LONG-TERM ECOLOGICAL RESEARCH (LTER)

PROPOSAL TO THE DIVISION

OF BIOTIC SYSTEMS AND RESOURCES

NATIONAL SCIENCE FOUNDATION

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The ecology and developmental biology of nitrogen fixation in
actinomycete-nodulated angiosperms

DEB-81-06952 $139,788

8/15/81 to 1/31/84   John G. Torrey and John D. Tjepkema

Summary of Results:
    National Science Foundation support for research on the ecology
and developmental biology of nitrogen fixation in actinomycete-
nodulated angiosperms began in June 1977 under NSF research grant
DEB77-02249 with J. G. Torrey and J. D. Tjepkema as principal
investigators. A new grant continuing this research was initiated in
August, 1981 under grant number DEB-81-06952. A series of
publications acknowledging support of the National Science Foundation
began in 1978 and continued beyond the two successive grant periods.
Listed below are publications acknowledging the support from grant
DEB-81-06952.

    Three major areas of research were studied under this research
grant :the isolation, culture and biology of the filamentous
bacterium *Frankia* of the Actinomycetales, analysis of the infection
of susceptible woody dicot host plants and early nodule development,
and the ecophysiology of nitrogen-fixing actinorhizal plants,
especially members of the Myricaceae.

1. Isolation, culture and biology of *Frankia*. The first confirmed
isolation and successful culture of *Frankia* was achieved at the
Harvard Forest in 1977 by Callaham, DelTredici and Torrey and was
published in 1978 (Science 199 :899-902). Since that time a number
of successful isolations of *Frankia* strains from actinorhizal host
plants have been achieved. Berry isolated *Frankia* strain HFPArI3
from *Alnus rubra* in 1979 and Baker isolated *Frankia* strain Eull from
Elaeagnus umbellata in 1979. This list was extended significantly by
Zhang in 1984 (Zhang et al. 1984) by isolations of *Frankia* strains
from *Casuarina cunninghamiana* (HFPCcI3), from *Allocasuarina
lehmanniana* (HFPAI1I1) and from *Myrica gale* (HFPMgIl). These strains
all showed significant differences among themselves, not least of
which was their capacity to infect or to be non-infective on a range
of host species.

    Studies of the characteristics <u>in</u> <u>vitro</u> of these cultured
isolates led to identification of some of their distinctive features,
including diagnostic polar lipid contents and the nature of stored
free sugars (Lopez et al. 1983). The identification of trehalose as
a major microbial storage disaccharide (Lopez et al. 1984) led to
studies of its metabolism and of the enzyme trehalase that makes it
available as a substrate (Lopez and Torrey 1985, Arch. Microbiol.
143:209-215). Subsequent studies have pursued the metabolism of
glucose in *Frankia* (Lopez and Torrey 1985, J. Bact. 162:110-116).

2. Root hair infection and nodule development. Two types of
infection of host plants by *Frankia* are now known, viz., root hair
infection and direct intercellular penetration. The more common type
is probably via root hair infection, shown to occur in response to

seedling inoculations in *Comptonia peregrina*, in *Casuarina cunninghamiana* and in *Myrica gale* by Callaham, Newcomb, Torrey and Peterson (Bot. Gaz. 140(Suppl.) :S10-S14, 1979). Berry and Torrey (1983) extended these observations in studies of root hair infection in *Alnus rubra*, showing effects on root hair deformation followed by root hair penetration. Berry and Torrey (1985) demonstrated the practical use of pure cultured *Frankia* strain (HFPArI3) in seedling inoculation and establishment.

In some cases, inoculation with cultured *Frankia* or suspensions prepared from root nodules led to infection but no dinitrogen fixation. Such ineffective associations and the nodular development that accompanies such ineffectivity were studied by VandenBosch and Torrey (1983, 1984, 1985). Notable in these studies were the occurrence and detrimental effect of sporulation by the endophyte within the nodule in some host-microbial combinations.

3. Ecophysiology of nitrogen-fixing actinorhizal plants. In 1982 Schwintzer, Berry and Disney (Can. J. Bot. 60 :746-757) published a comprehensive phenological account of nodule development in *Myrica gale* growing in different field situations at the Harvard Forest. This research served as the introduction to our subsequent work, both in the field and in the greenhouse and in controlled environment chambers, on members of the Myricaceae, including especially *Myrica gale*, *M. cerifera*, *M. pensylvanicum* and *Comptonia peregrina*. Schwintzer et al. (1982) demonstrated the seasonal activity of dinitrogen-fixation in relation to seasonal changes in temperature which were reflected in nodule growth and in internal changes in the microbial endophyte. Subsequent studies by Schwintzer (1983) and Schwintzer and Lancelle (1983) defined environmental changes influencing and determining the levels of symbiotic nitrogen fixation in the peatland environment inhabited by *Myrica gale*.

VandenBosch and Torrey (1984, 1985) demonstrated that sporulation by *Frankia* in root nodules of *M. gale* and *Comptonia peregrina* led to premature senescence of endophyte vesicles and rapid cessation of nitrogenase activity.

Work on these experimental systems has continued since 1984 to the present time under other auspices than the National Science Foundation.

List of publications arranged by date:

Schwintzer, C. R. 1983. Nonsymbiotic and symbiotic nitrogen fixation in a weakly minerotrophic peatland. American Journal of Botany 70:1071-1078.

Schwintzer, C. R. and S. Lancelle. 1983. Effect of water-table depth on shoot growth, root growth, and nodulation of *Myrica gale* seedlings. Journal of Ecology 71:489-501.

Lopez, M. F., C. S. Whaling and J. G. Torrey. 1983. The polar lipids and free sugars of *Frankia* in culture. Canadian Journal of Botany 61:2834-2842.

Berry, A. M. and J. G. Torrey. 1983. Root hair deformation in the infection process of *Alnus rubra*. Canadian Journal of Botany 61:2863-2876.

VandenBosch, K. A. and J. G. Torrey. 1983. Host-endophyte interactions in effective and ineffective nodules induced by the endophyte of *Myrica gale*. Canadian Journal of Botany 61:2898-2909.

Murry, M. A., M. S. Fontaine and J. G. Torrey. 1984. Growth kinetics and nitrogenase induction in *Frankia* sp. HFPArI3 grown in batch culture. Plant and Soil 78:61-78.

Zhang, Z., M. F. Lopez and J. G. Torrey. 1984. A comparison of cultural characteristics and infectivity of *Frankia* isolates from root nodules of *Casuarina* species. Plant and Soil 78:79-90.

Lopez, M. F., M. S. Fontaine and J. G. Torrey. 1984. Levels of trehalose and glycogen in *Frankia* sp. HFPArI3 (Actinomycetales). Canadian Journal of Microbiology 30:746-752.

VandenBosch, K. A. and J. G. Torrey. 1984. Consequences of sporangial development for nodule function in root nodules of *Comptonia peregrina* and *Myrica gale*. Plant Physiology 76:556-560.

VandenBosch, K. A. and J. G. Torrey. 1985. Development of endophytic *Frankia* sporangia in field- and laboratory-grown nodules of *Comptonia peregrina* and *Myrica gale*. American Journal of Botany 72:99-108.

Berry, A. M. and J. G. Torrey. 1985. Seed germination, seedling inoculation and establishment of *Alnus* spp. in containers in greenhouse trials. Plant and Soil 87:161-173.

RESULTS FROM PRIOR NSF SUPPORT - DAVID R. FOSTER

DPP-8312160 $19,547   Peatland Development in Northern Sweden

9/1/83 to 2/28/85   D. R. Foster and H. E. Wright

This grant from Polar Programs was used in conjunction with travel funds from the Fulbright Foundation and a research stipend from the Swedish National Research Council to fund one year of post-doctoral research on mires for D. R. Foster at Lund University. The research concentrated on Krackelbacken Fen in central Sweden. Results included a numerical analysis of the modern flora and pollen assemblages, a detailed description of landform features in relation to height above the water table, the completion of a regional pollen diagram, and stratigraphical analysis of long cores. This project demonstrated the utility of a comparative study of mires in northern Europe and North America.

Results from this project have been presented at meetings of the Ecological Society of America (Foster 1985b) and International Geological Correlation Program (Foster and Wright 1987), at a mire

workshop in Abisko, Sweden (Foster 1986), and in recent publications (Foster and Fritz 1987, Foster and Wright 1987, Foster, King and Santelman 1988).

Foster, D. R. and S. C. Fritz. 1987. Mire development, pool formation, and landscape processes of patterned fens in Dalarna, central Sweden. Journal of Ecology 75:409-437.

Foster, D. R. and H. E. Wright. 1987. Mire development in eastern North America and central Sweden. Paleohydrological changes in the temperate zone in the last 15000 years. Lundqua Report, University of Lund. 26:37-39.

Foster, D. R., G. A. King, and M. L. Santelman. 1988. Patterned mires in western Labrador: floristics, landscape features, and development. Canadian Journal of Botany. In press.

INT-8503849 $24,550   Patterns in Boreal Peatlands

2/15/85 to 5/31/87   H. E. Wright, D. R. Foster and P. H. Glaser

   This grant initiated comparative paleoecological studies on peatland landforms and development in Ireland, Sweden and Labrador. P. H. Glaser and H. E. Wright have been responsible for the Irish sites in collaboration with W. A. Watts and R. Bradshaw at Trinity College, Dublin. D. R. Foster and H. E. Wright have been responsible for the Swedish and Labrador work.

   Sites representing nearly the complete range of mire types (fen, bog and palsa) and mire surface pattern found in the boreal and subarctic region were selected in Sweden for comparison with North American mires. Studies have included vegetation analysis, water chemistry, and topographic description of the mires and macrofossil and pollen analysis of long peat cores. Results have been presented at International Symposia (Foster 1985. Foster and Wright 1987) and are in press (Glaser and Foster 1985, Foster and Glaser 1986, Foster et al. 1988, Foster and Wright 1988, Aaby and Foster 1988).

Glaser, P. G. and D. R. Foster. 1985. Vascular flora of raised bogs in southeastern Labrador and its phytogeographical significance. Canadian Journal of Botany 62:1361-1364.

Foster, D. R. 1985. The origin and development of patterned mires in Labrador, Canada. *In* Future Directions for Research in Nouveau -Quebec. McGill Subarctic Research Paper No. 39:61-75.

Foster, D. R. and P. H. Glaser. 1986. Raised bogs in Labrador, Canada: classification, distribution, vegetation, and recent dynamics. Journal of Ecology 74:47-73.

Foster, D. R., H. E. Wright, M. Thelaus and G. A. King. 1987. Bog development and the dynamics of bog landforms in central Sweden and eastern Canada. Journal of Ecology. In press.

NSF-BRRP $75,795   Facility Support at Harvard Forest

08/15/87-01/31/89   J. G. Torrey, E. M. Gould, Jr. and D. R. Foster

    This current grant is being used to upgrade research, computer and archival facilities at the Harvard Forest with particular emphasis on forest ecology, geographic information systems (GIS), and forest microbiology. The purchase of an IBM PS/2 model 80, line digitizer, pen plotter, laser printer and related equipment is serving as the core of our efforts to develop GIS and implement it in research as well as data management. GIS research focuses on four spatial scales: landscape-scale patterns of vegetation, forest dynamics and disturbance processes, stand-scale analysis and modeling of canopy gap formation and regrowth, organism-scale mapping and modeling of meristem location, type and reiteration in contrasting herb, shrub and tree species and sub-organism scale analysis of root growth.

    Data management tasks handled with the new equipment by our computer manager, Emery Boose, include on-line bibliographic searches of the Harvard Forest Library, GIS-based maps of the Harvard Forest for decision-making and data storage, and records of Forest inventories and research activities.

    Additional facilities improvements include: expansion and upgrading of our fire-proof vault for archival storage; modernization of photographic and darkroom facilities; conversion of a garage bay into a walk-in laboratory for handling bulk soil samples and plant materials, purchase of a walk-in refrigerator and large freezer, and construction of a 2400 sq. ft. pole barn for storage of large machinery and equipment.

    Institutional support from the Dean of the Faculty of Arts and Sciences has contributed significantly to this facilities improvement and labor expenses have been kept to a minimum by the use of our woods and maintenance crew for building construction and renovation.

RESULTS FROM PRIOR NSF SUPPORT - PAUL A. STEUDLER

    Sulphur gas fluxes between temperate and boreal forest soils and the troposphere (Grant #ATM-8505280 - $234,700; renewed ATM-8714673 - $477,457 for 3 years).

P. A. Steudler and J. M. Melillo.

    A two-year pilot study of COS and CS_2 fluxes initiated in 1985 was organized around the following questions: 1) What are the spatial and temporal variabilities associated with the COS and CS_2 fluxes between the soil and the atmosphere at a single site? and 2) Is there significant difference in the magnitude of sulfur gas fluxes between the soil and the atmosphere at forest sites receiving different levels of acid precipitation? and 3) Is it possible to demonstrate

through experimental manipulation that nitrogen inputs to a forest
soil have an influence on sulfur gas emissions from that soil?

Results from four replicate chambers in each stand indicate
considerable spatial and temporal variability in sulfur gas fluxes.
Spatial variation ranged from a minimum of 17% to a maximum of 47%
standard error of the mean hourly value. Diurnal variations were
also recorded suggesting that a few measurements made during any one
time of the day may not be sufficient to adequately estimate daily
fluxes. In addition, since the emissions appear to have strong
seasonal patterns with high releases in spring and early fall,
measurements must be made on several seasons not just during one part
of the year to obtain a good annual flux estimate. Studies along
transects in North American and Scandinavia suggest that there is a
positive correlation between the magnitude of S and N inputs in
precipitation and the rates of COS and CS_2 emitted from the sites.

RESULTS FROM PRIOR NSF SUPPORT

Aber and Melillo received three sequential awards beginning in
1978 for the study of organic matter and nutrient dynamics in
northern temperate forest ecosystems:

1. DEB 7804260, DEB 7908250
   Decomposition Processes in Forest Soils
   June 1978-May 1980 $170,000

2. DEB 8005081
   Organic Matter and Nitrogen Dynamics in Forest
    Ecosystems
   June 1980-November 1983 $375,000

3. BSR 8317531
   Carbon-Nitrogen Dynamics and Rates of Below Ground
   Turnover Along a Nitrogen Availability Gradient
   in Forest Ecosystems
   February 1984-August 1986 $608,000

These have allowed study of most of the important processes of
nitrogen and organic matter transformation in the systems examined,
many of them at the Harvard Forest. Measurements have included:
nitrogen mineralization and uptake, primary production and
allocation, decomposition, denitrification, and water use. A list of
selected publications follows. A more complete list can be found in
the CVs of Aber and Melillo.

Publications

Aber, J. D. and J. M. Melillo. 1980. Litter decomposition: Measuring
     relative contributions of organic matter and nitrogen to forest
     soils. Canadian Journal of Botany 58:416-421.

Aber, J. D. and J. M. Melillo. 1982. Nitrogen immobilization
in decaying hardwood leaf litter as a function of initial nitrogen
and lignin content. Canadian Journal of Botany. 60:2263-2269.

Aber, J. D., J. M. Melillo and C. A. Federer. 1982. Predicting the
effects of rotation length, harvesting intensity and
fertilization on fiber yield from northern hardwood forests in
New England. Forest Science 28:31-45.

Aber, J. D., J. M. Melillo, K. Nadelhoffer, C. A. McClaugherty and J.
Pastor. 1985. Fine-root turnover in forest ecosystems in
relation to quantity and form of nitrogen availability: A
comparison of two methods. Oecologia 66:317-321.

McClaugherty, C. A., J. D. Aber and J. M. Melillo. 1984.
Decomposition dynamics of fine roots in forested ecosystems.
Oikos 42:378-386.

McClaugherty, C. A., J. D. Aber and J. M. Melillo. 1982. The role of
fine roots in the organic matter and nitrogen dynamics of two
forest ecosystems. Ecology 63:1481-1490.

McClaugherty, C. A., J. Pastor, J. D. Aber and J. M. Melillo. 1985.
Forest litter decomposition in relation to soil nitrogen
dynamics and litter quality. Ecology 66:266-275.

Melillo, J. M. and J. D. Aber. 1984. Nutrient immobilization in
decaying litter. In: Research opportunities in ecology in the
1980's. NATO conference series: Ecology Vol. 6. Plenum Press.

Melillo, J. M., J. D. Aber and J. M. Muratore. 1982. Nitrogen and
lignin control of hardwood leaf litter decomposition dynamics.
Ecology 63:621-626.

Melillo, J. M., J. D. Aber, P. A. Steudler and J. P. Schimel. 1983.
Denitrification potentials in a successional sequence of
northern hardwood stands. Ecological Bulletin (Stockholm)
35:217-228.

Nadelhoffer, K. J., J. D. Aber and J. M. Melillo. 1985. Fine root
production in relation to net primary production along a
nitrogen availability gradient in temperate forests: a new
hypothesis. Ecology 66:1377-1389.

Nadelhoffer, K. J., J. D. Aber and J. M. Melillo. 1983. Leaf litter
production and soil organic matter dynamics along a nitrogen
availability gradient in southern Wisconsin (USA). Canadian
Journal of Forest Research 13:12-21.

Pastor, J., J. D. Aber, C. A. McClaugherty and J. M. Melillo. 1984.
Above ground production and N and P cycling along a nitrogen
mineralization gradient on Blackhawk Island, Wisconsin. Ecology
65:256-268.

HARVARD FOREST LTER

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ABSTRACT

The Harvard Forest in central Massachusetts has been an active research facility for the study of forest ecosystems since 1907. A group of researchers representing 5 institutions proposes that the Harvard Forest be added to the LTER network.

The central theme of the Harvard Forest LTER is a comparison of historically-important physical disturbances and recent and projected chemical disturbances in terms of their effect on forest ecosystem structure and function. One fundamental question is whether chronic, low-level additions of pollutants can result in more lasting alteration of ecosystem function than does the historical regime of disturbance to which components of the system may be adapted.

Four core experiments involve: 1) re-creation of physical types of disturbance, including catastrophic hurricane blowdown, smaller windthrows and selective mortality of overstory species, 2) simulation of chronic chemical disturbance by altering inputs of important nutrients or pollutants, 3) interactions between physical and chemical disturbances, and 4) repetition of treatments to assess the range of variation in organism and ecosystem response. Synthesis of the research will be achieved through the application of remote sensing, geographic information systems, and modeling.

The integrated research group has a long history of interaction at the Harvard Forest and has expertise in physiological ecology, plant development, forest microbiology, paleoecology, ecosystem studies and atmospheric chemistry and experience with such research tools as remote sensing, geographic information systems, stable isotopes, ecosystem and atmospheric modeling, micrometerological techniques, and trace-gas measurement.

The Harvard Forest group seeks to integrate its expertise into the LTER network through active collaboration with researchers at other sites.

I. **INTRODUCTION** - The forests of central New England comprise a dynamic ecosystem that has been shaped through geological and historical time by climate change, natural disturbance, species elimination through introduced pathogens and human activity (Paillet 1982, Tweery and Patterson 1985, Davis 1986, Jacobsen *et al.* 1987). As documented in the paleoecological record, a series of species migrations during the Holocene produced major changes in the composition of upland and wetland forests. The temporary loss of hemlock from the forests 4800 yrs B.P. has been paralleled recently by the elimination of chestnut as a canopy tree and decline of elm and beech from introduced pathogens. In the recent past a major form of natural disturbance has been the creation of gaps of various size in the forest canopy by individual tree-death, wind-throw, and hurricanes (Griffith *et al.* 1930, Henry and Swan 1974, Oliver and Stephens 1976, Foster 1988b). The continuing productivity of forests in the region through this long history of change, attests to the resilience of these ecosystems in the face of physical or biological disturbance.

