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Abbreviations used in this proposal

HBES - Hubbard Brook Ecosystem Study
HBEF - Hubbard Brook Experimental Forest
USFS - United States Forest Service
USGS - United States Geological Survey
NADP - National Atmospheric Deposition Program
HASL - Health and Safety Laboratory
W# - watershed number
dbh - diameter at breast height
Al - aluminum
ANC - acid neutralizing capacity
Ca - calcium
Cl - chloride
F - fluoride
Fe - iron
H^+ - hydrogen ion
K - potassium
Mg - magnesium
Mn - manganese
Na - sodium
NH_4 - ammonium
NO_2 - nitrogen dioxide
NO_3 - nitrate
N_2O - nitrous oxide
NO - nitrogen oxide
HNO_3 - nitric acid
Pb - lead
PO_4 - phosphate
Si - silica
SO_4 - sulfate
Zn - zinc
DIC - dissolved inorganic carbon
DOC - dissolved organic carbon
TP - total phosphorus
TN - total nitrogen

Project Summary

Funding is requested for the initiation of a LTER Project at Hubbard Brook Experimental Forest, New Hampshire. The overall goal of the proposed research is a better understanding of the response of northern hardwood-conifer watersheds to large-scale disturbance, particularly with regard to (i) vegetation structure, composition and productivity; (ii) dynamics of dead organic matter; (iii) atmosphere-terrestrial-aquatic linkages; and (iv) heterotroph population dynamics. The research will be carried out on sites with contrasting disturbance history using experimental, survey, and long-term monitoring studies. It should provide valuable information on long-term ecosystem responses to disturbance, information needed by society to assess the effects of management and policy on the integrity of forest ecosystems.

Specifically, our research would examine (1) vegetation processes including neighborhood competition and gap-phase succession at different stages of development, and biomass and nutrient accumulation in the early stages of succession; (2) organic matter processing in streams and soils, decomposition of bole wood, and the formation and disruption of organic debris dams; (3) biogeochemical processes including wet and dry deposition, stream outflow, hydrologic modeling and hillslope hydrology, and construction of internal ionic budgets; and (4) population dynamics of breeding birds, phytophagous insects and a pathogenic fungus, and the nutritional ecology of white-tailed deer.

Results From Prior NSF Support

I. Timothy J. Fahey

A. NSF Award DEB 81-13546; $99,825; May 1982-May 1984

Title: Water and nutrient fluxes in lodgepole pine forests in Wyoming

Summary of Results: In this research we attempted to quantify the biotic and environmental factors regulating water and nutrient loss from lodgepole pine forests in the central Rocky Mountains. We discovered large variation in the biomass and leaf area of mature (>100 yr old) stands. The leaf area/sapwood area ratio for this species varied markedly among sites, primarily in response to stand density and crown form, and the root-shoot ratio also differed significantly among stands. Thus, potentially large differences in water use and nutrient uptake by mature stands occurs across the montane landscape.

The differences in stand structure were associated with sharply contrasting soil textural properties across the landscape, which led to concomitant variation in soil and plant water regimes. In general, close correlations were observed between soil water content, soil water potential and tree xylem pressure potential, but field and lab studies indicated that a more detailed understanding of the relationships between soil texture, soil water potential at various depths, and tree water stress is needed.

A physiological-based simulation model of water movement through lodgepole pine ecosystems (H2OTRANS) was parameterized for the sites described above to identify the biotic and environmental factors regulating water and dissolved solute fluxes. The simulations indicated that stands with different soil and meteorologic conditions experience markedly different water and element flux regimes. In particular, soil water storage capacity and stand leaf area index influence a number of control processes which determine the timing and magnitude of leaching. Thus, different parts of the montane landscape supply different portions of the water and nutrient yield of Rocky Mountain watersheds.

The nitrogen cycle is under particularly strong biotic control in the oligotrophic landscapes, because of extremely low inputs and periodic large losses in crown fires. Nitrogen accumulated in the N-poor leaf litter for up to 7 yr following leaf fall before significant mineralization occurred. Most of the N flux from forest floor horizon occurred via leaching of organic N which was retained in surface mineral horizons by precipitation/ adsorption. Subsequent mineralization of this fraction apparently provided most of the N available for root uptake, and little N was leached to subsoil and streams.

