switch from DOS to a UNIX-compliant operating system (QNX), allowing enormous streamlining of software. As in the past, both hardware designs and software will be made available to anyone requesting it. These efforts are intended to bring long-term flux measurements within reach of researchers at other LTERs and throughout the scientific community.

CO_2 sampling instrumentation - Gas analyzers are commonly used for purposes of environmental monitoring and control and for gas exchange measurements. A single analyzer is often connected to a bank of solenoids in order to maximize

its performance. These multiplexed systems are slow and for this reason are usually limited to six to ten channels. Efforts to improve the sampling rate by increasing the flow lead to pressure variations and loss of measurement accuracy.

We have developed a system that eliminates these problems with minimal mechanical complication. The design uses one additional solenoid to momentarily stop flow, allowing the analyzer sample cell to come to atmospheric pressure before a measurement is made. There are several important consequences of such a design. First, with zero flow the actual CO_2 measurement is made under ideal conditions and accuracy is maximized. Second, there is virtually no constraint on flow rate since the measurement is not made while gas is flowing through the sample cell. This allows the use of a powerful pump to rapidly purge the sample cell as each new channel is selected. Finally, because the measurements are made at atmospheric pressure, there is no need to balance the flow from different lines; sample tubes can differ somewhat in length and resistance, and the pump can be moved downstream of the analyzer.

A version of this sampling system has been reliably controlling CO_2 concentrations in the Bazzaz laboratory glasshouse since April 1992. This system has also been adapted for field measurement of CO_2 profiles in the Harvard Forest. Our field system presently has 18 channels and could be greatly expanded by adding additional channels. Both systems have sampling times of less than four seconds per channel. This type of system with a single analyzer is more economical than previous systems and is more reliable and accurate for comparative studies. This sampling method seems especially well suited for control of glasshouses, growth chambers, OTCs, and FACE experiments. Other potential applications include replicated gas exchange measurements and fine-scale microenvironmental studies.

Soil warming technology - We have successfully used buried heating cables to warm a series of 6 m x 6 m plots in a mixed hardwood stand. In the heated plot, the cables were installed in the upper mineral soil horizon at a depth of 10 cm and the soils warmed to 5°C above the ambient temperature of control plots. The soil temperature control system is completely automated and has been operating since July 1991. This technology has been adopted by other sites: the Hunting Forest in New York, the Howland Forest in Maine, and a sub-arctic woodland site in Abisko, Sweden. During 1991 a time domain reflectometry (TDR) system was designed, calibrated, and installed to replace our gravimetric technique for soil moisture.

Broad-scale ^{15}N applications - The development and use of ^{15}N tracers at ecosystem scales at the Harvard Forest and other New England sites (Sections A.3.a, B.4 and C.7) is a promising new approach to the study of N cycles and C-N interactions that could prove to be a powerful means of testing and improving our understanding of controls on biogeochemical cycles.

Hurricane models - The use of computer models to reconstruct hurricane wind conditions at remote forest sites (HURRECON) and to predict the wind-shielding effects of topography at a landscape scale (EXPOS) is a new and promising approach to a difficult problem: how to unravel the roles of storm meteorology, local topography, and vegetation in the complex patterns of forest damage created by hurricane winds. This approach can be tested directly against meteorological observations and forest damage assessments on a wide range of spatial scales.

C.12. Supplemental support

Supplemental funds awarded by NSF to the HF LTER grant during the current grant period have been used for the following purposes:

1. Computer hardware, software, and networking. Supplemental funds have revolutionized the Harvard Forest computer system, leading to greatly improved capability for GIS, remote sensing, data management and analysis, and electronic communications. Improvements include: computers (primarily 66 MHz 486 PCs with 400 MB hard disks and XGA graphics), purchase and upgrades of software, and 14.4 kbps modems. These improvements have been critical to ongoing research and file exchange over the Internet. Supplemental funds will be used to install Ethernet cable to all Harvard Forest offices and labs, and to cover the costs of equipment (Sun computer, router computer, 56 kbps modems) and installation for a full Internet connection and LAN.

2. Computer personnel. E. Boose was supported for one half year to install and support new computer systems and GIS software at the Harvard Forest (1989)

3. REU program. Funds from NSF-REU, Harvard Forest, and the Mellon Foundation have enabled the development of the Harvard Forest Summer Undergraduate Research Program, which involves over 30 students in independent and team-based research.

4. ROA program. Richard Bowden (Assistant Professor at Allegheny College) was supported to study trace gas fluxes in the simulated hurricane blowdown, the effects of soil moisture on methane uptake, and soil respiration in the DIRT plots (summer 1992). This opportunity launched a very active research program by Rich at the Harvard Forest. Annually he coordinates the Summer Undergraduate Research Program and supervises work by undergraduate students.

5. Aerial photo interpretation. A zoom transfer scope was acquired to transfer stereo photographic images to base maps for GIS analysis. This system now forms the base for extensive historical land-use reconstructions.

6. Systematics/biodiversity equipment. Two Cornell insect cabinets with drawers, two herbarium cabinets, field collection and curation equipment, and electrophoresis equipment were purchased to accommodate the growing plant and insect collections at the Harvard Forest and for population studies.

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