Disturbance of another kind now poses a contemporary threat to the continued health of New England forests. The global earth-atmosphere system is believed to be undergoing unprecedented change in response to broad-scale human activities (National Research Council 1983, 1986). Industrial and agricultural activities release pollutants, such as oxides of nitrogen and sulfur that change the chemistry of the atmosphere over vast scales. Released CO_2 and halocarbons are accumulating in the atmosphere and are expected to cause a marked warming of the climate and to reduce the stratospheric ozone layer. As a result of these global changes, the last 30 years has seen a significant increase in the deposition of different forms of air pollution to New England forests. An important question is: are these forests as resilient (or resistant) to chronic, chemical disturbance as they are to physical or biological disruption?

The central theme of the research proposed for the Harvard Forest LTER is a comparison of historically-important physical disturbances and recent and projected chemical disturbances in terms of their effect on ecosystem structure and function.

Fundamental questions addressed by the proposed research are:

1) How do ecosystems and the organisms comprising them respond to natural, episodic disturbance as opposed to chronic chemical disturbance?

2) Can chronic, low level additions of pollutants result in more lasting alteration of ecosystem function than does the historical regime of disturbance to which components of the system may be adapted? and

3) Are there significant interactions between physical and chronic chemical disturbance that cannot be predicted on the basis of each disturbance type independently?

Measurements of net trace gas emissions are given particular emphasis in this proposal as they represent the link between atmospheric deposition and the role of forests in atmospheric chemistry and the global heat balance. Comparing fluxes from control and physically versus chemically disturbed systems will determine the contribution of atmospheric deposition to increasing emissions of trace gases from forests in the region. This, in turn, will have major implications for atmosphere-biosphere interactions and global change questions, as well as revealing much about ecosystem function and stability.

The studies required to answer disturbance-response questions are, of necessity, long-term. They must allow for both the cumulative effects of chronic chemical disturbance and the long-term responses of the biota and soils. Physical disturbance initiates a long-term series of changes in ecosystems that will be compared with responses to chemical disturbance.

The core experiments proposed here include:

1) Re-creation of physical types of disturbance, including catastrophic hurricane blowdown, small canopy gap windthrow, and selective standing-death of dominant overstory tree species;

2) Simulation of chronic chemical disturbance by alternating inputs

of important nutrient or pollutants;

3) Interactions between physical and chemical disturbances to assess the role of chronic chemical deposition in changing the normal patterns of system response to physical disturbance;

4) Repetition of physical disturbance treatments to assess the role of chance variation in annual weather patterns and species' reproductive behaviors on the composition and function of the recovering ecosystem.

A set of complementary studies of long-term nature include:

1) The effects of litter addition/removal and coarse woody debris on biogeochemical circulation;

2) Monitoring the role of herbivory by large mammal (white-tailed deer) on community regeneration following hurricane windthrow; and

3) The effects of plant development and shoot architecture on deterministic versus opportunistic species' responses to disturbance.

The understanding gained through these studies will be placed in a comprehensive historical context through continued analysis of vegetation dynamics, disturbance regimes, and climate change and through the characterization of ambient levels of atmospheric pollution.

The disturbance and response patterns we propose to study occur on a variety of spatial and temporal scales, and require synthesis of information from many disciplines. We propose to provide a framework for integration of results through a combination of modeling, remote sensing and geographic information system (GIS) applications. We will incorporate macrometeorological data and modifications due to site and forest structure into models that predict micrometeorological patterns in intact and disturbed forests. We will synthesize current modeling efforts in environmental plant physiology and plant development and architecture to predict whole-plant response to above- and below-ground microenvironmental variation measured in the field. We will extend existing annual-time-step models of forest ecosystem function to include weekly-time-step models of highly variable events such as trace gas emissions, and of soil temperature, water, and labile carbon pools required to drive emission estimates. These same plot-level models will

be extended in the spatial domain by further development of an existing GIS for the Harvard Forest and by continuing on-going cooperative work with Harvard's Laboratory for Computer Graphics and Spatial Analysis and NASA's Ames Research Center. Prediction of biogeochemical changes over longer time scales, which must allow for changes in species composition, will be accomplished using a modified version of the FORTNITE model (Aber *et al.* 1982). Models of gap formation based on structural variables (T. Sipe, unpublished) will be expanded and linked to FORET-style simulation models to generate a cyclic forest growth and gap disturbance model. As this and other models employed in our project are very similar in structure to those employed in other LTER projects (e.g. FORET/Linkages: Shugart and West 1980, Pastor and Post 1986) we will coordinate our efforts with modelers at other LTER sites.

II. THE HARVARD FOREST AS AN LTER SITE – The proposed research at the Harvard Forest brings particular strengths to the LTER network of sites including: a) a broad-based interdisciplinary research team with especial expertise in physiological ecology of microbes and plants (Torrey and Bazzaz), population biology (Bazzaz), plant architecture and development (Tomlinson), paleoecology and community ecology (Foster and Patterson), ecosystem studies (Aber, Nadelhoffer) and atmospheric chemistry (Wofsy, McElroy, Steudler), and experience with a variety of state-of-the-art research tools such as remote sensing (Aber), geographic information systems (Tomlin), stable isotopes (Nadelhoffer), micrometeorological techniques used in the study of system-wide metabolism (Wofsy and McElroy), molecular sieves and gas chromatography used in the study of trace gas exchanges between the biosphere and the atmosphere, and ecosystem and atmospheric modeling (Aber and Wofsy respectively) (Table 1.); b) a diversity of extensively studied and well-documented ecosystem types; c) well-equipped and well-maintained facilities and an experienced support staff; and d) a long history of comprehensive research in ecological studies and a commitment to long-term study and data management. The scientific team comprising Harvard Forest LTER is eager to join the larger scientific team of the LTER network. We are ready to participate in intersite comparisons and we

are willing to share our scientific and technological skills with the network.

A. Interdisciplinary Research Team - Ongoing studies at the Forest by researchers from the Harvard Forest (Foster, Tomlinson, Torrey), Department of Organismic and Evolutionary Biology (Bazzaz), Department of Landscape Architecture (Forman) and Laboratory for Computer Graphics and Spatial Analysis (Tomlin) at Harvard University, the Ecosystem Center at Woods Hole (Melillo, Nadelhoffer, Steudler), the University of New Hampshire (Aber), Clarkson University (Antibus, Linkins, McClaugherty) provide a background and framework for the proposed research. This group is particularly strong in organismic, community and ecosystem studies and in cartographic analysis and modeling. A significant complement to this established research effort is brought by investigators from the Department of Earth and Planetary Sciences at Harvard University (McElroy, Wofsy) in atmospheric sciences and trace-gas analysis and from the Forestry Department at the University of Massachusetts (Patterson) in paleoecology. This group provides experience in long-term studies and a strong interdisciplinary background.

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Table 1. Research Components and Investigators for the Integrated Study of Forested Ecosystems

Research Component	Investigator
Vegetation, Climate and Disturbance	Foster, Patterson
History Macroclimate and Atmospheric	Wofsy, McElroy
Chemistry Forest Microbiology	Torrey, Antibus
Ecophysiology	Bazzaz
Micrometeorological Patterns	Bazzaz, Wofsy
Plant Development/Architecture	Tomlinson
Population Structure and Dynamics	Bazzaz
Community Structure and Development	Aber, Foster, Bazzaz
Structural Effects of Disturbance	Foster
Decomposition and Mineralization	McClaugherty, Aber, Nadelhoffer
Fine Root Dynamics and Soil Enzymes	Linkins, McClaugherty, Aber
Nutrient Cycling, N,S	Steudler, Nadelhoffer
Organic Matter Inputs	Nadelhoffer
Productivity and Biomass	Aber, Patterson
Atmospheric Exchange	Wofsy, McElroy, Steudler
Landscape Ecology	Forman

Geographic Information Systems	Tomlin
Remote Sensing	Aber
Modeling	Aber, Wofsy, Bossert
Data Management	Foster

B. Site Location and Description - The 1200-hectare Harvard Forest in north-central Massachusetts (Fig. 1) has been operated as a silvicultural and ecological research facility by Harvard University since 1907. The Forest lies in the New England Upland physiographic region, with moderate local relief ranging from 120m to 410m above sea level. A bedrock dominated by granite, gneiss, and schist is generally overlain by sandy-loam glacial till soils that are moderate to well drained, acidic, and average 3 meters in thickness. Local variations in parent materials, textures, alluvial and colluvial deposits, and slope produce poorly drained and excessively drained sites as well. The regional climate is cool temperate (summer mean 20°C, winter -4°C) and humid, with precipitation (annual mean 110cm) distributed fairly evenly throughout the year.

The Forest lies in the Transition Hardwood-White Pine-Hemlock forest region (Westveldt *et al.* 1956). Dominant species include red oak *(Quercus borealis)*, red maple (Acer *rubrum),* black birch *(Betula lenta),* white pine *(Pinus strobus),* and hemlock *(Tsuga canadensis).* On drier soils white oak *(Quercus alba),* black oak *(Q. velutina),* hickory *(Carya ovata)* and, formerly, chestnut *(Castanea dentata)* increase. Cool, moist, but well-drained sites support a northern mixed forest of yellow birch *(Betula lutea),* beech *(Fagus grandifolia)*, sugar maple *(Acer saccharum),* paper birch *(Betula papyrifera)*, ash *(Fraxinus americana)*, hemlock and white pine, whereas red spruce *(Picea rubens)*, black spruce *(P. mariana* and larch *(Larix laricina)* occupy oligotrophic peatlands. Approximately 7% of the Forest is occupied by plantations of diverse compositions and age. Detailed stand records, including prior site history, and repeated growth measurements are available for each plantation and many natural stands. A well-developed network of woods roads provides good access to all areas in the Forest.

C. Facilities - The physical plant of the Harvard Forest is unusually complete as a base for experimental research in forest ecology,

Figure 1. Forest Classification for New England (Westveld et al. 1956)
Showing the Location of the Harvard Forest.

NATURAL FOREST VEGETATION ZONES
OF NEW ENGLAND

COMPILED BY
COMMITTEE ON SILVICULTURE
SOCIETY OF AMERICAN FORESTERS
NEW ENGLAND SECTION

1955

HARVARD FOREST

LEGEND

1 SPRUCE-FIR-NORTHERN HARDWOODS *
2 NORTHERN HARDWOODS-HEMLOCK-WHITE PINE
3 TRANSITION HARDWOODS-WHITE PINE-HEMLOCK
4 CENTRAL HARDWOODS-HEMLOCK-WHITE PINE
5 CENTRAL HARDWOODS-HEMLOCK
6 PITCH PINE-OAK

0   50   100

MILES

ecosystem sciences and forest microbiology. The brick headquarters complex consists of Shaler Hall, the Controlled Environment Facility (CEF), a large garage and laboratory complex and the Fisher Museum.

Shaler Hall, nearly 15,000 square feet of space, contains offices, research laboratories, a seminar room, the Harvard Forest Archives and a library of 22,000 volumes. In addition Shaler Hall provides dormitory accommodation for twenty-five persons and dining room and kitchen facilities. Common research space includes a photographic suite and darkroom, a graphics and mapping room, a projection and film analysis room for video microscopy, and seven microcomputers with on-line access to the Harvard University computer center in Cambridge. Three laboratories in Shaler Hall are used primarily for physiological, morphological and nutrient studies. One laboratory has recently been renovated with funding from the Mellon Foundation for research in forest microbiology. A facilities grant from NSF is supporting the purchase of an IBM PS/80, digitizing board and related computer equipment for ongoing research in GIS.

The Controlled Environment Facility serves as the bridge between field experiments and the indoor laboratories for chemical and physical measurements and experimentation. An area of 4000 sq. ft. is comprised of a large head house, two research greenhouses, offices and laboratories. Three walk-in and five reach-in growth chambers provide a range of growing conditions with controlled light, temperature and humidity. A facility for microbiology and sterile culture work completes this self-contained center for whole-plant research. With support from NSF part of an adjacent garage complex is being converted into an additional laboratory for work with soil samples and bulky plant materials.

The woods crew of three men and the forest manager are fully equipped for experimental manipulations, forestry operations, construction, and maintenance. Large equipment including a back hoe, bulldozer, crawler, dump truck, flat bed truck, pick-up and van, are stored in garages and in a 2400 sq. ft. pole shed under construction. The staff operates a wood-working shop which serves as the center for building maintenance and a sawmill is operated seasonally.

University-owned houses and apartments include the Director's house and four residences currently occupied by faculty or post-doctoral fellows and their families. Two houses provide eight additional rental apartments for staff, graduate students and visiting scientists.

Fisher Museum houses the Harvard Forest Models, twenty-three dioramas portraying the history, ecology and management of central New England forests. A lecture hall with seating for fifty persons is also on the first floor. On the second floor are exhibits related to forest ecology: root biology, soil science, plant/pathogen interactions, the effects of disturbance on vegetation, and the local history of land-use in Petersham. Offices and a complete herbarium of the local flora also occupy the second floor. Thus, the Fisher Museum Building provides some 10,000 sq. ft. of space devoted primarily to public education and partly to scientific research.

C. History of Research and Established Data Bases - The Harvard Forest has a long and rich history in the study of forest ecosystems, vegetation history, and development. This research background, which is summarized below and extensively described in Appendix I, provides broad baseline data for the LTER project (Table 2).

Beginning in 1907 studies at the Forest focused on silviculture and forest production including mineral nutrition (Spaeth 1922, Mitchell and Chandler 1939) and early breeding experiments. By the 1930's research had expanded to include studies of forest nitrogen economy (Gast 1936, 1937), forest dynamics and succession (Fisher 1928, 1933, Griffith *et al.* 1930),soil morphology, mycorrhizal fungi (Finn 1942) and microclimate (Rasche 1953). S. Spurr increased the local interest in remote sensing, catastrophic disturbance (Spurr 1956b), and micrometeorology (Spurr 1956a), whereas M.B. Davis (1958), H. Raup (1937, 1964) and others (Goodlett 1954, Stephens 1955, Hack and Goodlett 1960) created a strong background in historical ecology and disturbance processes (Stephens 1956, Henry and Swan 1974, Oliver and Stephens 1977, Hibbs 1979, 1982).

Within the past 20 years studies have focused on organism-community-and ecosystem-level research. Particular strengths have been in tree physiology (Zimmermann 1978, 1983), plant development and

architecture (Tomlinson 1983, 1987), forest microbiology (Torrey et *al.* 1981, Tjepkema *et al.* 1981) and vegetation dynamics (Foster 1988a, 1988b). Research by investigators from Woods Hole (Melillo *et al.* 1983, Melillo and Aber 1984, Nadelhoffer *et al.* 1986, Steudler 1986), University of New Hampshire (Aber et *al.* 1983, Aber *et al.* 1985) and Clarkson University (McClaugherty *et al.* 1982, 1984, Linkins *et al.* 1984) have provided a very strong ecosystem component. The commitment to below-ground ecology was formalized in 1985 by the creation, jointly with the Yale School of Forestry and Environmental Studies, of the Program in Forest Microbiology, funded by the Mellon Foundation. Integrated research among the many groups using the Forest has contributed to a strong interdisciplinary understanding of forest processes.

III. Scientific Tasks and Major Research Areas

A. Overview.   The theme of the Harvard Forest LTER is a comparison of the effects of several important kinds of natural and anthropogenic disturbance processes on the structure and function of forested ecosystems. A major goal is to determine if the more recent anthropogenic chemical inputs cause fluctuations in system structure and function that are beyond the ranges produced by natural disturbances. A second major goal is to determine if there is a significant interaction between natural windthrow disturbance and chronic chemical deposition that could not be predicted from system responses to each factor independently.

   The disturbance processes we will investigate include:

(1) Catastrophic windthrow due to infrequent hurricanes;

(2) Small canopy gaps due to the more frequent windthrow of isolated individuals or groups of overstory trees;

(3) Selective loss of tree species due to pathogens, resulting in standing dead overstory trees;

(4) Chronic nitrogen and sulfur inputs through atmospheric deposition;

(5) Soil neutralization.

Four related research components will provide additional information with which to interpret system responses. These include:

(1) Addition/removal of litter on the forest floor, and its effects on biogeochemical cycling;

(2) The role of coarse woody debris in biogeochemical cycling;

(3) The movement of animals and birds in relation to forest patches, and large mammal (deer) herbivory inside and outside exclosures; and

(4) The role of plant development and architecture in deterministic versus opportunistic responses to disturbance.

   Historically, the primary forms of disturbance at the Harvard Forest have been physical disruption by catastrophic (hurricane) and small-scale windthrow and the recent (chestnut, elm and beech) and

mid-Holocene (hemlock) decline of major tree species due to pathogens. The size of disturbed areas has ranged from small canopy gaps to the destruction of whole stands by hurricanes. In order to provide a comprehensive historical context for interpreting our proposed experimental treatments the extensive historical records of the Harvard Forest will be combined with new research into forest dynamics throughout the Holocene.

Recent and future changes in the chemical loading experienced by central New England forests due to atmospheric deposition will alter rates of internal processes such as primary production and nutrient cycling, affect organism ecophysiology and interactions differentially, and will have profound effects on atmosphere-biosphere interactions through changes in trace gas fluxes. The hypothesis that chronic chemical disturbances, and/or their interactions with natural windthrow disturbance, cause greater variation in forest function than natural disturbance alone will be rejected unless the rates of function in the treated stands lie outside the range of values measured through the successional sequence following windthrow.

We will simulate the major disturbance types listed above in various ways. We propose to create one 1.0-hectare simulated hurricane blowdown every five years, using a model of susceptibility to windthrow developed at the Harvard Forest to design the treatments. We will also create six small multiple-tree gaps (200-300m^2) every five years, in the same years in which hurricane blowdowns are made. Likewise, we will selectively kill overstory trees in 1.0-2.0 ha stands on the same 5-year intervals. This plan will eventually yield an age-sequence of controlled large blowdowns and small-scale gaps in various stages of recovery in which measurements can be made simultaneously. This design will also allow us to investigate the role of weather and regeneration, since new blowdowns and small gaps will be created every five years. These studies will be integrated with the ongoing investigation of experimental tree-fall gaps, which is emphasizing microenvironmental measurements, ecophysiology and community dynamics (Hibbs and Sipe unpubl., Bazzaz and Sipe 1987).

We propose a series of alterations in element inputs as simulations of current and projected novel sources of stress. Chronic additions of nitrogen and sulfur in mixed hardwood stands and pine plantations will represent the eutrophication potential of increased N and S by atmospheric deposition and, through measurements of trace gas fluxes, will allow us to evaluate the contribution of temperate forests as a source for sulfur and nitrogen trace gases. Soil neutralization treatments through liming will allow us to study changes in mineralization processes and species responses "in reverse", i.e. in a system dominated by the natural long-term development of acidic soils, and at a point in time where recent atmospheric inputs are accelerating acidification.

We propose to study disturbance type interactions in two ways. First, we will study the interaction between physical canopy disturbance and chronic nitrogen input by adding nitrogen (1) to plots within the hurricane blowdowns and (2) to a third of the set of small canopy gaps. In reciprocal fashion, we will also establish small subplots containing seedlings of selected tree species in the chronic amendment sites, so that we can determine the effects of added nitrogen on tree physiology and growth in the intact forest independently of physical canopy disturbance. This same reciprocity involving windthrow and nitrogen addition will be repeated for windthrow and soil neutralization.

The effects of addition/removal of litter on belowground chemical fluxes will expand our understanding of the transformations between organic matter deposition and soil chemistry. This particular study will provide a comparison with a long-term experiment in Wisconsin and negotiations are currently underway to duplicate this design at six other LTER sites (K. Nadelhoffer, pers. comm.).