Finally, highly-decayed wood acted as an important substrate for tree roots and solute concentrations in this wood were quite high. The strongly-acidic nature of dissolved organic compounds in dead wood leachate implies a possibly important role in soil formation in temperate coniferous forests.

Publications:

Pearson, J.A., T.J. Fahey and D.H. Knight. 1984. Biomass and leaf area in contrasting lodgepole pine forests. Can. J. For. Res. 14:259-265.

Fahey, T.J. and D.R. Young. 1984. Soil and xylem water potential and soil water content in contrasting *Pinus contorta* ecosystems, southeastern Wyoming, USA. Oecologia (Berl.) 61:346-351.

Knight, D.H., T.J. Fahey and S.W. Running. 1985. Water and nutrient outflow from contrasting lodgepole pine forests in Wyoming. Ecol. Monogr. 55:29-48.

Fahey, T.J., J.B. Yavitt, J.A. Pearson and D.H. Knight. 1985. The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. Biogeochemistry 1:257-275.

Yavitt, J.B. and T.J. Fahey. 1985. Chemical composition of interstitial water in decaying lodgepole pine bole wood. Can. J. For. Res. 15:1149-1153.

Fahey, T.J. and D.H. Knight. 1986. Lodgepole pine ecosystems. Bio Science 36:610-617.

B. NSF Award BSR 83-16924; $222,288; April 1983-April 1985

Title: Water and nutrient loss from Rocky Mountain forest ecosystems

Summary of Results: This research project represents an extension of the activities described under DEB 81-13546. We continued measurements and data analysis for wet and dry precipitation, throughfall, forest floor and soil solution chemistry; we measured hydraulic characteristics of three of our intensive study sites; we performed field simulations of bark beetle epidemics and field studies of natural beetle infestations; and we developed subroutines for computer simulation of water and nutrient fluxes in lodgepole pine ecosystems.

Particularly for Ca and SO_4, dry deposition appears to be an important model of nutrient input with between 25 and 40% of canopy wash and canopy leaching accounted for as dryfall. In contrast, K is leached from leaves, mostly in the form of organic salts. Unexplained, but consistent, variation in the acid strength and the charge density of organic solutes in throughfall was observed, and experimental studies will be needed to determine the mechanisms causing this variation.

By combining these related measurements: leaching from the forest floor; long-term decay of leaf litter; and steady-state residence times in the forest floor, we were able to deduce several features of organic matter and nutrient dynamics. First, about 30% of annual C flux from the forest floor resulted from leaching of DOC. Second, most of the leaching of nutrient cations was attributed to ion exchange in the 02 horizons. Third, N appears to be translocated rapidly from subsurface horizons to 01 litter via heterotrophs. Finally, the flux of various organic fractions is mediated by both biological activity and solubility under the field circumstances.

Solute concentrations in root-zone soil solution decreased during the snowmelt period in a systematic manner, but marked differences in the rate of concentration decline, total ionic strength, and proportions of mobile anions were observed and appear to be related to soil textural differences. Soil clay content appears to play a critical role in regulating solute fluxes and other ecosystem properties in these forests.

Extreme spatial variation was observed in soil hydraulic properties in both glacially-derived and regolithic soils. This variation fit the lognormal distribution, and overall hydraulic conductivity estimates were comparable as measured by a pulsed-tracer method and an internal-drainage method, with over 50-fold differences between three soils of contrasting texture. It appears that soil hydraulic properties may affect soil solution chemistry during snowmelt run-off in these ecosystems.

A dendrochronologic model was developed to describe nutrient retention features of lodgepole pine ecosystems during succession following large-scale disturbance. For nitrogen, accretion in forest floor layers dominates as a retention mechanism, peaking at about age 50 yr, whereas for K and Ca accumulation in vegetation is most important and peaks somewhat earlier (about 35 yr).