The patch mosaic generated by canopy disturbance affects the movements and foraging of animals and birds. The high productivity, nutritive potential, and reproductive output of the regenerating community in gaps attract herbivores, and the effects of both small and large herbivores on plant success can be devastating. We will assess the effects of herbivores, and the interaction with soil

nitrogen and neutralization treatments, in two ways. First, we will construct one large-mammal (deer) exclosure in each of the hurricane blowdowns that bisects the blowdown from north to south, extends into the surrounding forest by 30-40m, and encloses one each of the nitrogen-addition, neutralization, and control plots. A second set of three plots will be left outside the exclosure. Small (insect) and large (deer) animal herbivory will be sampled inside and outside the exclosures as part of regular measurements of tree demography and growth in permanent plots. Second, herbivore damage will be recorded in other experiments where seedling demography and growth are sampled regularly, with emphasis on the contrasts between nitrogen-added and control plots. These herbivory measurements will be interfaced with data on the growth, gas-exchange, and nitrogen content of tree seedlings in selected study plots.

The question of whether and to what extent co-occurring species vary in resource requirements for their success is an important theme of the proposed studies on ecophysiology and population biology. Predictions have been made about the physiological responses of species that occupy different positions on successional and forest gap-understory gradients (Bazzaz 1979, Bazzaz and Pickett 1980, Bazzaz 1983, Bazzaz and Sipe 1987).

We will test several of these predictions in the proposed research by focusing our ecophysiological and population measurements on a carefully chosen suite of tree species. We will measure responses on naturally established seedlings where possible, and on controlled plantings where necessary, in all experimental treatments. The 7-species *Acer-Betula* system that is being used in ongoing studies of experimental gaps (Bazzaz and Sipe) spans the shade-tolerance spectrum and will be emphasized here as well. To this set we will consider adding an important dominant *(Quercus borealis,* red oak), a pair of congeners that are early and mid-successional *{Prunus pennsylvanica,* pin cherry; *Prunus serotina,* black cherry); and a locally-abundant species *(Fraxinus americana,* white ash). *Prunus serotina* and *Fraxinus americana* are demanding in their resource requirements (especially

soil moisture and nutrients), and this will be contrasted with other target species that are less demanding.

The ecophysiology of these co-occurring species can be compared and modeled only if detailed data on above- and belowground physical and chemical fluxes are available. We will secure these data through a combination of (1) intensive micrometeorological sampling using a portable system of electronic instrument stations and data loggers, and (2) extensive belowground sampling of physical conditions and nutrient fluxes, with emphasis on nitrogen and sulfur transformations.

The differences in species response to disturbance cannot be understood by measuring physiological processes of resource use alone. A particularly strong theme emerging from recent ecophysiological research is that plant development and architecture must be measured in conjunction with such variables as gas-exchange and nutrient allocation (Mooney and Chiariello 1984, Kuppers 1985). Research in plant morphology has converged on this theme as well (e.g., Givnish 1986, Tomlinson 1987), and rigorous techniques and models for quantifying the dynamics of plant form have been developed. The flexibilities and constraints of plant response in experimental intact and disturbed forest environments will be studied through comparative analysis of meristem systems in selected herb, shrub, and tree species. Ecophysiological measurements will be coordinated with architectural analysis as much as possible to enhance predictions about whole-plant response to changing environments.

In addition to data gathered on the set of target tree species across all experiments, we will establish sample plots in the physical disturbance treatments (hurricane, small gap. standing death) in which we will follow the performance of all tree species that regenerate naturally. We will monitor seed rain, germination, herbivore damage, and seedling growth and mortality. The population dynamics of tree species will be interfaced with data on gap geometry, microenviron- mental patterns, belowground resource availability, and physiological and architectural responses.

A core set of measurements (section III.D.) will be carried out across most experimental treatments and controls. These measurements

incorporate important linkages between above- and below-ground physical and chemical fluxes, ecophysiological performance, organism growth and development, population dynamics, and system productivity. We propose to synthesize the results from these experiments into a spatial analysis of ecosystem function and atmosphere-biosphere interactions, and also to project these through time. This goal will be achieved through a combination of modeling, geographic information systems (GIS), and remote sensing. By (1) restricting the number of experimental treatments, (2) carrying out an interfaced set of core measurements across all experiments, and (3) synthesizing the results in the three-pronged manner described in detail below, we will be able to predict with greater precision the effects of natural and chronic disturbances on the structure and function of central New England forests on spatial and temporal scales that span several orders of magnitude.

The proposed research is described in the next three sections (III.B. through III.D.), and all experiments are presented according to the same structure: Hypotheses, Background, and Methods. The Methods subsections do not include instrumentation and measurement techniques, since many of the measurements are repeated across experiments and would be repetitious if described under each experiment. The measurement details are summarized by category in section III.E.

B. The Historical Context for Ongoing and Proposed Research

1. Climate, Disturbance and Vegetation Dynamics

   a. Hypotheses
- (1) Paleoecological studies will document significant change in species assemblages and abundances on relatively short time intervals. The forcing agents behind this change will be different at different spatial scales of vegetation as detected by complementary methods of forest reconstruction.

    - a. Pollen stratigraphies from small lakes will record regional changes in vegetation resulting from continental-scale climate change driven by major alteration in atmospheric circulation.

    - b. Pollen from very small lakes will record landscape-level vegetation dynamics controlled especially by broad-scale

disturbance processes such as decline in tree taxa *(Tsuga
and Castanea)* from pathogens, catastrophic blow-down and
fire.

    c. Pollen from small hollows and forest humus layers, and
other methods of stand reconstruction will record
community-level vegetation change dominated by gap
processes and disturbance.

    d. The integration of a network of paleoecological sites of
different size and basin characteristics will enable the
identification of vegetation dynamics at spatial scales
ranging from the stand to region and will provide a
comprehensive understanding of long-term change.

b. Background. Palynological reconstructions of vegetation in
temperate regions indicate broad-scale and complex patterns of change
in the abundance and distribution of the major arboreal taxa (Bernabo
and Webb 1977, Davis 1983, Huntley and Birks 1986, Jacobson *et al.*
1987). Various factors are implicated as forcing vegetation dynamics
on different spatial and temporal scales, including: climate change,
species migration, soil weathering, natural disturbance and
anthropogenic activity (Aaby 1983, Wright 1984, Birks 1985, Davis
1986). The relative importance of these factors and the patterns of
vegetation detected in the historical record will depend on the
spatial scale sensed in the particular record (Webb *et al.* 1978).

    The spatial resolution of paleoecological studies is dependent on
the relative contribution of extra-regional, regional, and local
pollen to the sediments studied (Janssen 1973), which in turn is
largely controlled by the size and morphometry of the basin (Jacobson
and Bradshaw 1981). As the size of the basin sampling site decreases
(e.g. from large lake to small lake to pond) the component of local
pollen increases, as does the spatial resolution (Birks and Birks
1980, Prentice 1986). The extreme end point in this progression to
smaller basins is the analysis of soil humus or small hollows in
forests for which the pollen source area is approximately 0.1 hectare
(Andersen 1966, 1970, Bradshaw 1981a, Heide and Bradshaw 1982). By
selecting organic profiles ranging from 10 cm to more than 1 m in
depth that occur in humus and small forest hollows these very local
vegetation records can be extended from hundreds of years to millennia
(Andersen 1978, Aaby 1983, Schwartz and Davis 1985). Humus samples

recently analyzed at the Harvard Forest yield a detailed stratigraphy to approximately 500 years before settlement (Bradshaw and Miller 1988), whereas hollows contain an apparently continuous sediment record from the mid-Holocene.

Although the vegetation and disturbance history of the Harvard Forest is as well understood as any forest in northeastern North America, the record still has limitations in temporal and spatial coverage and resolution. To address this gap an integrated approach developed at the Harvard Forest and University of Massachusetts for reconstructing forest dynamics will be implemented for the Harvard Forest LTER (Foster 1988b, Clark and Patterson 1986, Patterson and Backman 1988). Integration is provided by the overlap in temporal length and spatial resolution of the techniques employed (historical records, forest reconstruction, pollen analysis of forest hollows and lake sediments; Fig. 2). This research will answer fundamental questions about the disturbance regime, community stability and ecosystem dynamics and will provide an important baseline for manipulation experiments used in the Harvard Forest LTER.

c. Methods. For the broad-scale analysis one small lake basin and one very small pond within 5 km of the Forest will be cored for the full Holocene record of regional change. Pollen, macrofossils and charcoal will be counted at very close intervals (1-2 cm) using standard methods (Cushing 1967, Clark 1982, Patterson *et al.* 1987). Temporal control will be provided by C-14 analysis, opaque spherules (Clark and Patterson 1984) and Pb-210. We will build a regional chronology of vegetation change and inferred climate history and a detailed understanding of fire history that can be placed in the context of other studies in this project and regionally (Patterson and Backman 1988, Backman 1984, Gaudreau 1987).

Within the Harvard Forest 16 forest hollows and mor humus samples will be cored in old-growth forests and representative examples of upland and lowland forest types. Sampling interval in the cores will typically be 1 cm and dating will be provided by C-14 and correlation with major cultural events (e.g. European settlement, c.f. Bradshaw

and Miller 1988). At each site reconstruction of the vegetation history within 20 m of the coring location using techniques developed at the Forest (Stephens 1955) will provide unusual ability to interpret the stratigraphic record. Interpretative power will be added by a complete set of regression equations between relative basal area and pollen representation of the major tree species (cf. Heide and Bradshaw 1982), which is being developed for central New England in the Ph.D. research of P. K. Schoonmaker.

The information derived in these studies across various spatial scales will be integrated locally into the Harvard Forest GIS and regionally into our (Patterson, Foster) on-going palynological studies in New England and the pollen data-base maintained by T. Webb III at Brown University.

2. Ecosystem Susceptibility to Catastrophic Disturbance

a. Hypotheses.

(1). The interaction of wind patterns, geomorphology, and vegetation distribution creates gradients in susceptibility to catastrophic wind-damage.

  a. Landscapes vary in their response and susceptibility to catastrophic storm depending on the developmental stage, structure, composition and distribution of vegetation types, and empirical models will verify this.

  b. Landscape patterns will be determined by the size, shape and composition of patches, within which forest structure and function will vary according to the degree of exposure to infrequent catastrophic blowdowns.

b. Background. Studies at the Harvard Forest document that catastrophic hurricane damage has been responsible historically for much of the structural pattern and dynamics of the upland forests in central New England (Cline and Spurr 1942; Stephens 1956; Henry and Swan 1974; Foster 1988b). Catastrophic storms occur about once every 70-100 years (Smith 1946; Neumann *et al.* 1978) and the most recent hurricane, in 1938, destroyed over 6 billion board feet of timber along a 100 km-wide path (NETSA 1943), including approximately *10%* of the timber at the Forest (Gould 1960).

Current research is assessing hurricane damage at the scale of the individual, stand and landscape (Foster 1988a, 1988b). For individual trees differences in susceptibility are controlled by autecological and architectural characteristics (Rowlands 1941). At the community scale the differential susceptibility of the major forest types is controlled by composition, age, height and density (Foster 1988b). Based on the documented relationships for species and stand susceptibility to wind, attention is currently focused on the landscape-scale features that add higher-order interactions to the disturbance process.

   c. Methods. This work is largely centered on GIS using the Map Analysis Package (MAP; cf. Tomlin 1983) and involves 1) completion of the digital cartographic data base depicting landscape features of the Harvard Forest and Petersham area before and after the 1938 hurricane; 2) derivation from these data of explanatory relationships between observed levels of wind damage and vegetational, site and landscape characteristics and 3) development and testing of a digital cartographic model embodying these relationships to simulate hurricane damage. A preliminary study on approximately a third of the Harvard Forest indicated that the data base has the necessary resolution to derive exacting relationships between site and landscape variables and wind damage (Fetherston 1986). The general applicability of these models is being tested through comparative studies of tornado damage to old-growth forests on the Allegheny Plateau (S. Pickett and D. Foster) and hurricane damage to tropical forests in Puerto Rico (Waide and Lugo 1988).

C. Experimental Treatments: Hypotheses, Background, Methods

  1. Physical Disturbances
  a. Catastrophic Hurricane vs. Small Canopy Gap Windthrow
    i. Hypotheses
        (1) Ecosystem process rates will change most rapidly and
            exhibit their widest range in the earliest stages (first

20 years) following both catastrophic and small gap windthrow.

(2) The range of variation in ecosystem process rates, as compared to the undisturbed state, will decrease with gap size.

(3) The influence of the regenerating community composition on ecosystem process rates will decrease with canopy gap size.

(4) Tree species differ in spatial and temporal patterns of seed dispersal into both large and small windthrow gaps.

(5) Germination and establishment of tree species in both large and small windthrow gaps are non-randomly associated with seedbed types (e.g., exposed tip-up mounds), and the level of non-randomness among species is inversely related to seed size.

(6) Tree species differ in the relative contribution of regeneration modes (seed rain, seed bank, advance establishment, resprout) between and within the understory and gaps of different size. However, when all species are considered together, there are consistent patterns of mode importance that vary with gap size.

(7) Tree species differ in survival and growth of established seedlings between the understory and gaps, and at different positions within gaps.

(8) Complex but orderly patterns of above- and belowground microenvironments exist along the gradient from the most exposed portions of large gaps to the full understory, and differential survival and growth of tree species can be largely explained by differences in physiological responses to this complex gradient.

(9) In contrast to (8), microenvironmental patterns in windthrows are extremely heterogeneous on scales appropriate to processes such as seed germination, and therefore much of the unpredictability in community composition following windthrow is due to chance establishment in microsites with conditions unrelated to the more orderly microenvironmental variation on larger spatial scales.

(10) Annual, essentially unpredictable differences in such factors as weather and reproductive behavior will result in significant variation in the composition of the regenerating tree community in windthrow gaps of all sizes.

(11) The diversity of tree species reaching reproductive age will be lower in a forest dominated by small windthrows than under a regime dominated by large windthrows.

   ii. Background. Ecologists are now viewing patterns of

disturbance and functional responses of species as a unifying link

between the widely divergent types of closed-canopy forest in the world (Whitmore 1982: Shugart 1984). This view has paralleled the increasing emphasis on disturbance regimes in all ecosystems, especially terrestrial (Sousa 1984, Pickett and White 1985). A powerful way to view any form of disturbance is through its effects on the physical and chemical fluxes of the undisturbed system. This permits direct linkage between organism- and ecosystem-level processes (Bazzaz and Sipe 1987).

The effects of the intact forest on the complex above- and belowground microenvironmental gradient from the centers of large gaps to the understory are pervasive. The breadth and steepness of this complex gradient are functions of disturbance frequency, size, and intensity. Disturbance frequency affects gradient breadth since the developmental status of the forest surrounding the disturbed area is a function of the time since the last disturbance. Disturbance size is critical since the gradient broadens as gap size increases. However, the strength of the disturbance agent (intensity) and the extent to which the pre-disturbance community is destroyed, including the seed bank (severity), must also be considered because of their effects on the nature of the remnant community and initial above- and belowground microenvironmental patterns. While there is a great deal of predictability in microenvironmental patterns across intact forest and canopy gaps, chance variations in such factors as seed production and dispersal, weather patterns, and interactions with other trophic levels (e.g., herbivores) can cause wide variation in the composition of the regenerating community.

The rates of important ecosystem processes will vary along this gradient, and will change through time as the community recovers. Several models of trends in ecosystem function following disturbance have been developed (e.g., Odum 1969, Bormann and Likens 1979, Vitousek and Reiners 1975, Van Cleve et al. 1983). These models differ mainly in the designation of the initial state of the system following distinct kinds of disturbance, such as old field, burned forest, or clearcut. All models suggest that the earliest stages of recovery are the most dynamic, with relatively open nutrient cycles,

high net primary production, and rapid changes in rates of function. Windthrows, especially catastrophic hurricanes, produce massive flushes of labile elements and organic matter inputs in a short period of time, and the patterns of element transformations in response to physical and biotic components may be expected to show wide ranges and change rapidly within a short time following blowdown.

Previous research here at the Harvard Forest suggests that some of the forested systems may be buffered against the losses of nitrogen, since the initiation of nitrate production may be delayed for a full year following disturbance (Vitousek et al. 1979, Aber et al. 1983). Measured denitrification potentials based on anaerobic incubations are also much higher in disturbed (trenched) plots than in undisturbed plots 2 to 3 years after disturbance. We are proposing to extend our work to include realistic physical disturbances that are important driving forces for our system.

We will simulate catastrophic (hurricane) and small canopy gap windthrows in order to test hypotheses on: (1) disturbance size and position within disturbed area, (2) system rate processes, especially over time, (3) tradeoffs among co-occurring species in response to spatial patterns of system fluxes, and (4) the effects of chance variations in regeneration on community development.

iii. Methods. Hurricane blowdowns and small canopy gaps will be made in the Prospect Hill compartment of the Harvard Forest where over 200 hectares of second growth maple-oak forest are available. One hurricane blowdown approximately 1 hectare in size will be created every five years. Site selection will be based on existing maps of stand susceptibility to hurricane that incorporate forest composition, structure, and site variables. Manipulations will be undertaken by the Harvard Forest woods crew utilizing established techniques to simulate natural disturbance and minimize machine damage to the vegetation and soil.

Guidelines for felling individual trees will be derived from extensive empirical information on disturbance events in the Harvard Forest (Rowlands 1941, Stephens 1955, Foster 1988a). On a given site the major variables affecting tree susceptibility and therefore used as

selection criteria include species-specific factors (e.g. crown and root architecture, wood strength, stem flexibility), size (height and crown shape) and stand composition. Selection criteria will be applied repeatedly in the simulated downwind direction until the desired gap size is reached and all trees are marked. The location, size and orientation of the six small canopy gaps will be carefully controlled to eliminate excessive variation in gap geometry, site conditions, and the surrounding forest matrix.

The selected trees will be pulled down using a technique developed by our woods crew to simulate windthrow. A 1.5" steel cable run from a 230 Timberjack skidder with a Hyster winch situated just outside the study area is attached to the bole of a tree 3-5 m above the ground. As the cable is tightened the upper bole and crown of the tree add leverage to pull the tree over, generally through uprooting. Occasional breakage of the bole, especially on damaged or decayed trees, simulates natural breakage. Trees will be left in place where they fall. This method provides a reasonable simulation of windthrow in terms of soil disturbance by uprooting, snapping of weakened boles, parallel orientation of downed trees and the absence of machine-damage to the soil or vegetation. Trees up to 60 cm dbh have been uprooted by our own crews with the rental of the skidder.

b. Selective Mortality of Dominant Overstory Species

i. Hypotheses.

(1) Pre-gap micrometeorological patterns aboveground and element fluxes belowground will exhibit less variation among the set of standing-death sites than among the small windthrow sites of comparable size, due to the consistent influence of the single gap-making species in the former and variable influence of gap-making species in the latter.

(2) Post-gap micrometeorological patterns aboveground and element fluxes belowground will exhibit less variation among standing-death sites than among windthrow sites of comparable size not only due to lower pre-gap variation (hypothesis #1), but also to the less variable effects of standing death versus treefall on gap geometry and damage to the remnant community.

(3) For canopy openings of comparable size, standing-death gaps will exhibit a greater proportion of stems regenerating from advanced growth, and smaller proportions from seed rain and seed bank, than in windthrow gaps.

(4) As a consequence of (1)-(3) above, the composition and structure of the regenerating community will be more strongly related to the composition of advance growth, will vary less, and will therefore be more predictable than in windthrow gaps of comparable size.

(5) Organic matter input rates to the forest floor will be lower, but the period of higher inputs than control levels will last longer, in standing-death gaps than in either the small or large windthrow gaps.

(6) As a consequence of (4) and the absence of soil disruption, decomposition and mineralization processes will be less affected in the standing-death gaps than in either of the windthrow treatments.

(6) As the size of standing-death canopy openings increases, the heterogeneity of above- and belowground microenvironments and the potential for differential growth rate expression among tree species will increase.

ii. Background. There are four converging reasons for proposing to selectively kill overstory stems to produce patches of standing dead trees. First, pathogens have selectively attacked tree species several times in our system during the last 5000 years *(Tsuga canadensis, Castanea dentata, Fagus grandifolia, Ulmus americana).* Second, selective insect herbivores periodically reach epidemic proportions and cause widespread mortality (e.g. gypsy moth *(Lymantria dispar)).* Third, the effects of standing tree death versus windthrow on regeneration and on organic matter deposition and nutrient cycling are probably quite distinct, although little is known about these differences. Finally, there is a growing interest in the potential of dominant plant species to alter rates of nutrient cycling and basic soil characteristics in their sphere of belowground influence (eg. Alban 1982 and Binkley *et al.* 1984).

We propose to selectively kill overstory stems of *Quercus borealis* (northern red oak) every five years through the bole

application of systemic arbocide (Tordon). We have chosen red oak for three reasons: (1) it is a widespread dominant, and suitable study sites are available; (2) it is one of the preferred food species for gypsy moths and is killed in large numbers following epidemic outbreaks; and (3) in our system, red oak is arguably most like American chestnut (*Castanea dentata)* in its widespread dominance and autecology, allowing us to reasonably simulate the historical loss of a formerly dominant species.

iii. Methods. Stands of 2-3 ha will be chosen in which northern red oak accounts for 40-60% of the basal area in order to generate a range of gap sizes within an adequate forest matrix. Several standing-death gaps of size and orientation similar to those in the small gap windthrow experiment will be included. Trees to be killed will be marked in the field and plotted on a detailed GIS map of the study area. Several overstory red oak stems will be exempt from arbocide application to serve as controls. Permanent sample plots will be established in and around the marked trees, including positions within the future canopy openings and well into the surrounding intact forest. Above-ground micrometeorological patterns and belowground nutrient fluxes will also be measured in subsets of these plots before deadening.

All marked trees will be injected with Tordon, a very effective systemic arbocide that does not escape into the soil from roots and the temporal pattern of mortality will be recorded. Changes in above- and belowground physical and chemical fluxes, and survival and growth of tree seedlings in plots will be sampled regularly. The frequency of sampling will be greater during the remainder of the first year than in subsequent years in order to capture the rapid changes that are expected to occur early in the recovery period. The core measurements made on these standing-death gaps will be compared to data from all other experimental treatments, but with an emphasis on the two windthrow experiments.

2. Chemical Disturbances

a. Chronic Nitrogen Addition

Because mineral nitrogen is an important growth-limiting nutrient in forested systems, chronic increasing deposition of N from the atmosphere may alter rates and patterns of forest N cycling, plant physiological responses, differential species growth rates, plant-herbivore interactions, primary production, and trace gas emissions to the atmosphere as hypothesized below.

i. Hypotheses.

(1) Nitrification will be induced at low soil pH.

(2) Relative and absolute alterations in the emissions of trace sulfur and nitrogen gases will occur.

(3) Fine root biomass will decrease markedly, and fine root turnover will increase.

(4) Nitrate reductase activity in leaves will increase.

(5) System primary productivity will increase.

(6) Overall, plants will have higher leaf N contents, higher photosynthetic capacities, net diurnal carbon gain, greater water-use efficiencies, lower root:shoot ratios, and higher growth rates.

(7) Because of the reduction in fine root biomass and root:shoot ratios, plants growing under higher soil N will exhibit lower net carbon gain and greater drought stress, including mortality, during periods of low precipitation and soil moisture.

(8) Co-occurring tree species will differ in their responses to varying levels of soil nitrogen (especially nitrate), and this will result in changes in the relative growth rates among species in both intact and windthrown forest.

(9) Herbivore feeding preferences, and the absolute and relative amounts of damage to plants, will change in both short- and long-term as plants adjust physiologically to N addition and herbivore populations respond to these adjustments.

ii. Background. A major novel source of stress on forest ecosystems is eutrophication by the addition of high levels of nutrients through atmospheric deposition. For example, "nitrogen saturation" in excess of biotic demand or uptake potential, has been linked to various pathological conditions in trees, and to forest decline (Nihlgard 1985, Freidland *et al.* 1984). Excess availability may also stimulate or trigger increased trace gas fluxes (Steudler *et al.* 1988), and so affect global climate as well as local ecosystems.

At the level of plant physiology, the forms and amounts of available nitrogen probably have differential effects on co-occurring plant species, involving costs of nitrate versus ammonium assimilation and tradeoffs in nitrogen allocation among photosynthetic enzymes, nitrate reductase, N-based defensive chemistry, and many other metabolic demands (Mooney and Gulman 1982). The effects of increased foliar nitrogen contents on herbivore feeding can also vary among plant species depending on the ways in which such factors as C:N ratios, defensive chemistry, and herbivore population dynamics respond (Coley *et al.* 1985). For these reasons, an increase in total soil nitrogen and/or a shift in the primary form to nitrate will most likely alter growth rates and competitive relationships among tree species, and therefore alter community composition. We may also expect the recovery process to occur faster in physically disturbed sites, since growth rates by the community as a whole should increase with soil nitrogen content.

iii. Methods. We will test the above hypotheses by carrying out measurements on sets of control and fertilized plots in undisturbed mixed-hardwood stands and pine plantations. We have in place experimental plots in both types of intact forest which are receiving applications of 50, 100, and 150 kg N/ha/yr as NH_4NO_3 in six equal doses over the growing season. Plots are 1 ha each and are replicated three times in each stand type. Nitrogen has been applied to these plots for 5 years now.

Within each of the treatment and control plots we will establish several 1x2m subplots and plant seeds and/or transplant seedlings (bare-rooted) of tree species chosen from the target group. Regular measurements of comparative demography, growth, architecture, herbivore damage, gas-exchange, and whole-plant carbon and nitrogen allocation will be supplemented by foliar analysis for allocation of nitrogen to nitrate reductase, ribulose bisphosphate carboxylase, and free amino acids.

b. Soil Neutralization

We propose to investigate the effects of artificial increases in soil pH on system function through liming, in order to complete our

understanding of system biogeochemistry by exploring a reversal of the
natural and anthropogenically-accelerated trend toward soil
acidification. The effects of elevated soil pH on element fluxes in
soil and plant response are complex and manifold. Specific
predictions can be made about the effects on nitrogen transformations,
and general predictions about species responses.

i. Hypotheses

(1) As soil pH rises, net nitrogen mineralization will increase.

(2) As soil pH rises, soil nitrification rates will increase.

(3) Due to increased nitrification, fine root biomass will
decrease and fine root turnover will increase, leaves will
exhibit greater nitrate reductase activity, and emissions of
nitrogen and sulfur trace gas fluxes will increase (see
hypotheses for chronic nitrogen addition).

(4) Due to the effects of increased nitrification on fine root
structure and turnover, the forest floor will convert over a
long term from mor to mull type.

(5) Unlike chronic nitrogen addition, the increased nitrification
caused by elevated soil pH will not increase net primary
productivity. However, higher soil pH will lead to greater
productivity due to more favorable supply of other nutrients,
such as phosphorus, potassium, and calcium.

ii. Background. Forest N economies vary with respect to the
dominant form of mineral N available in soil. Extremely acid soils
(pH<4.0) typically release ammonium rather than nitrate to soil
solution. We hypothesize that experimentally increasing the pH of an
extremely acidic soil to levels greater than pH 4.5 will cause several
changes in plant response and system function. Previous work at the
Harvard Forest and elsewhere has suggested that the distinction
between nitrate and ammonium economies in forest ecosystems has
significant implications for carbon allocation, fine root dynamics,
and nitrate reduction (Novoa and Loomis 1981, Aber et *al.* 1985,
Nadelhoffer *et al.* 1986, Al Gharbi and Hopkins 1984).

Nitrification processes are not the only factors affected by
elevating soil pH above 4.5. Organic matter decomposition and
mineralization rates for other nutrients should also increase.

Overall, the stocks of nutrients limiting for plant growth should rise, and so should average community productivity. However, we may expect that relative growth rates and competitive abilities among species will change with pH.

iii. Methods. To test these hypotheses we will continue lime applications (9000 kg/ha yr) to 30m x 30m plots in both a mixed hardwood and a red pine stand that were begun in 1985. Rates of N mineralization, nitrification, trace gas emissions, fine root turnover, nitrate reductase activity, and net productivity will be measured on both control and limed plots. We will also sample soils regularly for concentrations of other nutrient elements, including phosphorus, potassium, sulfur, and calcium.

We will establish several lmx2m subplots within control and limed plots in stands, and plant seeds and/or seedlings of tree species chosen from the target group. These seedlings will be used for the comparative studies on demography, growth, and biomass and nutrient allocation.

3. Interactions between Physical and Chemical Disturbances a. Windthrow and Chronic Nitrogen Addition

In contrast to nitrogen additions to intact forest stands, where light and other resources are limiting, increasing soil nitrogen content in windthrown stands may cause significant alterations of the normal pattern of system recovery. This experiment is designed to test this possibility.

i. Hypotheses.

(1) The effect of increased soil nitrogen in windthrows will be greater after the normally-observed nutrient flush from fast mineralization of non-resistant litter than before this flush.

(2) Increased nitrogen will buffer the recovering system from normally low nutrient levels after the initial flush, and consequently the rate of community regrowth will be faster.

(3) Increased nitrogen will alter the relative growth rates among co-occurring tree species and change the composition of the regenerating community.

ii. Background. Predictions on system behavior following either nitrogen addition to intact forest or windthrow independently may not

be accurate when these disturbances interact. Since chronic atmospheric nitrogen input is expected to continue, forest recovery after catastrophic or small canopy gap windthrow will likewise take place under gradually increasing levels of soil nitrogen.

Additional nitrogen can be expected to have only a minor effect in the early phases of recovery, when a pulse of nutrient ions occurs, and when the regrowing community is still adjusting to the changed conditions. However, after this pulse the concentrations of nutrient elements normally drops dramatically as they are assimilated by the community and the C:N ratio in the soil slows mineralization. It is during this second phase that chronic additions should have their greatest influence. The results may be a faster recovery rate and shifts in dominance among the eventual dominant species on the site.

iii. Methods. Two pairs of 15mx15m plots will be established within the simulated hurricane blowdowns. One pair will be inside the large mammal exclosure (see III.C.5.c. below) and the other outside. One member of each pair will receive 150 kg/ha/yr of NH_4NO_3 in six equal doses and the other will serve as a control. Two of the six small windthrow gaps will be randomly assigned to this same nitrogen addition rate, and two will serve as controls (the remaining two will be limed - see III.C.3.b. below). The suite of nitrogen mineralization and fine root measurements will be used here. Likewise, plant growth, demography, gas-exchange, leaf nitrogen contents, and herbivore damage will be sampled regularly in tree seedling subplots.

b. Windthrow and Soil Neutralization.

i. Hypotheses

(1) Soil neutralization will enhance decomposition and mineralization rates and result in larger quantities of available nutrient ions, especially those increasingly mobilized at higher soil pH.

(2) As a consequence of (1), primary productivity will be greater and the recovery time for community regrowth will be shorter.

(3) Due to differential soil pH preferences, the relative growth rates among co-occurring tree species will be altered by

neutralization, resulting in changes in the composition of the regrowing community.

ii. Background. The predictions for species and system responses to soil neutralization in intact forest stands (III.C.2.b.) apply in general here. But since the composition of the future forest is determined by species interactions early on in recovery following disturbance, the differential responses of species to higher soil pH will have a more profound effect on future system structure and function.

iii. Methods. We will test for a significant interaction between windthrow and increased soil pH in a manner analogous to that for windthrow and nitrogen addition. Two pairs of 15mx15m plots will be placed in the hurricane windthrow, one pair inside and one pair outside the large mammal exclosure. One member of each pair will be limed at the rate of 9000 kg/ha/yr. Two of the six small canopy gaps will be selected at random to receive the same liming rate. The set of measurements to be made on belowground processes and plant species responses in neutralized intact forest plots (III.C.2.b.) will be made in the windthrows as well.

4. Forest-Atmosphere Trace Gas Fluxes in Undisturbed and Chemically Disturbed Stands

  a. Canopy Productivity and O_3 Uptake

  i. Hypotheses

  (1) The forest receives significant input of nutrients, acids, and phytotoxic chemicals (e.g., O_3) from the atmosphere.

  (2) Rates of pollutant uptake and damage to the forest depend on the physiological states of individual trees, which in turn depend on soil moisture, temperature, solar irradiance, and nutrition.

  (3) The chronic addition of nitrogen to forests will alter the rates of pollutant uptake and damage by trees through its effects on plant nutrient balance and ultimately on photosynthetic gas-exchange.

  ii. Background. The kinds and magnitudes of chemical exchanges between forest and atmosphere must be understood in order to have a

predictive understanding of forest ecosystem function, and especially if the predictions are to be made about landscape or even global effects of local fluxes. This involves both characterization of (1) the atmospheric inputs to the system in question and (2) the more complex exchanges and transformations between physical and biological components in the system.

The atmospheric chemical climate in forested areas is poorly known and present knowledge of pollutant levels (means, extremes, spatial and temporal distributions) is limited. In addition, though there are now numerous studies on the physiological and growth effects of direct application of atmospheric pollutants on crop plants and forest trees, the vast majority of this work has been done in controlled laboratory environments. Consequently, we know very little about uptake of pollutants by plants under normal pollutant levels in the field. Virtually no studies have been completed that follow the internal dose of pollutants through stomatal exchange to potential effects on internal tissues.

However, it has been known for many years that plants take up pollutants such as O_3 and SO_2 mainly through stomata, and therefore potential damage to plants depends not only on pollutant levels but also on the metabolic activity of the trees (Wesley *et al.* 1977, Reich and Amundson 1985, Winner *et al.*). In recent studies in Amazonia (S. Wofsy, unpublished) the rates of CO_2 and O_3 uptake were measured in a tropical forest over a 2-week period using the eddy correlation technique (cf. Wesley *et al.* 1978, Matt et *al.* 1988). Uptake rates for these gases were strongly correlated over diurnal cycles, indicating stomatal control of O_3 entry.

Net CO_2 uptake for the stand as a whole was calculated directly, and represented total flux over a 3-6 ha around the central measurement point. Measurements of this sort allow determinations of gross and net primary productivity for the site without any traditional gas-exchange sampling. However, when coordinated with such sampling and knowledge of the physiological status of the trees in response to site conditions, it should be possible to define algorithms that predict the net inputs of gaseous pollutants to the

forest based on measurements of ambient pollutant concentrations in concert with data on temperature, solar irradiance, and soil moisture.

iii. Methods. Four phases of measurements will allow us to address the hypotheses and develop predictive models of net productivity and pollutant uptake by the forests of central Massachusetts. First, we will set up an air pollution monitoring site for O_3, NO, NO_2, total other N-species, CO_2, and meteorological variables at an undisturbed location in the Harvard Forest or in the adjoining Quabbin Reservation. This site will operate from computer control and will provide a complete climatology for the Harvard Forest region. These baseline data will serve as a background for the remaining three phases.

The second phase will determine the net fluxes of CO_2 and H_2O from stands in the Harvard Forest using the eddy correlation technique. The measurements utilize fast response chemical sensors for CO_2, H_2O and O_3 coupled to fast-response measurements of the three directional components of wind above the forest canopy. This will allow us to observe in real time how the forest responds as a whole to fluctuations in physical inputs, such as solar radiation or water stress. These data will be used to model and predict CO_2 and H_2O fluxes using temperature, humidity, irradiance, time of day, time of season, and soil water potential.

The third phase will shift attention to the long-term perturbations imposed on the system by atmospheric inputs of phytotoxic gas species. The measurements made in the second phase, when applied to O_3 reactivity within the forest (Wofsy 1988a), will allow us to calculate the actual dose of O_3 to the forest as it is modified by the physiological activity of trees.

Finally, the fourth phase will address the question of the effects of chronic nitrogen addition to the soil on forest physiological activity and consequently on gaseous fluxes of CO_2 and O_3. Nitrogen (as NH_4NO_3) will be added to a 5.0-hectare stand in coordination with ongoing work involving nitrogen additions to smaller plots (III.C.2.a.). A structurally relatively uniform stand will be chosen and baseline measurements of CO_2, H_2O and O_3 flux will be

measured at several points on the stand to characterize undisturbed conditions. After nitrogen addition, gaseous uptake will be measured at both the center and at the edges of the treated stand. The significance of interactions between two kinds of chronic atmospheric pollutants, O_3 and NO_X, will then be determined.

b. Sulfur Gas Fluxes

i. Hypotheses

(1) COS and CS_2 fluxes from the soil to the atmosphere are increased by the chronic addition of nitrogen to forest stands at rates that saturate the soil-forest system.

(2) There is a significant synergistic interaction between chronic nitrogen and sulfur addition to forest stands in their influence on the fluxes of COS and CS_2 from soil to atmosphere.

(3) The forest canopy may act as a sink for atmospheric COS and CS_2, depending on the nitrogen and sulfur status of the soil and the metabolic activity, especially photosynthetic gas-exchange, of the trees.

ii. Background. Preliminary measurements indicate that gaseous sulfur compounds are emitted from both plants and soils in forest ecosystems (Steudler et al. 1985). The magnitudes of these emissions are not well documented and we know little about the factors that control either the magnitudes or the species of sulfur gases emitted. Since certain sulfur gases, even in trace amounts, have a major impact on the chemistry of the atmosphere, it is important to measure these fluxes and understand the biological and physical controls on them.

The number of sulfur gas flux measurements from upland soils are few. Adams et al. (1981) made a preliminary survey of sulfur emissions from a number of soil orders in the eastern U.S. and Steudler et al. (1985) have monitored sulfur gas fluxes from soils in the Harvard Forest. CS_2 and COS appear to be the dominant forms emitted from undisturbed acidic upland soils.

The addition of sulfur to upland forests is predicted to increase the fluxes of sulfur gases, to the atmosphere, including COS and CS_2. However, no studies have explored the possible controls that nitrogen exerts on gaseous sulfur from the soil or from plants. In nitrogen-

limited systems, plants accumulate excess sulfate in their leaves, which is reduced to H_2S via photosynthetic pathways and emitted through stomates to the atmosphere. In nitrogen-saturated systems, most of the sulfate in leaves is incorporated into carbon-bonded sulfur, such as amino acids (Turner et al. 1980). Most of the carbon-bonded sulfur will fall to the forest floor in plant litter, where microbes transform the sulfur-containing amino acids into a number of compounds, including COS and CS_2, which escape to the atmosphere.

At present, there is much discussion over the identity of the "missing sink" needed to balance the global COS budget (e.g., Lamb et al. 1987). Net influx into trees during photosynthesis may account for a significant fraction of this imbalance. There are currently no published data on the net exchanges of COS and CS_2 between forest vegetation and the atmosphere. The last hypothesis will address this need.

iii. Methods. Sulfur gas fluxes from soil to atmosphere will be made in control plots and in plots where either nitrogen alone or nitrogen plus sulfur are added. The chronic nitrogen treatments are described elsewhere in this section (III.C.2.a.). The experimental N x S plots are part of a separately funded grant to researchers at MBL (P. Steudler and J. Mellilo), and will be running concurrently with the nitrogen plots. Spatial and temporal variability in trace sulfur gas fluxes from the soil will be determined by using replicated soil-surface chambers and sampling schedules appropriate to daily and seasonal cycles. These measurements will begin in year one and continue through the five-year period of the LTER grant.

During year two, we will begin developing a steady-state gas-exchange system that will allow simultaneous measurements of photosynthetic carbon uptake and COS and CS_2 exchange between the forest canopy and the atmosphere, in coordination with F. A. Bazzaz at Harvard. During years three through five, forest-atmosphere fluxes will be measured in a 90-year-old mixed hardwood stand and a 30-year old pine plantation, including plots treated with nitrogen or nitrogen plus sulfur addition.