Modelling subroutines simulating throughfall flux and forest floor processes have been developed and are being incorporated into the hydrologic model (DAYTRANS). Also, a photosynthesis subroutine has been completed, incorporated and partially validated. Work is proceeding on development of soil solution chemistry and nutrient uptake subroutines in conjunction with an EPRI-funded project. Also, we have collected parameter and validation information for applying the DAYTRANS model in a relict population of lodgepole in the San Jacinto Mountains, and work towards this extension of the modelling effort is proceeding in conjunction with colleagues at Cornell University.

Finally, field studies of the effect of natural and simulated bark beetle infestations have been carried out. These studies suggest that nutrient losses associated with partial overstory mortality are minimized by the dispersed root systems of the trees, so that "root gaps" are not created by the demise of individual trees, and also by the temporary retention of partial shading buffering against increased soil temperatures. In contrast, large-scale disturbance (clear-cutting) resulted in ten to hundred fold increases in soil solution nitrate concentrations, following a one to two year delay.

Publications:

Fahey, T.J. and D.H. Knight. 1986. Lodgepole pine ecosystems. Bio Science 36:610-617.

Romeme, W.H., D.H. Knight and J.B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? Amer. Nat. 127:484-494.

Yavitt, J.B. and T.J. Fahey. 1986. Litter decay and leaching from the forest floor in _Pinus contorta_ (lodgepole pine) ecosystems. J. Ecol. 74:525-545.

Pearson, J.A., D.H. Knight and T.J. Fahey. 1987. Patterns of biomass and nutrient accumulation during ecosystem development in _Pinus contorta_ forests, southeastern Wyoming. Ecology, in press.

(Note: Five additional manuscripts are submitted or in the final stages of preparation for publication.)

II. Charles T. Driscoll

A. NSF Award: CME-8006733; $39,996; 5/15/80 to 10/31/82

Title: Significance of aluminum in the fate of trace metals

Summary of Results: Elevated concentrations of trace metals within acidic lake ecosystems may have deleterious effects on aquatic biota. As a result, there is interest in understanding the chemistry and transport of these solutes. We hypothesize that "in-lake" formation of particulate aluminum is an important mechanism regulating trace metal transport within acidic lakes. To evaluate the fate of lead, copper, zinc, and manganese, two experimental approaches were utilized. First, lake manipulations by base addition were accomplished to induce hydrolysis of aluminum. Subsequent changes in trace metal chemistry were evaluated. In our second and more extensive experiment the chemistry and transport of trace metals were monitored within an acidic lake (Dart's Lake in the Adirondack region of NY) over an annual cycle. In this latter study we evaluated the fluxes and pools of particulate and aqueous metals.

Results of our research suggests that there are dramatic temporal and spatial variations in the pools and fluxes of trace metals within acidic lakes. In addition there are major differences in the transformations of individual metals. For example, in Dart's Lake there is considerable internal cycling of lead. Lead transport appears to be closely linked to aluminum cycling. Conversely, zinc was relatively conservative within the acidic lake environment. In lake systems manipulated by base addition (pH>6), lead, copper, and zinc were readily removed by sorption to particulate matter.

Publications:

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2. Schafran, G.C., J.R. White, and C.T. Driscoll. 1982. The response of dilute acidic surface waters to strong base addition. Northeast Environ. Sci. 1:151-160.
3. White, J.R., G.C. Schafran, and C.T. Driscoll. 1984. Lead cycling in an acidic Adirondack lake. Proc. of the Sec. New York State Symp. on Atmos. Deposition, Ithaca, NY. 151-158.
4. White, J.R., and C.T. Driscoll. 1985. Lead cycling in an acidic Adirondack lake. Environ. Sci. Technol. 19:1182-1187.
5. White, J.R., and C.T. Driscoll. 1986. Manganese cycling in an acidic Adirondack lake. Biogeochemistry. 2:(in press).
6. White, J.R., and C.T. Driscoll. 1987. Zinc cycling in an acidic Adirondack lake. Environ. Sci. Technol. (in press).