5. Related Treatments of Long-Term Value

a. Vegetation Influence of Soil Organic Matter Accumulation and Quality

ii. Background - Vegetation strongly influences soil properties, primarily by contributing organic matter to soil as litterfall and fine root detritus (Jenny 1980). Disturbances that alter the rates and patterns of primary production inevitably affect both the formation of soil organic matter and the amount and quality of organic matter in a forest soil. We propose to establish a set of long-term experiments, using plots in different forest types on a variety of soils at the Harvard Forest, that will allow us to identify and quantify relationships between litter input amounts and rates of both soil organic matter formation and soil processes.

The proposed experimental design is based on a plot manipulations started in two central Wisconsin oak forests in 1956 (Nielsen and Hole 1963) and continued to the present time. The Hole-Nielsen plots are 3m x 3m and are located under oak-dominated canopies. Experimental treatments are referred to as "NO LITTER", "2X LITTER", and "A-LESS". The NO LITTER treatment consists of preventing leaf litter inputs by frequent raking during autumn. 2X LITTER plots receive 2 times natural leaf litter inputs, with the litter removed annually from the NO LITTER plots being used for additions to the 2X LITTER plots. The A-LESS treatment consists of: 1) severely depleting soil organic matter stocks by physically removing 0 and A horizons, 2) restoring the soil surface to its pre-disturbance level with B horizon material, and 3) allowing soil organic matter stocks to recover by permitting natural levels of leaf litter and fine root inputs after the soils are experimentally impoverished in steps 1 and 2. The Wisconsin plots are now providing valuable information on the effects of leaf litter inputs on soil organic matter pools, on forest soil fertility in forests, and on microbial processing of organic C and N in forest soils (Fry and Nadelhoffer 1987, Nadelhoffer *et al.* 1987). Once established, experimental plots such as these require minimal maintenance (none for ALESS) to continue the experimental treatments. Nonetheless, they constitute a resource that is extremely useful for

addressing critical questions about controls on rates of soil and ecosystem processes.

Sustained experimental manipulation of plant litter inputs to soils together with repeated measurements of soil organic matter in experimental plots will allow us to identify the fraction of total litter that is ultimately stored as stable organic matter in a variety of forest soils. In addition, our recent work suggests that we will be able to identify the pool sizes of rapidly cycling C and N using shifts in stable isotope abundances (^{15}N and ^{13}C) that should result from altering the amount of litter inputs (Fry and Nadelhoffer 1987; Nadelhoffer and Fry, submitted). Therefore, if the litter addition/removal plots are established, we will propose to use the isotopic compositions of plant available N and respired C02 released from soils to determine the relative contributions of fresh litter and older humus to these fluxes. We also plan to use controlled additions of maize litter (a C4 plant that has higher 13C:12C ratios than the C3 plants that dominate forest litter inputs) as a method for measuring the sizes and turnover of labile and refractory organic matter (Balesdent and Mariotti 1987*).*

iii. Methods. We propose to establish plots in the Harvard Forest similar to the existing Hole-Neilsen experiment. In addition to their treatments (CONTROL, NO LITTER, 2x LITTER, A-LESS), we will establish new treatments by preventing root ingrowth to a subset of control and experimental plots. This will be done by trenching around plots to a depth at least 1 m and backfilling around corrugated fiberglass barriers. All plots would be instrumented with: a) 4 tube lysimeters to for collecting subsoil water samples; b) thermocouple arrays to allow for construction temperature profiles; and c) neutron probe access tubes to allow for non-destructive moisture determinations.

We will compare vegetation-soil interactions in a diversity of rest ecosystems by establishing replicated experimental plots in at

least forest ecosystem types: 1) deciduous forests with mull forest floors; 2) deciduous forests with mor forest floors; 3) pine stands; and 4) spruce stands. Addition of root exclusion treatments will allow for determining the relative influence of above- vs. below-ground inputs on soil organic matter pools and soil processes.

Negotiations are currently underway to replicate this experiment other LTER sites (e.g. Kellog, Coweeta, Hubbard Brook, Taiga, Andrews), Establishment of these experimental plots will allow for research that dresses the five core themes of the national LTER program (cf. Callahan 84*, Brenneman and Blinn 1987*) as follows.

b. The Role of Coarse Woody Debris in Biogochemical Cycling

i. Coarse Woody Debris - Coarse woody debris is often abundant forest ecosystems and is deposited in large amounts during many types of disturbance. The fate of this material and its importance in ecosystem recovery, nutrient cycling and soil genesis is poorly understood and is a major focus at other LTER forest sites. Unusual baseline information for this study is provided by the Harvard Pisgah Tract in southwestern New Hampshire, where the complete destruction of old-growth forest in 1938 provides a 50-year experiment in various forest types. Surveys of this material were made in 1968 (Henry 1968, Henry and Swan 1974) and in 1984 (Foster 1988b) in hemlock-white pine and northern hardwood forests. Methods for this work will continue to follow those in other LTER's (Harmon *et al.* 1986) and the Forest would participate in the exchange of woody debris among LTER sites (Franklin 1986).

Some work has also been done on the nitrogen balance of decaying logs at the Harvard Forest. Aber *et al.* (1983) found no change in total nitrogen content of decaying birch logs in both mixed hardwood and red pine stands through 80% of original weight loss, suggesting that this substrate is not an important component of the annual nitrogen cycle. A litter bag decay study using well-rotted birch wood material (approx. *20%* original weight remaining) has been in place for 5 years. The material continues to decay very slowly and exhibit little change in nitrogen content. We will continue to collect these samples as part of the Harvard Forest LTER project.

c. Effects of Large Mammal Herbivore Exclosures on Community Recovery Following Catastrophic Windthrow

i. Background. The recovery of vegetation following disturbance is often strongly affected by large mammal browsing. This has been shown dramatically at the Quabbin Reservoir Watershed near the Harvard Forest, where electrified fence exclosures were constructed in 1985 in clearcut stands. Seedling and sprout regeneration inside the exclosure are abundant and vigorous, while regrowth outside is nearly absent.

White-tail deer populations at the Forest have been moderately high for at least two decades. This poses a both a problem and an opportunity for the proposed LTER experiments. The problem is that intensively sampled study plots will need to be protected from potentially serious browsing. The opportunity involves taking advantage of the herbivore pressure to investigate the effect of browsing on species survival and growth and community composition. We will address both problem and opportunity by constructing an electrified strip exclosure across the catastrophic windthrow treatments to enclose a portion of all study plot types.

ii. Methods. In both the Quabbin Reservoir Watershed and in ongoing research at the Harvard Forest a relatively low-cost, low- maintenance and effective exclosure has been constructed from 5-stranded electrical fence 5-6 feet high (Gallagher spring-tight system). We will construct a 30-m wide electrified spring-tight exclosure in each catastrophic windthrow, running N-S to bisect the opening and extending into the surrounding forest by 40 m. This design will permit analysis of both herbivore (deer) activity and browse damage along the spatial gradient across a large canopy opening and into the understory. The exclosure will be installed immediately after windthrow creation.

Browse damage will be sampled in permanent plots before and after windthrow creation and tabulated by species and quantity in the control, chronic nitrogen and neutralization plots, inside and outside the fence. Differences between plant species in browse levels and the effects on community recovery will be related to: (1) position within the gap; (2)

nitrogen and neutralization plot treatments; (3) time of year; (4) deer population estimates; and (5) community composition and structure.

d. The Role of Plant Development and Architecture in Deterministic vs Opportunistic Response to Disturbance

Differences in whole-plant response involves the flexibilities and constraints inherent in developmental processes and resulting architectural form. The abilities of species to adjust to disturbed environments can be predicted with greater precision by addressing the following hypotheses.

i. Hypotheses

(1) Co-occurring species differ in the deployment of meristems in ways that produces differential buffering from negative effects of disturbance events.

(2) Early-successional tree species are capable of extensive vegetative regeneration via new meristems, mid-successional species deploy reserve meristems, and late-successional species redeploy existing meristems.

ii. Background. A major shift in plant morphological research in recent, decades has been the incorporation of plant form into demography and vegetation structure. This has been motivated by an increasing emphasis on environmental controls of plant form (Dirzo and Sarukhan 1984). To date, however, few detailed analyses of functional plant morphology have been attempted.

A central problem is the way in which complex forms are to be quantified to allow comparisons among taxa. One direct approach is to use the shoot apical meristem as the fundamental unit, since this can be located and counted. Even superficial analysis shows that species deploy meristems in different numbers and arrangements, and this often relates directly to their responses to disturbance. Detailed analyses are needed to determine the population dynamics of different types of meristems within each species, their longevities, their response to various disturbances, and the extent to which active and inactive meristems are segregated within such clonal populations (Oldeman 1983, White 1985). The concept of "meristem investment" has been exploited in a preliminary way (e.g., Maillette 1982a, b), but must be extended

to all life history phases, since each phase must be capable of responding to disturbance.

Within forests meristem proliferation in two dimensions is relatively easily analyzed in understory herbs, with a major contrast between linear and branched strategies (Bell 1974, Bell and Tomlinson 1980). Trees are more complex to analyze since primary growth, which otherwise provides clues to meristem demography, is obscured by secondary growth. Nevertheless, assessments of meristem reserve populations among tree species are feasible along the lines attempted for *Acer rubrum* (Wilson 1966).

iii. Methods. Of the 100+ major species of the Harvard Forest, several herbaceous and woody taxa will be selected for analysis. This will include common species amenable to precise quantification (e.g. *Lycopodium;* cf, Reutter 1988). Tree species from three successional categories (early, mid, late) including the genera *Tsuga, Fagus, Acer, Populus, Betula,* and *Prunus* will be used as will several species of *Viburnum.* Finally, species with distinctive architecture will be included, such as *Cornus alternifolia.*

Analyses of plant architecture will be coordinated with the core measurements (especially ecophysiological) made across experiments, though there will be an emphasis on architectural response to physical (windthrow) disturbance. For the rhizomatous herbs, clonal branching will be mapped in the field, and genealogical histories for individual clones will be assembled. For trees and shrubs, destructive sampling of seedlings or small saplings will yield data on shoot organization and crown development. Data entry into the GIS will permit efficient and flexible representations of architectural form.

After analysis, we will model the development of selected species to simulate examples of deterministic versus opportunistic processes within each life form. This has been attempted for abstract representations of rhizomatous herbs, using the axis as the unit of construction (e.g., Bell 1986). But it is possible to generate more realistic models if the apical meristem is used as the fundamental unit, if meristem demography is understood, and if opportunistic

developmental features are incorporated on the basis of known field responses.

D. Measurements

1. Overview

Section III.C outlined several types of experimental manipulations that provide an opportunity for measurement of processes listed as central to the LTER concept. The techniques we will use in these measurements are described below.

2. Micrometerology

Micrometeorological sampling will use a portable, system of electronic instruments and dataloggers with direct interfacing to IBM-PC compatible microcomputers. This system was developed by T.W. Sipe for ongoing studies of microenvironments and physiological ecology in experimental gaps at the Harvard Forest. Photosynthetic photon flux density (PPFD), air temperature, vapor pressure and deficit, windspeed, soil temperature (at two depths), and soil moisture are measured simultaneously by each station. The instruments are mounted on angled aluminum supports which are lightweight and easily transported to field sites for setup in any spatial array. They are connected to a Campbell CR21X datalogger and AM32 Channel expansion unit, which are housed in a weatherproof picnic cooler. Each datalogger can receive inputs from five stations. The angled supports can be extended above the ground to allow three-dimensional characterization of spatial variations in forest microclimates.

The start and stop times and sampling and storage intervals can be set to any desired values by the investigator. We have typically sampled all variables every 5 seconds, and stored 5-minute means continuously over periods of as much as 72 hours. The system can be moved as frequently as desired, depending on the experimental need.

Data are automatically dumped to cassette tape in the field, and transferred to microcomputer through a Campbell Scientific PC201 cassette-read card installed in the computer. Other software converts datafile formats and allows transfer of data in ASCII format to spreadsheet, statistics, or graphics software for analysis and visual presentation.

3. Ecophysiology

Ecophysiological measurements fall into two general categories: (1) physical/chemical exchanges with the environment, and (2) growth and allocation. The first category focuses on infrared gas analysis (IRGA) of photosynthesis, transpiration, and trace gas exchange. Several experiments call for periodic sampling of photosynthesis and water use of tree seedlings in the field. We will use a portable Li-Cor 6200 IRGA system, which measures photosynthesis, transpiration, leaf and air temperature, photosynthetic photon flux density (PPFD), ambient $[CO_2]$, and calculates water-use efficiency. The microprocessor capabilities of the Li-6200 allow relatively rapid measurements and extensive data storage for later dumping to computer. Fluxes of O_3 and sulfur gases between the forest canopy and the atmosphere will be measured using a Bingham Interspace steady-state IRGA system.

For selected species, we will measure curves of net photosynthesis versus PPFD, temperature, and $[CO_2]$. We will measure leaf nitrogen content of seedlings during response curve analysis in order to calculate potential photosynthetic nitrogen-use efficiency.

Whenever possible, field gas-exchange measurements will be coordinated with micrometeorological sampling. Connecting these data with the photosynthetic response curves will allow us to modify existing models of leaf photosynthesis and apply them to our target species in order to predict gas-exchange rates across a wide range of physical conditions.

The growth and allocation measurements form two logical categories. First, standard measurements of dimension growth (height, stem diameter, etc.) and biomass allocation will be done across the permanent sampling plots to yield comparative data from which to draw conclusions on the ultimate success or failure of co-occurring species under many different conditions. Depending on the particular experiment and question, we will occasionally harvest seedlings of selected species from the field in order to separate plants into root, stem, and leaf components and thereby quantify biomass allocation. For questions involving nitrogen use, we will analyze portions of the harvested leaves for nitrogen contents.

The second category of growth and allocation measurements involves the architecture of tree seedlings, and focuses not only on the allocation of mass to basic plant components but also on the arrangement of that mass in space. Such variables include the number of leaves, leaf dimensions, individual and total leaf areas, branch numbers and lengths, leaf orientations, leaf area index, and the ways in which these factors change luring the growing season and with seedling age. Some of these variables will be measured non-destructively on seedlings in permanent sample plots and the data will be related to gas-exchange performance. Destructive variables such as leaf area will be done on harvested seedlings. In the case of leaf areas, we will use a Li-Cor 3100 leaf area meter. Coordination with the proposed research on plant development and meristem architecture will allow exploration of the developmental constraints on whole-plant physiological performance and realistic refinements of predictions made by photosynthetic models for shoot carbon gain and water use.

4. Population Biology & Community Dynamics

All of the measurements of population fluxes and community structure and dynamics will be done on a system of permanent small (0.5mx0.5m) to medium (5mx5m) sized sample plots established for the experimental treatments. This will include the chemical disturbance treatments in the intact forest, but we will emphasize the windthrow treatments. We will monitor successive life historical stages in these plots, including seed dispersal, germination, seedling survival and growth, and mortality. These measurements will be done on all tree species present in the naturally-regenerating community.

The measurements of seed rain will give us the densities, timing, and spatial dispersal patterns of seed distribution of the major tree species at the Harvard Forest. The pattern of seed rain in relation to the proximity of parents and especially in relation to the position of the large litter components will be necessary in order to understand variability among species in patterns of seedling recruitment. The measurements of seed rain will be achieved through $0.25m^2$ aluminum tray seed traps covered with wire mesh to deter predation. Traps will be arrayed in the large and small windthrow

gaps along transects that will allow us to quantify dispersal patterns in relation to gap geometry. Traps will also be placed in the understory to quantify seed fall there. Seeds will be collected periodically, identified, counted, air-dried, and weighed. The sample schedule will follow the patterns of seed maturation in the field.

Germination rates will be measured and recruited seedlings will be identified, tagged and recorded within several germination plots. Each germination plot will be $0.25m^2$ and the plots will be arrayed along transects parallel to the seed traps. Measurements of seedling growth and mortality will initially be sampled on a biweekly schedule, and modified later according to need. Causes of death will be identified where possible.

In addition to the small-plot studies of seed dispersal and germination, we will tag and record all tree stems in a number of larger (2mx2m or 5mx5m) plots in the intact forest and gap sites. The regeneration mode (seed, advance establishment, resprout) of each individual will be recorded and data will be analyzed across all modes and within modes. Plots will be placed in the nitrogen-added, soil neutralization, and control treatments in both intact forest and hurricane windthrow, including both sides of the large mammal herbivore exclosure in the latter. Sampling of demography and growth will be done in these plots at intervals ranging from 4 to 8 weeks. Herbivore damage will be periodically sampled on these plots, with an emphasis on the nitrogen treatments and controls, following protocols developed in conjunction with M.D. Bowers and R. Forman at Harvard.

Community composition on the permanent plots will be summarized via standard importance values. The patterns of abundance and growth rates among species will be linked to measurements of aboveground and belowground microenvironmental conditions wherever possible. After a time-series of sampling on the permanent plots has accumulated, we will calculate transition matrices for each sample site and explore the variability in successional recovery as a function of gap size, position within gap, interaction with chemical (nitrogen or neutralization) treatments, and initial community composition. These data will be used to adapt the FORET-style stand simulation model in

order to predict forest regeneration following disturbance of various types.

5. Soil organic matter and nutrient dynamics

Nitrogen mineralization will be measured using a modified on-site incubation technique (Ellenberg 1978, Nadelhoffer *et al.* 1983, Pastor *et al.* 1984). Soil samples will be collected from both the O horizon and the top 20 cm of mineral soil at each site. Half of the samples from each horizon will be composited, well mixed, and taken to the laboratory for extraction (2N KC1, 24-48 hours) of ammonium and nitrate. The remaining twenty will be placed in thin polyethylene bags, returned to their original soil position, and left to incubate for 6 weeks. Incubated soils will be retrieved and analyzed for extractable ammonium and nitrate. Sequential incubations will continue throughout the year to allow calculation of net mineralization and nitrification for the entire period.

Carbon stocks in sampled soils will be determined by ashing. Total nitrogen will be determined initially by modified kjehldahl analysis, but we will pursue development of Near Infrared Spectroscopy (Section F.2.) or measurement of both C and N in soils samples.

6. Atmosphere-biosphere interactions

a. Eddy Correlation – Net fluxes of C02, H20 and 03 will be measured using the eddy correlation technique as described above (Section III.C.4).

b. Gaseous Sulfur Flux – We will make several additional gaseous sulfur flux measurements each year by deploying four replicate chambers in N and N + S fertilized and non-fertilized plots. All four chambers will be operated simultaneously and continuously for 24 hours. The flux measurements will consist of a series of eight three-hour integrated sampling intervals over a period of 24 hours. The eight sampling intervals will be distributed over the 24-hour period in a way that allows us to derive a clear picture of the effect of daily insolation and temperature cycles on the COS and CS_2 emissions. We will take frequent illumination data and air and soil temperatures during the flux samplings. The gaseous sulfur flux measurements will be made using a modified FEP Teflon flow-through chamber developed by

Steudler and Peterson (1985) to cover the soil surface. The chamber is operated so that ambient air is continuously drawn through it at a constant velocity and the difference in the gaseous sulfur concentrations between the chamber input and output are used to calculate the net gaseous sulfur uptake or release. The chamber design allows the sulfur gases in the incoming ambient air to interact with the soil that net fluxes (emission minus uptake) are measured.

We will analyze the gaseous sulfur compounds in the laboratory using the analytical method developed by Steudler and Kijowski (1984). This method simultaneously preconcentrates the gaseous sulfur compounds (COS and CS_2 as well as H_2S, CH_3SH, DMS and DMDS) on a trap containing the solid adsorbents Molecular Sieve 5A and Tenax GC. A Chromosil 330 column and sulfur specific FPD-GC will be used to separate and analyze the sulfur compounds.

c. Nitrous Oxide Emissions - Several types of N_2O measurement techniques from soils have been employed.