B. NSF Award: DEB 82-06980; $159,916; 7/15/82 to 1/1/85

Title: Alummo-ligand interactions in a forested ecosystem prior to and following a deforestation disturbance

Summary of Results: There is currently considerable concern and controversy over the impact of man's activities on forest ecosystems. Of particular interest in the northeastern U.S. are the effects of acidic deposition and forest clearcutting (whole-tree harvesting). The intent of this investigation was to evaluate the processes regulating the concentration of acidic substances prior to and following a clearcutting disturbance at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire.

In the presence of current loadings of acidic deposition, acidification of soil and stream solutions has occurred at the HBEF. However, the nature and extent of acidification is modified by intra-watershed processes. For example, in the spruce-fir zone which is characteristic of high elevations (>730m) at the HBEF, the large foliar surface area facilitates SO_4^{-2} deposition and recalcitrant litter results in considerable organic acid production. The high concentrations of sulfuric and organic acids produce extremely low pH values (4.1) in soil and stream solutions. Below the coniferous zone, hardwood vegetation produces lower concentrations of organic acids but elevated concentrations of nitric acid. Within this zone, mineral acid inputs leach high concentrations of inorganic aluminum from soil, which is potentially toxic to fish and other organisms. As water drains to lower elevations, soil depth increases and is neutralized by the release of basic cations from soil.

Deforestation at the HBEF enhances the decomposition of organic matter producing nitric acid. Immediately following the whole-tree harvest, release of basic cations from soil was adequate to neutralize nitric acid inputs. However, within 6 months readily-available pools of basic cations were depleted causing acidification of soil and stream solutions (pH below 4.7), the release of high concentrations of potentially toxic inorganic aluminum (greater than 40 $\mu mol \cdot l^{-1}$) and the retention of sulfate. Results of this study indicate that there is extreme variability in the processes regulating solute concentrations in drainage water within watersheds. Furthermore, acidic deposition and forest clearcutting facilitate the acidification of surface waters in the northeastern U.S.

Publications:

1. Van Breemen, N., J. Mulder, and C.T. Driscoll. 1983. Acidification and alkalinization of soils. Plant and Soil. 75:283-308.

2. Driscoll, C.T., N. van Breemen, J. Mulder, and M. van der Pol. 1983. Dissolution of soil bound aluminum from the Hubbard Brook Experimental Forest, New Hampshire. Proceedings of Acid Precipitation--Origin and Effects, An International Conference. Lindau, FRG Verein Deutscher Ingenieure. pp. 349-361.

3. Driscoll, C.T. 1984. A procedure for the fractionation of aqueous aluminum in dilute acidic waters. Int. J. Environ. Anal. Chem. 16:267-283.

4. Van Breemen, N., C.T. Driscoll, and J. Mulder. 1984. Acidic deposition and internal proton sources in acidification of soils and waters. Nature. 307:599-604.

5. Driscoll, C.T. 1984. Aluminum chemistry and potential effects in acidic surface waters. In: D.D. Hemphill (ed.) Trace Substances in Environmental Health--XVIII. Columbia, MO. pp. 215-229.

6. Johnson, N.M., G.E. Likens, M.C. Feller, and C.T. Driscoll. 1984. Acid rain and soil chemistry. Science. 255:1424-1425.

7. Driscoll, C.T., N. van Breemen, and J. Mulder. 1985. Aluminum chemistry in a forested Spodosol. Soil Sci. Soc. Am. J. 49:437-444.

8. Fuller, R.D., M.B. David, and C.T. Driscoll. 1985. Sulfate adsorption relationships in forested Spodosols of the northeastern U.S. Soil Sci. Soc. Am. J. 49:1034-1040.

9. Fuller, R.D., M.J. Mitchell, H.R. Krouse, B.J. Wyskowski, and C.T. Driscoll. 1986. Stable sulfur isotope ratios as a tool for interpreting ecosystem sulfur dynamics. Water, Air, Soil Pollut. 28:163-171.

10. Lawrence, G.B., R.D. Fuller, and C.T. Driscoll. 1986. Aqueous aluminum chemistry in the streams of two upper elevation watersheds in the White Mountains of New Hampshire. Biogeochemistry. 2:115-135.

11. Schindler, S.C., M.J. Mitchell, T.J. Scott, R.D. Fuller, and C.T. Driscoll. 1986. Incorporation of ^{35}S-sulfate into inorganic and organic sulfur constituents of two forest soils. Soil Sci. Soc. Am. J. 50:457-462.