Previous studies have used several techniques to measure N_2O emissions from soils, including: 1) incubations of soil horizons or intact soils cores with or without the presence of acetylene (Firestone *et al.* 1980; Melillo *et al.* 1983; Robertson and Tiedje 1984); 2) sampling of the headspace such as used for CO_2 (Kanemanu *et al.* 1974) and radon (Pearson *et al* 1965); 3) use of both open and closed circulation chamber systems in the field (Denmead *et al.* 1979); and 4) closed chamber designs (Matthias *et al.* 1980; Mosier and Hutchinson 1981; Duxbury *et al.* 1982; Goreau 1982; Keller *et al.* 1983; Goodroad and Keeney 1984), which involve chambers placed on or inserted into the soil surface with measurements made of the change in N_2O concentration in the enclosed headspace over time.

Most of these estimates are short-term, non-continuous experiments which do not measure N_2O releases over a whole day, nor do most of the field studies make measurements over an entire year. We now believe that there are large seasonal (spring through fall) changes in the rates of N_2O production in soils (Goreau 1982; Keller *et al.* 1982; Melillo *et al* 1983; Goodroad and Keeney 1984; Goodroad *et al.* 1984). Conrad et *al.* (1983) were successful in using two

alternating closed chambers to measure the N_2O releases semicontinuously over a whole day and observed a diurnal pattern of N_2O emissions that coincided with the pattern of soil temperatures.

We propose to use closed chambers placed on the soil surface to make the field N_2O emission measurements. We will use the alternating open and closed adjacent chamber technique developed by Conrad *et al.* (1983) to continuously measure the emissions over a whole day. The headspace of the closed chamber will be sampled several times over the one hour closed period and the N_2O concentrations determined in the laboratory using a gas chromatograph with a 63Ni electron capture detector.

We will deploy three replicate chambers to ascertain the spatial variability at each N fertilized and non—fertilized plot. The flux measurements will consist of a series of sampling intervals distributed over a 24-hour period in a way that will allow us to observe the effects of the diel insolation and temperature cycles on the emission of N_2O. Measurements will be coordinated with extensive micrometeorological information.

The timing and frequency of field sampling are crucial as emissions may occur in pulses following snow-melt or heavy precipitation events. We propose to measure nitrous oxide emissions several additional times during each of the years. These will be scheduled to sample both the seasonal cycle of background N_2O emissions, and to attempt to catch pulse events.

d. Energy, water and mineral nutrient fluxes

In selected stands we will use a soil water balance technique to estimate annual evapotranspiration (Fownes 1985). The basic data are soil water content in 25cm increments through to the bottom of the rooting zone, as measured with a neutron probe. Water inputs to the soil are measured as throughfall collected below the forest canopy. Movement below the root zone is described by a soil drainage equation based on measured water loss from the soil during the dormant season as a function of soil water content. During the growing season, evapotranspiration (ET) between two soil water measurements (1 week) is estimated as: $ET = (W_i - W_f) + Th - D$ where W_i and W_f are initial

and final water content, respectively, Th is throughfall input and D is drainage. In intact forests, surface runoff inputs and outputs are generally very small. Evaporation is also minimal during the growing season such that ET is approximately equal to transpiration.

Precipitation monitoring - The Harvard Forest maintains a level 3 Weather Service Station. We will carry out daily collection of precipitation samples for analysis of ammonium and nitrate content to determine inputs of mineral N to the experimental systems. Analyses will be carried out on the TRAACS system at the University of New Hampshire.

Leaching losses - Leaching losses of nitrogen from certain plots will be determined by suction cup lysimeters placed below the rooting zone and sampled monthly during the growing season. Nitrate and ammonium concentrations will be measured on the TRAACS system at the University of New Hampshire.

e. Soil and Vegetation Chemistry - Collection of fresh leaves, recently senesced leaves, leaf litter, forest floor, and the upper 10 cm of mineral soil will be made several times a year. These samples will be analyzed for total sulfur, organic carbon and total nitrogen. We will use Leco C and S analyzers (with IR detection) to measure total sulfur and organic carbon on soil and vegetation samples. Total nitrogen will be determined by a standard semimicro-Kjeldahl method with the ammonium determined by a Technicon autoanalyzer. Field-moist soil samples, leaf litter and vegetation samples will be analyzed for the amount of sulfur as carbon-bonded sulfur (C-S). Carbon-bonded sulfur will be determined by the Raney-Ni procedure (Lowe and Delong 1963, Freney *et al*. 1970, 1975). This procedure determines sulfur containing amino acids. Periodically, we will analyze soil and vegetation samples for ester-sulfate (C-O-S) using the hydroiodic acid, formic acid and hypophosphorus acid reduction (HI-S) procedure (Fitzgerald 1976, Freney 1961). This method includes inorganic sulfate and the C-O-S pool. A Dionex ion-chromatograph or a Technicon autoanalyzer will be used to analyze extracts of soil and vegetation samples for soluble and sorbed SO_4, NO_3 and NH_4 using standard

procedures. Soil pH will be determined by a glass electrode (1:2.5) in 0.01M $CaCl_2$.

7. Net primary production and carbon, nitrogen allocation

Above ground net primary productivity will be measured as the sum of litter fall plus woody biomass increment. Litter fall will be measured using 5 1/2 m x 1/2 m litter traps per plot which will remain in place year round. Woody biomass increment will be estimated as measured changes in dbh of trees converted to biomass using summary allometric equations available for each species (Pastor *et al.* 1984; Whittaker et *al.* 1974; Tritton and Hornbeck 1982).

Biomass of fine roots will be measured twice each year by hand sorting of 10 soil cores collected from each plot. Times of collection will be based on seasonal fluctuations in biomass measured by McClaugherty *et al.* (1982). We will not attempt to estimate productivity by sequential changes in biomass (e.g. McClaugherty *et al.* 1982, Vogt *et al.* 1982, Aber *et al.* 1985). Rather we will use the N budgeting technique of Nadelhoffer et al. (1985) to predict N allocation to fine roots. Measured N concentration in fine roots will be used to calculate NPP of roots, and turnover will be calculated as mean fine root biomass divided by biomass allocated.

E. Project-wide Support Measurements - LTER Core Areas

A major goal of the LTER activity is to develop coherent data sets that allow for the analysis of long term dynamics in a single ecosystem type and for comparisons among all LTER sites. In the following paragraphs we summarize the various measurements that we will make as part of the basic, project-wide support data base. The measurements are organized into the five core research areas that form the basis of the LTER activity at NSF (Callahan 1984).

1. Pattern and Control of Primary Production

In this section we include direct measurements of the components of above-ground production and the indirect measurements of below-ground production of vegetation in both the control and manipulated plots. Above-ground production measures include litterfall and woody increment. Fine root production and turnover will be estimated using an N-budgeting technique. We will use these various types of

information on production to estimate total NPP. In addition we will use the eddy diffusion technique to calculate net ecosystem production for large forest tracts.

2. Spatial and Temporal Distribution of Populations

The population dynamics of tree, shrub and herb species will be an integral part of the LTER program of the Harvard Forest in conjunction with other permanent plot studies and long-term monitoring programs. In the tree gap and hurricane disturbance components of the research, we will establish permanent plots in which we will monitor seed rain, germination herbivore damage, growth and mortality for all tree species that regenerate naturally. Detailed analyses will be made of population dynamics of meristems for common species and these will be related to ecophysiological measurements.

3. Organic Matter Dynamics

Plant litter and soil organic matter will be measured on a routine basis on the various experimental sites at Harvard Forest. We will use several indexes including the lignocellulose index and stable isotope ratios of carbon and nitrogen to detect changes in litter and soil organic matter quality. Long-term changes in accumulation rates for organic matter in lake sediments, peatlands and small forest hollows will be studied in the paleoecological studies.

4. Nutrient Cycles

We will follow changes in nutrient pools in plant biomass and changes in inorganic and organic nutrient pools in the soil. We will also study intersystem exchanges of nutrients including nutrient inputs in precipitation and nutrient losses in solution and in gaseous forms.

5. Patterns and Frequencies of Disturbance

The theme of the proposal is disturbance. We are focusing on a finite set of disturbances that have been, are, or are likely to be important to the forest landscape of southern New England - wind damage at several spatial scales, nutrient saturation as a consequence of chronic air pollution, and the loss of key species. We will evaluate the effects of these different types of disturbance on both short-term system properties such as nutrient outputs as well as on

long-term attributes such as soil organic matter quantity and quality and trends in NPP and NEP.

F. Synthesis: Modeling, Remote Sensing and Geographic Information Systems

We will extend the results of our experimental treatments in both space and time to develop a synthetic, landscape-level view of ecosystem dynamics at the Harvard Forest. Existing process models will be modified to extend predictions in time. Spatial extension will be through cooperative remote sensing research with NASA's Ames Research Center and through continued development of GIS research and development in coordination with the Harvard Laboratory for Computer Graphics and Spatial Analysis.

1. Computer Modeling - Data synthesis will occur through continued development of existing models of ecosystem function. The first is a data-driven model of nitrogen and water interactions which has been developed using information from stands in Wisconsin and at the Harvard Forest. The model has two components: a production module which converts water and nitrogen availability into net primary production by leaves, wood and fine roots, as well as calculating water and nitrogen uptake, and a decomposition module which follows the decomposition process continuously through five states of decay for each type of litter produced. This model has been used to predict equilibrium nitrogen cycling rates for ecosystems based on the relative water-, nitrogen- and light-use efficiencies of species present, and the water holding capacity of the soil. The structure of this model was designed around existing data bases. For example, the decomposition module accepts information on the five stages of decay defined on the basis of carbon and nitrogen dynamics measured in actual decomposition studies (Melillo and Aber 1984).

This simplified model is designed to work at an annual time step, but over relatively short time periods in which changes in species composition are not significant. We propose to modify this model to a weekly time step in order to encompass shorter time scale events important in modeling soil moisture conditions and trace gas fluxes. A hydrologic budget will be incorporated using the methods of Fownes

(1985), where soil water content is used to determine both initial leaf conductance and its reduction during the course of a day. Intra-annual data on litter decay and leaching losses (McClaugherty and Aber 1984) will be used to determine labile carbon pools available to drive trace gas emissions. This model structure will continue to be tightly connected to the measurement methods used in the field, so that compatibility between field results and model will be maximized.

We have also extended this model to include soil chemical interactions and cycling of all major nutrients (Aber 1985), and have used this to project effects of different acid deposition scenarios on various forest ecosystem types. We will continue development of this part of the model as it is an area not covered by most existing forest ecosystem models.

A second modeling approach is designed to lengthen the time scale of prediction, and also provide interaction and integration with other LTER sites. John Pastor (Cedar River site), Hank Shugart (Virginia Coastal site) and Bill Parton (Pawnee site) are coordinating efforts in combining the Century model for grasslands (Parton et al. 1986) with the Foret/Linkages forest models (Shugart and West 1980, Pastor and Post 1986) to provide a single model dealing with both types of ecosystems and ecotones as well. Our group has developed the FORTNITE model (Aber et al. 1982) which is very similar in structure and processes to the Linkages model. We propose to interact with these investigators and sites in the development of this integrated model. In terms of the Harvard Forest LTER, this type of model will provide for prediction over longer time scales where changes in vegetation and climate may be significant.

2. Remote sensing - A major part of the on-going research in nutrient cycling at the Harvard Forest is the development of remote sensing technologies for detection of nitrogen saturated stands, and for predicting biogeochemical cycling rates based on chemical characteristics of forest canopies. Infrared spectroscopy has recently gained wide acceptance as a method for quantitative analysis in agricultural research and commercial operations (Rotolo 1979). The near infrared (NIR) reflectance properties of organic materials are a

summation of the characteristics of individual components (e.g. proteins, cellulose, etc., Marten et al. 1985) combined with the radiation-scattering properties of the sample material. The early research of Ben-Gera and Norris (1968) demonstrated the utility of NIR analysis for predictions of forage and grain nutritional values (e.g. crude protein, fiber, digestible dry matter; Hymowitz et al. 1974; Norris et al. 1976). Analytical errors by NIR analysis are within the range of wet chemistry repeatability (Norris et al. 1976; Winch and Major 1981). In addition, the speed of measurement allows handling of much larger sample sizes, actually reducing the total variance associated with the sum of sampling error and analytical error.

In the past year we have drawn on our extensive set of green and senescent foliage samples to calibrate a NeoTec model 51A Scanning Filter System which samples between 1594 and 2354 nm at roughly 1 nm intervals. The technique predicts the quantity of specific compounds within a ground sample by measuring absorption at multiple wavelengths and entering measured reflectance values into multivariate equations derived from a large set of samples with known chemistry. We analyzed over 200 samples for which nitrogen and lignin content had been measured by standard wet chemical methods (McClaugherty et al. 1985). NIR spectra for these samples were measured and then used to develop the calibration equations for predicting nitrogen and lignin content from NIR reflectance.

The results of the calibration have been extremely encouraging. Using linear combinations of reflectance at five wavelengths, the standard error of estimation for nitrogen was 0.11% N with an R-squared of .98 between measured and predicted. For lignin, six wavelengths were used to obtain a SEE of 2.90% with an R-squared of .78. These values compare with laboratory repeatability errors of .12% for N and 2.28% for lignin. Again, by increasing the number of samples which can be processed, this method will reduce the total error due to both sampling and analytical error substantially. The wavelengths used in the regressions all represent known absorbance features for pure compounds of the type being assayed, or features of other important components of plants which must be accounted for in

the spectra of the tissue. For both nitrogen and lignin, a single equation applied to the entire range of materials tested. It was not necessary to develop separate equations for green foliage versus litter, conifer versus broad-leaved, etc. With NIR analysis the lignin and nitrogen content of leaf material can be determined in 5 minutes.

While the technique of near infrared reflectance analysis is well established, we are apparently the first group to apply this method to non-crop plant materials. In the research proposed here, we will both apply the current regressions and will measure lignin content of whole forest canopies, and from this to predict rates of nitrogen cycling in undisturbed stands (e.g. Wessman *et al*. 1987). We propose here to link these advanced remote sensing tools to the GIS effort, using remote sensing results to add difficult-to-measure parameters such as productivity and nutrient cycling to the GIS data base. As the models dealing with soil status and trace gas fluxes are extended and refined, we hope to be able to predict spatial variation in trace gas flux using remote sensing data entered into the GIS as the basis for an aerial extension of results in experimental plots.

3. Geographic Information Systems will be an important integrative tool at the Harvard Forest LTER for research application and data management. Recent expansion in microcomputer capability and new development in GIS software for these systems (e.g. MAP on IBM PC and APPLE; Tomlin 1987) make it feasible for all participants in the Forest LTER to operate the Forest GIS in their own labs, thereby enhancing possibilities for data exchange and research development within this project. The emphasis on GIS development by the Forest LTER will also encourage integration and interaction within the LTER system where the utility of computerized cartographic systems is clearly recognized (Franklin, ed. 1987).

The GIS at the Forest consists of computer hardware and software specifically designed for encoding, storage, manipulation, and display of cartographic data. In assembling a system appropriate to the needs of the Harvard Forest LTER and similar facilities, a number of considerations have been taken into account. In particular, the

system: 1) must be able to provide up-to-date capabilities; 2) is affordable in terms of both acquisition and ongoing maintenance costs; 3) is accessible to users of other systems and users with little experience; and, 4) is adaptable to future changes in both hardware and software technology. We have specifically chosen to base our system on IBM-compatible microcomputers to enhance its availability to all researchers in our group and to encourage extensive exchange of data and development of new capabilities. The major hardware components of the GIS include data input and output devices, an IBM PS/2 80 central processing unit, and a mass storage device, specifically: a Calcomp model 9100 line digitizer, a Tektronix model 4125 color graphics display terminal, a pen plotter, a IBM PS/2 80 with micro-Bernoulli and WORM storage.

The software components of a GIS provide for input, transformation, and output of cartographic data. The encoding, editing, and maintenance of cartographic materials are handled with the ARC/INFO program of Environmental Systems Research Institute. This widely-used and well-supported program can manage cartographic data with high precision and manipulate non-spatial attributes with great flexibility and power.

The ARC/INFO comprises the core of the Harvard Forest GIS, performing all routine storage and retrieval functions. Though this program will also be used for particular research projects, it is anticipated that such projects will often rely on project-specific software, especially the Map Analysis Package (MAP). MAP is a widely-used program which provides a flexible set of modeling capabilities (Tomlin 1980, 1986).

To translate existing line-drawn maps at the Harvard Forest into GIS format original maps will be digitized directly into ARC/INFO and then be stored as part of a permanent archive. Once in digital form each map will also be rescaled, reprojected, and reorganized to conform to the conventions of common cartographic data base for the Harvard Forest area and will conform to the Universal Transverse Mercator projection system. This area encompasses all of the Harvard Forest property and all of the town of Petersham. Ultimately, the

data base will include overlays of general characteristics (e.g. topographic elevation, slope, aspect, soils characteristics, hydrology, vegetation, roads, buildings, and political boundaries) as well as overlays of more specific characteristics (e.g. timber stand treatments, land use history, population densities, chemical concentrations) associated with particular research projects.

   b. Data management with GIS. With over 80 years of research history and increasing activity and demands on the land base at the Forest the continued development of a GIS is seen as a critical step in administration and data management. With a data base including physical features, vegetation and research history the managers and administration of the Forest LTER will be able to plan and conduct research according to the established management plan.

   c. Research Applications of GIS. Data from research across a variety of spatial scales can be stored within the subsequent analysis or exchange. At the finer scales we have done some preliminary work mapping soils and root distribution and plant architecture. Mapping of individuals within permanent plots can be used for following changes in populations and community structure. At the broader scale maps of the entire forests have been analyzed for landscape elements, for historical changes in broadscale patterns of vegetation (Fetherston 1986) and for analyzing patterns of soil, landscape position and vegetation type. As our efforts at modeling forest dynamics progress we will seek to integrate the individual and stand-based models with landscape models on the GIS. At the very broadest scale we will tie the atmospheric science component of the Forest LTER into the regional network of sites using regional GIS and modeling efforts.

IV. RESEARCH SCHEDULE AND WORKPLAN

   The research schedule (see Table 3) summarized here outlines in broad terms the structure of the 5-year work plan. More specific scheduling is described under each of the scientific tasks in Section II.The five-year schedule for the Harvard Forest LTER involves 4 broad components:

   (1) continuation of ongoing experimental treatments and studies;

(2) site selection and baseline monitoring of pre-treatment system function for new experiments during years 1 and 2; and

(3) initiation of physical and chemical disturbances in year 3, followed by a comprehensive schedule of regular sampling, on our experiments; and

(4) synthesis of results in years 4 and 5 through modeling, GIS application, and remote sensing.

YEARS 1 and 2

Ongoing studies include paleoecological and catastrophic disturbance histories, and chronic N and N + S additions to small plots in hardwood and pine stands, which will be continued and expanded as described in Section II. Site selection and baseline monitoring prior to new experimental treatments include regional atmospheric chemistry, above- and below-ground microenvironments and nutrient fluxes, plant architectural systems, sampling of community composition and structure, and development of forest-atmosphere COS and CS_2 measurement technique.

YEAR 3

The windthrow and disturbance interaction treatments will be initiated in year 3 to achieve synchronization and valid cross-treatment comparisons. The large mammal herbivore exclosure will be constructed immediately after windthrow creation. Models of canopy CO_2 and H_2O flux will be developed from eddy correlation measurements in control and pre-N addition stands, and measurements of COS and CS_2 flux from canopy to atmosphere will commence.

YEAR 4

Chronic N additions will begin in the 5.0 hectare site, and eddy correlation measurements of the effects of N on canopy fluxes will start as well. Measurements of O_3 uptake as affected by forest physiological status (begun in year 3 if feasible), will continue on the control and N amended sites. Preliminary development or

modification of ecophysiological and geochemical models (e.g.
FORTNITE) will begin where possible in year 4.

YEAR 5

All experimental treatments and measurements will now be in
place, and in addition to regularly scheduled sampling, attention will
be turned more toward synthesis through the modeling, GIS, and remote
sensing efforts described in Section II.E.

Table 3
HARVARD FOREST LTER RESEARCH SCHEDULE

Proposal Section	Major Research Area	Ongoing	1989	1990	1991	1992	1993+
III.B.2	Paleoecology	******	****	****	****	****	****
	Catastrophic Disturbance	******	****	****	****	****	****
C.1.a.	Catastrophic and Small Windthrows		----	----	****	****	****
1.b.	Selective Mortality		----	----	****	****	****
2.a.	Chronic.N & (N+S) small plots	******	****	****	****	****	****
	Additions large 5.0 ha plot		----	----	****	****	****
2.b.	Chronic Neutralization	******	****	****	****	****	****
3.a.	Windthrow vs. Nitrogen		----	----	****	****	****
3.b.	Windthrow vs. Neutralization		----	----	****	****	****
4.a.	Canopy Productivity and O_3 Uptake						
	i. Baseline atmospheric chemistry		****	****			
	ii. CO_2, H_2O fluxes and model				****		
	iii. CO_2, H_2O, and O_3 uptake				----	****	
	iv. Chronic N - 5.0 ha plot					****	****
4.b.	Sulfur gas fluxes						
	i. From (N+S) - amended soils	*******	****	****	****	****	****
	ii. Canopy-atmosphere exchange			----	****	****	****
5.a.	Organic Matter Accumulation/Quality			****	****	****	****
5.b.	Coarse Woody Debris			****	****	****	****
5.c.	Large Mammal Herbivore Exclosure			----	****	****	****
5.d.	Plant Development/Architecture						
	i Intact forest		****	****	****	****	****
	ii. Windthrown sites				****	****	****
F.1.	Modeling	-------	----	----	----	****	****
2.	Remote Sensing		****	****	****	****	****
3.	GIS	*******	****	****	****	****	****

NOTE: (----) represents baseline monitoring or technique development
       (****) represents experimental treatment initiation and subsequent
              regular measurements

Table 2. Summary of Existing Data Bases for Harvard Forest LTER

Map series (1" = 400') of topography, soils, land-use history, forest stands (at 10-15 year intervals since 1907), disturbance history, experimental manipulations, permanent plots and study locations;

Geographic Information System with Map Analysis Package installed on IBM XT and PS/2 80; overlays (e.g. soils, forest types, topography, waterbodies) encoded for Tom Swamp tract and the town of Petersham;

Computerized databases for more than 800 published and 475 unpublished studies;

Aerial photography (1:4000 to 1:25000 scale) from 1937, 1939, 1944, 1955, 1968, 1972, 1986; nearly 3000 photographs of stands since 1922;

Daily temperature and precipitation records since 1913; comprehensive study of forest temperature regime; ongoing microclimatological characterization (light, wind, humidity, temperature) of intact forest and forest gaps; seasonal record of CO_2 levels in all forest strata;

Petersham and Harvard Forest floras; herbarium; bird checklist (1948, 1969); studies on vertebrate dynamics, herbivory and damage to forests; entomological collections dating to 1940's; fungal pathogens as of 1950's; phenological study of major tree species; survey of mycorrhizal associations in major forest types;

Paleoecological record of post-glacial vegetation and climate dynamics from 3 basins; post-settlement to modern pollen record from soil humus; ongoing comparison of last millennial dynamics at HF and Pisgah Forest;

Record of land-use history for entire area including original ownership and use patterns, agricultural history, and stand-level documentation of vegetation type and silvicultural activity since mid-1800's;

Eighty years of information on pre- and post-hurricane vegetation at virgin Pisgah Forest in SW New Hampshire: permanent plots, forest reconstruction, repeated measurements, and analysis of woody debris;

Vegetation inventories on 10-15 year intervals; periodic growth measurements on all plantations and many natural stands; long-term silvicultural experiments; volume and growth tables for all major species; long-term permanent plots to study vegetation recovery from hurricane and gypsy-moth; complete stem maps of 4 ha area periodically sampled since 1966;

Hydrological study of one watershed on Harvard Forest; Metropolitan District Commission records for Quabbin Reservoir watershed includes monitoring of 4 weirs on Cadwell Creek since 1962;

Physiological measurements and hydraulic architecture, for major tree species; seedling physiology for *Acer* and *Betula*; physiology and demography of *Viola* spp; developmental studies on major tree, shrub, herb and *Lycopod* spp;

Nitrogen budget, nutrient cycling, above and below-ground productivity, fine root dynamics, decomposition rates, hydrology, soil enzyme activity for red maple-oak forest and red pine plantation;

Survey of mycorrhizal associations in hardwood and conifer forest; counts, anatomical descriptions, root phosphatase activity and respiration for mycorrhizal morphotypes; effects of liming and burning on mycorrhizal abundance and types.

V. MANAGEMENT AND ORGANIZATION

A. Administration of the Harvard Forest LTER Program - The organization of the LTER will utilize and augment the existing management structure at the Harvard Forest. The administration will consist of a <u>Program Director</u> (John G. Torrey, Director of Harvard Forest) and an <u>Executive Committee</u> (J. Torrey, D. Foster, F. Bazzaz, S. Wofsy, J. Aber, P. Steudler and K. Nadelhoffer) that will be responsible for supervising research decisions in accordance with the long-term management plan of the Forest. The entire group of collaborators (see V.D.) will comprise the <u>Research and Policy</u> Committee. This group was responsible for framing the objectives of the current proposal and will meet annually in order to review research activities, formulate new strategies and collaboration, and to discuss policy issues. An annual meeting will be held at the Forest for three days during mid-winter and will consist of scientific presentations and discussion. Attendees will include all collaborators, appropriate agency officials, invited participants from related projects and other LTERs, and the <u>Harvard Forest Advisory Committee</u> (see V.G.).

John Edwards (M.S. in Forestry), currently the <u>Harvard Forest Manager</u> will be responsible for field logistics, coordinating experimental manipulations and site maintenance and will arrange contracts with outside technicians. Edwards has four years of experience at the Forest managing the physical plant, coordinating field activities and overseeing construction projects, ecological experiments and silvicultural activities. Logistics regarding housing for visiting scientists, the use of laboratory space, and scheduling of meetings and conferences will be arranged by Edwards and the <u>Administrative Secretary</u>. Equipment purchases and deliveries will be initiated by staff at the Forest in conjunction with the financial office of the Department of Organismic and Evolutionary Biology.

Our <u>Computer Manager</u>, Emery Boose, will be responsible for data management and computer implementation and will work closely with Foster and Tomlin. Boose has an undergraduate degree in mathematics and a Ph.D. from Harvard. He is extremely knowledgeable in the fields

of computer technology, data management and software applications. During his six years as computer manager at the Harvard Forest he has installed all of the current hardware and software, implemented the data management systems for the forest inventory, financial records, and library, written software for GIS editing, analysis and display and has instructed all newcomers and staff in the use of the microcomputer system.

   B. Data Management at the Harvard Forest - The organizational structure and facilities for storing long-term data at the Forest have been in place for nearly 80 years. Implementation of data management for the LTER therefore can be accomplished with moderate expansion of support staff and increased emphasis on GIS and computerization of data bases. The existing data structure and archive facilities are described below. In the following ion (V.C.) the specific protocol for LTER data management is presented.

   i. Data Organization - Information relating to the land base of the rest is organized geographically by compartments, which are 30-50 ha in area. Forest stands, research activities and experiments are keyed onto compartment base maps (1" = 400'). Standard data sheets are used by all searchers to record the type of research activity, site descriptions, and data. Unpublished studies, including raw data, notes and manuscripts, are led chronologically and indexed on a computer data base where they can be referenced by subject keyword, author, date, and geographical location. A companion data base contains a bibliography of all papers published about the Harvard Forest or by resident scientists.

   ii. Cartographic Data - In addition to compartment-based maps cording specific experiments or studies, nearly 500 maps document land- e history, vegetation, edaphic features and hydrology of the Harvard Forest. Original maps are stored in a fire-proof vault; duplicates are available in common map cases. Each map is indexed on a computer data base by location, subject, date, scale, author and storage location.

   iii. Physical Storage - A fire-proof vault in Shaler Hall serves as a permanent archive under the direction of D. R. Foster. Original

data, manuscripts and maps are stored in the vault along with
photographic archives, financial records and a complete back-up of all
computer tapes id diskettes.

   iv. Library - Approximately 22,000 volumes comprise the forestry
library of the Harvard University Library system in Shaler Hall.
Holdings, which are particularly strong in forestry, soil science,
ecology and conservation, are entered on the Distributable Union
Catalog (DUC) of the University library system. Microfiche is
available for the DUC as well as le holdings of the forestry libraries
at Yale and the University of Massachusetts. The card catalogue of
the Harvard Forest library has been converted to an IBM PS/80 with
support from NSF. Bibliographic searches may be made by author, date
and subject. Acquisitions, cataloguing and library exchanges are made
by a part-time librarian-secretary.

C. Data Management For The Harvard Forest LTER - Data management for
the LTER will expand on the protocol described above by: **i)**
implementing a formal protocol for experimental design and
coordination, ii) establishing a uniform computer data structure, and
iii) establishing efficient and secure provisions for permanent
storage and exchange.

   i. Experiment and Data Design - Currently all field research at
the Forest is approved by a group of resident scientists in accordance
with a Long-term management plan. The plan assigns specific-use
classification to each forest area based on the following
considerations: past history of research at the site; rarity of the
site type, or vegetation; cultural use and visibility; and, type of
research activity. This protocol is a necessary part of long-term
research as it ensures site security and maximizes the availability of
different site types.

   The protocol for handling site requests by researchers will be
formalized under LTER to assist in planning and data management. A
standard form will be submitted by a researcher to the <u>Harvard</u> <u>Forest</u>
<u>Manager</u> outlining the research (objective, experimental design,
personnel, equipment), describing the specific combination of site and
vegetation requirements including a map of the proposed site, and

giving details of the expected configuration of the data set. Decisions concerning experimental location will be made by the Executive Committee.

   ii. Data Storage - Data entry is the responsibility of the individual researcher. Our data system will interface with IBM PC microcomputers and all utilize dBase-III and LOTUS 1-2-3 as the standard software.   This hardware/software combination was chosen for the following reasons: i) Harvard University has selected IBM as its emphasized microcomputer system, hereby arranging inexpensive prices and compatibility throughout the University, ii) IBM-compatibility is shared by many microcomputers, which will ensure ease of data exchange among researchers, and iii) dBase-III and LOTUS provide a flexible, widely-used data base package that will be accessible to many researchers at other LTER sites.

   Each file header will include an ID number (e.g. year-xxx), keywords, date, location (Forest compartment number), vegetation type, collector and file size (rows x columns). The location designator will provide appropriate spatial information such that the corresponding GIS file can be accessed easily and new GIS overlays can be generated rapidly from the experimental data. Data received from an investigator will be loaded on the Harvard Forest system and will be stored in triplicate: an original floppy disk will be stored in the vault, an active version will be accessible on hard disk/optical disk, and the entire data base will be backed up on a micro-Bernoulli in the vault along with hard-copies of the data.

   iii. Data Analysis and Exchange - Data from dBase and LOTUS files on the hard disk can be sorted by e.g. keyword, ID number, or location to provide the entire data or an abstract. A current list of Harvard Forest data sets and the original data will be available to the LTER network using BITNET.

   Data analysis will be the responsibility of the individual researcher is expected that collaborators will have access to a variety of software currently available at the Harvard Forest including: simple graphical and statistical capabilities through e.g. Lotus 1-2-3; SYSTAT, a comprehensive PC-based statistical package; Map

Analysis Package (MAP), the GIS used for Harvard Forest cartographic information; and a series of display, outputting and spatial statistical software for use with MAP.

D. Principal Investigators, Co-Investigators and Research Collaborators - Currently five projects involving the principal investigators and major collaborators are on-going at the Harvard Forest. Each will contribute significantly to the proposed LTER plan and renewal of these grants or new proposals for related studies will be pursued in the future. Melillo, Aber, Nadelhoffer, Steudler and others have been studying nitrogen cycling, sulfur gas fluxes and organic matter dynamics in these forests for nearly 10 years. Their current project (NSF - ATM) will continue until 1991. Torrey has three more years of funding (Mellon Foundation, USDA, DOE and NSF) for his study of <u>Frankia</u> and soil microbiology. Linkins and McClaugherty have been studying decomposition rates and soil enzyme activity for 10 years and have a proposal for continuation of this work under review by NSF. Ecophysiological studies of birch and maple (Bazzaz and Sipe) have NSF funding through 1989 with a strong possibility of a renewal proposal being submitted at that time. One project, involving GIS development and modeling of landscape dynamics with Foster and Tomlin (NSF Biological Resources and Facilities grant) will continue through 1988.

The principal investigators are based at Harvard within the departments of the Harvard Forest and Organismic and Evolutionary Biology, it the Ecosystems Center at Woods Hole, and at the University of New Hampshire in the Complex Systems Research Center. Co-investigators and research collaborators come from within Harvard and from six other institutions and most have a history of research at the Forest. All collaborators would actively contribute time and data to the LTER program, many would receive some support from LTER funds, and all would participate in the integration of research results.

E. Control of the Site - Since its establishment the three-fold mission of the Forest has been to serve as a center for research, education, and demonstration related to forest biology. Harvard University and the administration of the Forest have recognized that

these goals could be achieved only through long-term commitment to experiments, forest management and teaching. As the accompanying letter from Dean Michael Spence (Appendix III) indicates, Harvard University is committed to maintaining the Harvard Forest as a center for long-term research and views the proposed LTER project as a natural extension of its historical mission.

As the successful continuation of past experiments for up to 65 years indicates, site security can be well maintained at the Forest. Trails are restricted from vehicular traffic and the woods crew services these paths for walking and cross-country skiing. An agreement with the local rod and gun club provides additional security and surveillance of our waterbodies and some trails. We have been very successful in maintaining undisturbed control sites and anticipate no future problems with site security.

F. Institutional Cost Sharing - As the research efforts of the Harvard Forest center around long-term studies, the Forest and Harvard University are strongly committed to sharing in the costs of managing the Forest as an LTER site. This institutional cost-sharing takes two forms: 1) direct annual contribution of income from Harvard Forest endowment (see sample budget below) and 2) the application of indirect costs from research grants to maintain the Forest. In fiscal year beginning 1989 earnings from the Harvard Forest endowment committed to the budget of the Forest will be ~$350,000 per annum. In addition to operational expenses and maintenance costs this budget covers salaries for the Harvard Forest Manager and Fisher Museum Coordinator, Computer Manager, Three-member woods and Maintenance crew, Caretaker and an Administrative Secretary. Funds for the Director's and other faculty salaries come from the Faculty of Arts and Sciences, whereas 2-4 annual fellowships for visiting faculty in forest sciences are provided by Bullard Fellowship funds. Additional support for the Forest comes from research grants from federal and state agencies or foundations. In accordance with past practice, the indirect costs from such grants, including an LTER grant from NSF, will be divided between the administrative costs in Cambridge (~15%) and the maintenance costs incurred in the operation of the Petersham facility

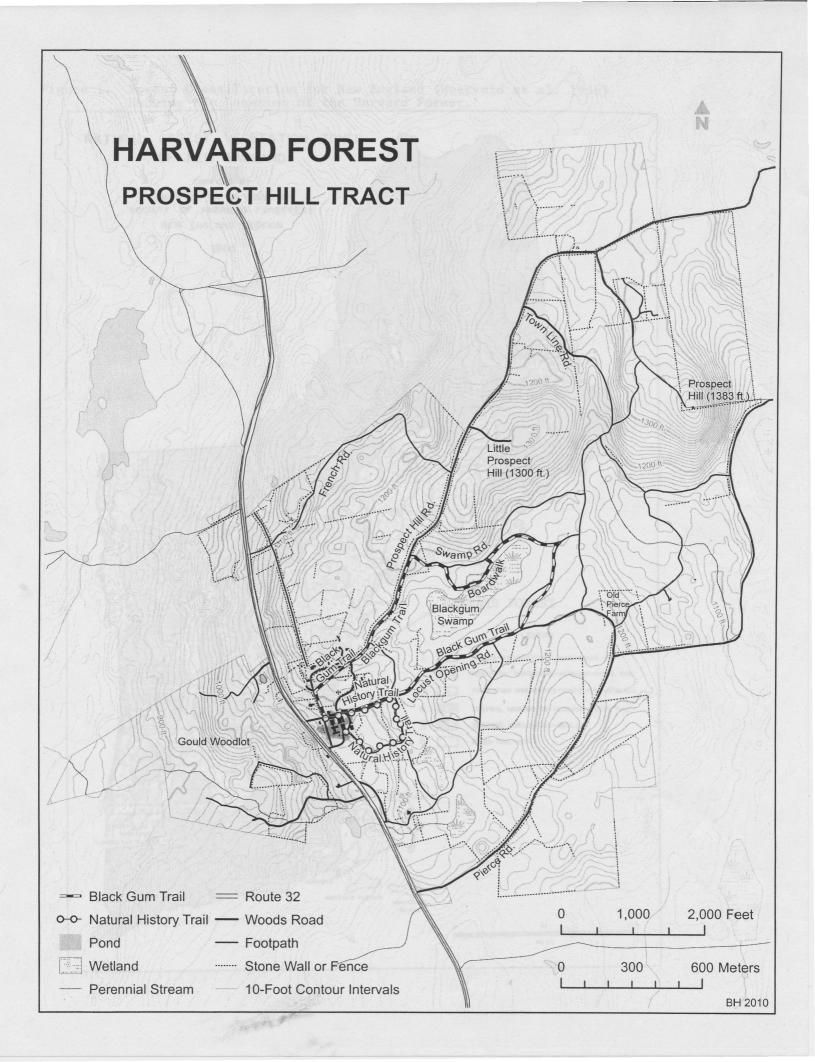(~85%). Therefore, indirect costs will be specifically applied to the research operation at the Forest.

G. Advisory Committee - The Harvard Forest is regularly reviewed Visiting Committee to the Department of Organismic and Evolutionary Biology. The most recent review was in 1986 by a Sub-Committee including H. Mooney, Stanford University, C. Stillman, Rutgers University, R. Waring, Oregon State, J. Gordon, Yale University and J. Boyer, Texas A & M University

   To provide advice and review for the LTER a separate Committee of Advisors has been appointed including (H. Shugart, U. of Virginia; H. Mooney, Stanford; S. Chapin, U. of Alaska; J. Melillo, Woods Hole; T. Webb III, Brown University). This group has reviewed the current proposal and will attend the annual meeting of investigators at the Harvard Forest.

 H. Public Awareness - The mission of the Harvard Forest involves a commitment to public education, which is predominantly represented by activities of the Fisher Museum. Each year thousands of visitors including student groups (elementary to graduate school), professional societies, local residents, and tourists come to see the dioramas and museum exhibits and to walk the self-guided nature tours. In addition over thirty scientific and professional meetings are conducted annually in the museum lecture room, with participants housed in Shaler Hall. As a contribution to these educational activities, results and demonstrations from the LTER project will be incorporated by the Museum Coordinator into exhibits to increase public understanding of ecological research. Rotating exhibits will be displayed and some of the basic manipulations (e.g. gap formation) will be replicated near the self-guided trails with detailed descriptions. We have found that visitors respond enthusiastically to demonstrations of current research at the Forest and we feel that the LTER project will integrate well with this tradition.

Flood Disaster Protection

   The Harvard Forest headquarters in Petersham, Massachusetts has been identified as having no special flood hazards and therefore requires no special protective measures or insurance under the

National Flood Insurance Act of 1968 as specified by the Flood Disaster Protection Act of 1973. (see Firm Flood Insurance Map of Petersham, MA, Community Panel Number 205327 0002 B, effective date 1/23/79).

HARVARD FOREST
PROSPECT HILL TRACT

N

Prospect Hill (1383 ft.)

Town Line Rd.

1200 ft.

1300 ft.

Little Prospect Hill (1300 ft.)

1300 ft.

1200 ft.

French Rd.

1200 ft.

Prospect Hill Rd.

Swamp Rd.

Boardwalk

Blackgum Swamp

Black Gum Trail

Old Pierce Farm

1200 ft.

1100 ft.

1000 ft.

Black Gum Trail

Blackgum Trail

Locust Opening Rd.

Natural History Trail

900 ft.

Gould Woodlot

Natural History Trail

1100 ft.

Pierce Rd.

Legend

- ▬ Black Gum Trail
- ○-○-○ Natural History Trail
- ▨ Pond
- ▦ Wetland
- ― Perennial Stream
- ═ Route 32
- ▬ Woods Road
- ― Footpath
- ⋯ Stone Wall or Fence
- ― 10-Foot Contour Intervals

0   1,000   2,000 Feet

0   300   600 Meters

BH 2010

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APPENDIX 1. Research at Harvard Forest (1907-1988)

1. Paleoecology and geomorphology - Benninghoff's pollen analysis of
the sediments of Tom Swamp in the late 1940's was the first
paleoecological study at the Forest and among the earliest in central
New England. Shortly thereafter M. B. Davis (1958) described the
post-glacial dynamics of the vegetation and climate and contrasted the
local development of three large wetlands. Subsequent studies
investigated the relationship between the pollen content of surface
sediment samples from lakes and the composition of the surrounding
forest communities (Davis and Goodlett 1960). Recent and ongoing
research focuses on: late-glacial climate and vegetation (Gaudreau
1987, Gaudreau and Webb 1985), late-glacial macro-fossil and sub-
fossil bryophyte assemblages (N. Miller, in prep.), mor-humus analysis
of pre- and post-settlement vegetation (Bradshaw and Miller 1988), and
comparison of regional and local vegetation dynamics at the Pisgah
Tract in southwestern, New Hampshire (Foster and Schoonmaker 1986,
Schoonmaker, unpubl.). All of the wetlands and waterbodies on and
adjacent to the Forest have been cored and basic stratigraphic
profiles are available (HF Archives).

Geomorphological studies at the Harvard Forest were initiated
through the collaboration of Hugh M. Raup (former director), Kirk
Bryan (geology department), and their students. In particular,
awareness of the dramatic climatic change during the Quaternary led
Raup and others to locate relic periglacial features in the temperate
landscape (Stout 1952, Denny 1956, Lyford *et al.* 1963). John
Goodlett, a student of Raup's, characterized the glacial landforms in
detail, initiated a series of studies relating vegetation and soil
processes to landform shape and type, and explored the similarities
between the development of ecological and geomorphological theory
(Goodlett 1954, Hack and Goodlett 1960).

2. Soil Science - Historically, soils research at the Harvard Forest
has had two main interests: the effect of soils in controlling the

composition and productivity of forests (Spaeth 1920, Stout 1952, Lyford *et al.* 1963) and the influence of vegetation on soil development, especially physical and chemical characteristics. Progress in the latter area was contributed significantly by P. R. Gast, working in collaboration with Henrik Hesselman of Sweden on forest nitrogen economies (Gast 1936, 1937). In addition, the effect of converting hardwood forest and old fields to white pine, through secondary succession and silviculture, was compared to natural dynamics in old-growth forests by Fisher and others (Fisher 1928, 1933, Branch *et al.* 1930, Griffith *et al.* 1930, Gast 1937, Whitney and Foster 1988).

   A complete mapping of the soils (1" = 400') of the Harvard Forest was finished in 1936 (Simmons, unpubl.). This baseline information enabled the soil/forest production question to be addressed in specific studies evaluating site concepts (Goodlett 1960), yield and productivity (Spurr and Cline 1942), and soil characteristics (Stout 1952, Lyford 1975). Current studies are emphasizing below-ground biological processes and nutrient cycling (see section 4).

3. Macro- and Microclimates - Basic macroclimatological data including precipitation and temperature have been collected at the Forest since 1913. Daily records are sent to the U. S. National Weather Bureau where monthly and annual summaries are available. In the Quabbin Reservoir Watershed 10 km to the west of the Forest, collaborators at the University of Massachusetts operate a station in the National Atmospheric Deposition Program. These data and the record from the meteorological station at the University of Massachusetts in Amherst (1870 - present; Bradley *et al.* 1987) will be available to the Harvard Forest LTER.

   Microclimatological variation across sites and vegetation types was studied first by Rasche (1953) and Spurr (1956a) and emphasized temperature variation as controlled by canopy characteristics, topographic position and local air movement. Ongoing studies focus on

microclimatological variation within closed canopy forest and across gaps (Sipe unpubl. Bazzaz and Sipe 1987), using a portable, efficient system of instrument stations and electronic dataloggers. Measurements recorded as frequently as every second on 15 stations include temperature, wind speed, relative humidity, soil moisture, soil temperature and irradiance.

4. Forest Microbiology - Early efforts at the Harvard Forest to apply scientific principles to forestry centered on the effect of site on tree growth (Fisher 1928, Griffith, Hartwell and Shaw 1930, Stout 1952), direct fertilization of forest stands (Mitchell and Chandler 1939) and experiments on mycorrhizal fungi (Finn 1942). When W. H. Lyford joined the Forest staff in 1960, emphasis turned toward soils in relation to roots and the rhizosphere, including concern for mineral nutrient supply and biotic influences on tree growth via effects on root systems. Studies detailed the rhizography of several hardwood species (Lyford and Wilson 1964, Lyford 1980), the occurrence and importance of mycorrhizae in root systems of hardwood species (Lyford 1966, 1980) and the structure of fine roots and their turn-over (Lyford 1975).

With J. G. Torrey's move to the Harvard Forest in 1971, interests in root biology turned to symbiotic nitrogen fixation by nodulated plants infected by actinomycetes. Isolation and culture of the actinomycete *Frankia* that nodulates *Comptonia peregrina* and the successful reinoculation of seedling roots was reported for the first time in 1978 (Callaham *et al.* 1978). In 1981 Tjepkema *et al.* (1980, 1981) and Torrey *et al.* (1981) reported that *Frankia* growing in pure culture could be induced to form vesicles by withdrawing all sources of reduced nitrogen substrates. In the period from 1979-1984, Torrey, Tjepkema and Schwintzer, pursued a collaborative effort at the Harvard Forest to gain a better understanding of the biology of *Frankia* and actinorhizal plants and the ecological significance of their associations.

In 1985 the commitment of the Harvard Forest to research in forest below-ground ecology was formalized in the creation jointly with the Yale School of Forestry and Environmental Studies of the Program of Forest Microbiology (PFM) funded in part by the A. W. Mellon Foundation and by DOE, and the USDA Competitive Grants Programs. Several major themes were outlined by the PFM including analysis and improvements of microbial genetic diversity, study of organic matter dynamics in the soil, improvement of ecosystems analysis of below-ground biology, and development of optimum symbioses for forest trees.

Research on mycorrhizae was renewed with studies on the culture of ectotrophic and vesicular-arbuscular mycorrhizal (VAM) fungi initiated by Dr. B. Mosse and extended by R. Berliner and A. Lodhi. A survey of mycorrhizal associations occurring in hardwood and conifer stands and on burned and unburned sites in the Harvard Forest has begun and experimental research on tripartite associations (host plant-*Frankia* and VAM) is ongoing. Current studies by R. Antibus and P. Linkins, Clarkson University, have involved an examination of the effects of liming on fine roots and mycorrhizae since 1983. This work has sought 1) to determine whether liming influences the numbers and morphological types of mycorrhizae, 2) to assess the resulting physiological changes by measuring root respiration, acid phosphatase activities and phosphorus uptake capacities and, 3) to integrate the mycorrhizal work with studies on soil enzymes (Antibus, Linkins, McClaugherty) and organic and nutrient dynamics (Aber, Melillo, Nadelhofer). The hypothesis underlying this research is that lime applications influence P availability, which should be reflected in changes in the types and/or functional characteristics of the mycorrhizae. To date, the following information has been collected on control and limed plots: repeated counts of mycorrhizal numbers in soil cores, separated by morpho-types; detailed anatomical information on individual morpho-types; estimates of root net production; data on root phosphatase activity for the common morpho-types on a root dry weight and areal basis; pH responses of surface acid phosphatase from

several morpho-types; and, respiration by excised mycorrhizal morpho-types.

5. **Fine Root Dynamics and Soil Enzyme Activity** - Fine root (less than 3 mm diameter) production and turnover have been studied in a red pine plantation and a mixed hardwood forest on the Prospect Hill section of the Harvard Forest since 1978. Detailed measurements of monthly changes in live biomass have been used to estimate annual primary production and seasonal occurrence of starch storage (McClaugherty *et al.* 1982). Ongoing studies continue to emphasize the importance of fine roots in soil organic matter production and nitrogen cycling. Decomposition of fine roots has been examined through comparative studies at the Harvard Forest and other study sites in Virginia and Wisconsin. Mass loss and nitrogen concentrations of roots in mesh litter bags has been followed at the Harvard Forest for the past nine years. The exceedingly low rates of root decay reported by McClaugherty *et al.* (1984) have been substantiated by the nine-year data set and further support the conservative methods of calculating root productivity presented by McClaugherty *et al.* (1982).

Activities of cellulases, chitinase, laccase and peroxidase have been measured in four soil horizons at five different times of the year in four different stands at the Harvard Forest. Experimental addition of lime changed the pH of the forest floor by 1 to 2 pH units but had generally small effects on soil respiration, enzyme activity and enzyme pH response curves. The results suggest that the <u>function</u> of the microbial decomposers does not change rapidly following the application of large doses of lime in contrast to results from lab soil core experiments. Temperature response curves have also been determined for the same four enzymes in two stands at the Harvard Forest (McClaugherty and Linkins, submitted).

6. **Tree Physiology, Plant Development and Ecophysiology** - Research at the Harvard Forest on tree physiology, initiated under the leadership of the late Martin H. Zimmermann, has been centered on problems of

long distance conduction within the xylem and phloem. A team of
recent collaborators (Ewers, Fisher, Lewis, Sperry, Tyree) are
extending this work by examining plants of different habit (e. g.
trees versus lianes) or contrasted environments (e. g. wetland and
upland species). An important concept generated by these studies is
that of "compartmentalization" of the conducting tissues and
ultimately the whole plant, which is fundamental to understanding how
the plant recovers from some dysfunction of the conducting system.
Compartmentalization means that the attacks of pathogens can sometimes
be contained, the effects of herbivores minimized, and repair
mechanisms, brought into play when the plant is stressed or damaged
mechanically, can become locally operative (Zimmermann 1983).

   The view of a balance between "safety" (containment of embolism)
and "efficiency" (maximizing flow rates) grew out of these studies
(Zimmermann 1983, Lewis 1987, Ewers and Cruizat in press) and resulted
in the development of innovative techniques of cinematography, paint
and dye injection, acoustic detection of cavitation (e.g. Ewers and
Cruziat, in press; Sperry *et al.* in press; Zimmermann 1978, Zimmermann
et al. 1983), and conductivity measurement. These studies and
techniques can be extended to show contrasted strategies of
disturbance response in plants.

   Physiological research has been complemented by the extensive
comparative study of plant form carried out by P. B. Tomlinson where
the emphasis has been on total organization (architecture) and has
drawn on examples from many ecosystems (New England forest, tropical
forest, mangroves and seagrasses, e.g. Halle *et al.* 1978; Tomlinson
1974; Tomlinson 1986). The net result has been to emphasize the
contrast between opportunistic and deterministic processes in plant
development (Tomlinson 1982). Deterministic processes are established
by a careful analysis of the total form of the plant, often involving
all ontogenetic changes. Opportunistic processes are observed when the
underlying form is modified by natural or artificial disturbance. The
functional unit in these contrasted processes is the shoot apical

meristem, and the plant can be treated, in demographic terms, as a set of meristems, some active, some dormant, whose relative numbers are controlled partly by environmental factors and partly by inherent deterministic traits. Viewed in this way the study of plant morphology and development can be taken out of its classical comparative-systematic context and placed firmly in the field of plant ecology and population biology (Tomlinson 1987). The present need is for studies of the responses to stress in individual species at contrasted stages in succession. These studies have intriguing evolutionary implications, because survival may depend more on opportunistic than deterministic aspects of plant construction.

Recent ecophysiological studies of vegetation recovery following disturbance have emphasized leaf-level and whole plant responses to changes in physical and chemical fluxes (Bazzaz and Sipe 1987). Current studies focus on the understory survival and gap-response of co-occurring species of maple *(Acer rubrum, A. saccharum, A. pensylvanicum)* and birch *{Betula lenta, B. allegheniensis, B. papyrifera, B. populifolia)* that span the entire range of shade tolerance. The major goals of this comparative research are to determine (1) the degree to which congeneric co-occurring species differ in physiological and growth responses to microenvironmental patterns in the mature forest and canopy gaps of different sizes, and (2) the effects that similarities and differences among these species may have on community diversity and the predictability of forest composition.

This research integrates several levels of organization (leaf, whole-plant, population) in four kinds of experiments (controlled field experiments, growth chamber experiments, common garden experiments and the sampling of natural microenvironments and seedling populations). Extensive information is being collected on diurnal and seasonal forest floor microenvironmental patterns (irradiance, temperature, wind speed, relative humidity, soil temperature, and soil moisture) within and between the understory and gaps, gas exchange,

biomass allocation, leaf phenology, growth, plant architecture, demography, and population structure of these species.

7. Disturbance History and Community Dynamics - The dynamic nature of the plant community was recognized early at the Forest by the first Director, R. T. Fisher (1918, 1928, 1933) and his students (Patton 1922, Spaeth 1922, Hawes 1923). Subsequent studies have examined the role of disturbance processes including anthropogenic activities (Marshall 1927, Raup and Carlson 1941, Lutz and Cline 1947, Gould 1960, Whitney and Foster 1988) and such natural factors as fire (Stephens 1947, Norberg 1964, Henry and Swan 1974), wind (Brake and Post 1941, Goodlett 1956, Spurr 1956, Raup 1964, Hibbs 1983a and b), herbivory (Hosley 1928, 1931, Jenkins 1975), ice (Abbott 1952, Raup 1971), and pathogens (Kittredge 1913, Cline and Baker 1936, Paillet 1987).

These studies have advanced techniques for detecting disturbance and its effect on vegetation. Documentation has relied on air-photo interpretation (Spurr 1948, Foster 1987a), dendrochronology (Marshall 1927, Oliver and Stephens 1977), historical records (Raup and Carlson 1941, Lorimer 1977, Whitney and Davis 1986), forest reconstruction (Cline and Spurr 1942, Stephens 1955, Henry and Swan 1974), soil analysis (Stephens 1956, Lyford and MacLean 1966) and palynology (Davis 1958, Davis and Goodlett 1960, Bradshaw and Miller 1988). Vegetation development has been studied over long time sequences through resurveys of the vegetation (Mitchell and Hosley 1936, Spurr 1956, Gould 1960), the use of permanent plots (Spurr 1956a, Hibbs 1983, Foster 1987), growth analysis (Swan and Gill 1970, Primack 1973, Oliver 1978, Kelty 1984, Rich 1985), demographic studies (Harper and White 1974, White 1979, Hibbs 1979), morphological analysis (Wilson 1968, Halle, Oldeman and Tomlinson 1978, LaFrankie 1985a) and multivariate analysis (Swan 1970). Ongoing studies concentrate on vegetation response to wind damage (Foster 1988a, b, Foster and Boose unpubl.), the use of pollen analysis to reconstruct vegetation and disturbance history at a range of spatial and temporal scales

(Schoonmaker unpubl.), and the historical role of fire in New England forest (Patterson *et al.* 1987, Patterson and Backman 1988, Patterson and Sassman 1987).

8. **Forest Canopy Gaps** - Throughout the history of the Harvard Forest there has been a consistent interest in forest dynamics in response to canopy removal by man and natural factors, including wind and fire. Early studies, through the 1940's, concentrated on gap creation for silvicultural purposes (Fisher 1918, Cline and Lockard 1925, 1935). Openings ranging from single-tree removals to large clear cuts were the focus of research on reproduction (McKinon *et al.* 1935), growth response (Marshall 1927), form and development (Gevorkiantz and Hosley 1931), species interactions (Holsoe 1947, 1948), and forest yield (Lutz and Cline 1947). Through these studies the basic silvical characteristics of dominant tree species was acquired and current silvicultural practises were established. Following the 1938 hurricane the emphasis of research on gap dynamics turned to more basic and ecological orientation (Spurr 1956, Stephens 1955, Oliver 1975, 1978, Kelty 1984). Much attention has been given to vegetation response to natural disturbance (Oliver and Stephens 1975, Hibbs 1979, 1981, 1982) and experimental manipulations were made to simulate natural gaps such as arising from wind damage (Hibbs 1982, a and b). Such ongoing gap experiments include a set of 12 circular gaps ranging in size from 30 m^2 to 700 m^2 for studying population and community-level responses in oak-red maple forest (Hibbs unpubl., Sipe unpubl.) and 12 gaps of 75 m^2 and 300 m^2 size to study the physiological response of birch and maple to gaps (Bazzaz and Sipe 1987; Sipe, unpubl.). The latter experiment is particularly noteworthy as the basic model developed for creating those gaps will be used in the design of the LTER openings. This considerable history of studying and creating gaps provides a strong background for the manipulations planned in the LTER.

9. **Nutrient Cycling and Productivity** - Nutrient cycling, primary production and biomass allocation has been studied at the Forest for

ten years. Intensive research has been done in a red pine plantation and a maple-oak forest on similar soils, including measurements of effects of disturbance on nitrate leaching (Vitousek *et al.* 1979, Aber *et al.* 1983) and trace gas fluxes (Melillo *et al.* 1983), basic measurements of productivity and nitrogen cycling (Aber *et al.* 1983), with emphasis on the role of fine roots (McClaugherty *et al.* 1982, 1984, Aber *et al.* 1985), and on litter decomposition and humus formation (Melillo and Aber 1984). On-going studies include long-term alterations of nutrient cycling through application of $CaCO_3$ and NH_4NO_3, as well as shorter-term studies on root retranslocation and nitrate reductase activity.

10. Geographic Information Systems – During the past eight years research and development of GIS applications at the Forest have progressed in conjunction with the Yale School of Forestry and the Laboratory for Computer Graphics at the Harvard Graduate School of Design (Tomlin 1980, Tomlin and Berry 1981, Tomlin 1986). Initial efforts focused on the generation of a mathematical structure for digital cartographic modeling (Tomlin 1980), with subsequent research defining techniques for analysis of cartographic distance and spatially-defined neighborhoods (Berry and Tomlin 1979, Tomlin and Berry 1982). Resource-related applications of GIS included modeling of spatial allocation of timber harvesting activity (S. Tomlin 1981, Tomlin and Tomlin 1982), development of cartographic techniques for assessing timber availability (Berry and Tomlin 1979) and cartographic analysis of wildlife habitat utilization (Tomlin *et al.* 1983). Recent applications development have involved converting a major mainframe-based GIS (MAP) to IBM and Macintosh systems (Tomlin 1986) and developing greater display, outputting and statistical capabilities. Research has meanwhile become oriented towards landscape-scale analyses of vegetation patterns, particularly those resulting from broadscale disturbance (Fetherston 1986). The studies of disturbance processes complement ongoing efforts at the individual, population, community and ecosystem level and involve comparative studies in other

temperate (Pickett and Foster, in prep.) and tropical (Waide and Lugo 1987) forests.

11. Remote Sensing - Research sites at the Harvard Forest are scheduled for use as ground-truth areas for experimental remote sensing research using new imaging spectrometer sensors under development by NASA (Goetz *et al.* 1985, Wessman *et al.* 1987). In the summer of 1988, NASA will fly the AVIRIS sensor (advanced visible infrared imaging spectrometer) over the Harvard Forest seeking to detect subtle changes in canopy chemistry which may have been caused by experimental manipulations and may reflect changes in production and nutrient cycling.