12. Fuller, R.D., C.T. Driscoll, S.C. Schindler, and M.J. Mitchell. 1986. A kinetic model of sulfur transformations in forested Spodosols. Biogeochemistry. (in press).

C. NSF Award: ECE-8351959; $312,500; 10/1/84 to 10/31/89

Title: Presidential Young Investigator Award: Drainage basin ecosystem response to inputs of sulfuric and nitric acids in the northeastern U.S.

Summary of Results: There is currently much concern over the role of atmospheric deposition of strong acids in the acidification of drainage waters. Although studies of surface water acidification have largely focused on sulfuric acid, inputs of nitric acid during spring snowmelt can significantly contribute to surface water acidification. The objectives of this study are to 1) determine the source of nitric acid inputs to "acid-sensitive" surface waters, and 2) assess intraregional differences in the duration and peak concentrations of NO_3^- events in the Adirondack region of New York.

Results of this ongoing study indicate that during snowmelt, solutions are enriched in H^+ and NO_3^- following transport through the forest floor. Evidently, decomposition and mineralization coupled with reduced biological assimilation results in an accumulation of solutes within the forest floor over the winter period. The influx of water associated with the initial phase of snowmelt appears to transport elevated concentrations of nitric acid to the lower mineral soil and to surface waters.

There is considerable regional variation in the extent and magnitude of spring nitric acid events. Future work will focus on an assessment of this variability.

Publications:

1. Rascher, C.M., C.T. Driscoll, and N.E. Peters. 1987. The concentrations and flux of solutes from snow and forest floor during snowmelt in the Adirondack region of New York. Biogeochemistry. 3:(in press).

2. Browne, B.A., J. McColl, and C.T. Driscoll. Speciation of aqueous aluminum in dilute acidic waters using morin. Part I. The chemistry of morin and its complexes with aluminum. J. Environ. Qual. (in review).

3. Browne, B.A., C.T. Driscoll, and J. McColl. Speciation of aqueous aluminum in dilute acidic waters using morin. Part II. Principles and procedures. J. Environ. Qual. (in review).

D. NSF Award: BSR 8046634; $416,000; 11/1/84 to 11/1/88

Title: Hydrologic-nutrient cycle interaction in small undisturbed and man-manipulated ecosystems

Summary of Results: Hardwood-conifer ecosystems in the northeastern U.S. are exposed to multiple stresses, including both anthropogenic and natural disturbances. The objectives of this ongoing study (with F.H. Bormann and G.E. Likens) are to evaluate 1) biogeochemical inputs and their effects on the terrestrial and aquatic ecosystem and 2) examine and compare the role of disturbance in regulating the structure, function, and development at the Hubbard Brook Experimental Forest in New Hampshire. Activities include 1) ongoing long-term monitoring of precipitation inputs, stream outputs, and vegetation, 2) research on the regulation of soil and drainage water acidification, 3) process-level studies on the biogeochemistry of N, Al, S, and P, and 4) an evaluation of the effects of disturbance from whole-tree harvesting on soil and drainage water quality.

Publications:

1. Driscoll, C.T. 1985. Aluminum in acidic surface waters: chemistry, transport, and effects. Environ. Health Persp. 63:93-104.
2. Nodvin, S.C., C.T. Driscoll, and G.E. Likens. 1986. Simple partitioning of anions and dissolved organic carbon in a forest soil. Soil Sci. 142:27-35.
3. Nodvin, S.C., C.T. Driscoll, and G.E. Likens. 1986. The effect of pH on sulfate adsorption by a forest soil. Soil Sci. 142:69-75.
4. Nodvin, S.C., C.T. Driscoll, and G.E. Likens. Soil processes and sulfate loss at the Hubbard Brook Experimental Forest. Biogeochemistry. (in press).
5. McDowell, W.H., J.J. Cole, and C.T. Driscoll. 1987. A simplified version of the ampoule-persulfate method for the determination of dissolved organic carbon. Can. J. Fish. Aq. Sci. (in press).
6. Fuller, R.D., C.T. Driscoll, G.B. Lawrence, and S.C. Nodvin. Processes regulating sulfate flux following whole-tree harvesting of a northern forested ecosystem. Nature. (in review).
7. Lawrence, G.B., R.D. Fuller, and C.T. Driscoll. Release of aluminum following whole-tree harvesting at the Hubbard Brook Experimental Forest. J. Environ. Qual. (in review).
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9. Simone, D.M., C.T. Driscoll, and R.D. Fuller. Effects of whole tree harvest on trace metal chemistry and transfer in a northern forested ecosystem. Can. J. For. Res. (in review).
10. Driscoll, C.T., R.D. Fuller, R.C. Santore, and G.B. Lawrence. 1987. Speciation of ions in acidic soil solutions. Proc. Int. Soil Sci. Soc. (in review).
11. Lawrence, G.B., C.T. Driscoll, and R.D. Fuller. 1987. Hydrologic control of aluminum chemistry in an acidic headwater stream. Wat. Resour. Res. (in review).

INTRODUCTION

Society, through the National Science Foundation (NSF), invests in long-term ecological research (LTER) to obtain basic information on the structure, function and development of ecosystems, as well as to defend against unanticipated ecological disasters. Experience has shown us that unforeseen changes in ecosystems can have social and economic significance. The recent identification of large scale environmental problems, such as groundwater and surface water contamination, regional air pollution and forest decline, have had far reaching effects on society.

Long-term ecological research has been conducted at the Hubbard Brook Experimental Forest (HBEF) since it was established in 1955 by the U.S. Forest Service, as a center for hydrologic research in New England. In 1963, the U.S. Forest Service and Dartmouth College (through G.E. Likens and F.H. Bormann) developed a cooperative agreement to conduct studies of element cycling at Hubbard Brook as the first step in a comprehensive study of a northern hardwood-conifer ecosystem. Since its inception, the Hubbard Brook Ecosystem Study (HBES) has made major contributions to environmental science (e.g. Likens et al. 1977; Bormann and Likens 1979; Likens 1985) which have facilitated policy decisions regarding the management of terrestrial and aquatic ecosystems. Over the past 23 years the NSF has continuously provided support for the HBES. Through the HBES the following long-term research goals have been developed to provide a scientific basis for management and policy decisions regarding the future of the northern hardwood-conifer ecosystem.

1. To evaluate the changing nature of biogeochemical inputs to the northern hardwood-conifer ecosystem and their effects on the terrestrial ecosystem and interconnected aquatic ecosystems.

2. To examine and compare the role of disturbance in governing the structure, function and development of the northern hardwood-conifer ecosystem. This research includes disturbances which are both anthropogenic (various types of forest harvesting, fire, road building, agricultural land clearing and abandonment, conversion to non-forest land use, inputs of air pollutants) and natural (insect and disease outbreaks, wind, fire) in origin.

3. To develop ecological principles governing the structure, function and development of forested watersheds and to work closely with specialists in economics, policy and conservation to attempt to incoporate these principles in decision-making processes.

We propose to continue the pursuit of these goals through the establishment of a Long-Term Ecological Research (LTER) program at the HBEF, a research site which is well suited for this program because:

(1) the HBEF is representative of northern hardwood-conifer forests in eastern North America, which are impacted by elevated loadings of atmospheric pollutants,

(2) long-term measurements of meteorology, hydrology, precipitation, drainage water quality, plant tissue chemistry, biomass, and productivity have been made using carefully standardized methods,

(3) drainage basins in the HBEF are virtually water-tight (Likens et al. 1977) allowing for accurate water and element budgets that are critical to verify ecosystem and plot-level processes studies,

(4) the entire Experimental Forest is under the jurisdiction of the U.S. Forest Service, which maintains the site for long-term scientific research, and

(5) within the HBEF a series of whole-watershed and sub-watershed treatments have been made since 1965 (Appendix I.A), facilitating the study of ecosystem recovery following disturbance.

I.A Theme of the Hubbard Brook Experimental Forest LTER Program

Odum's (1969) postulates of the changes in ecosystems as they develop have helped stimulate detailed research on the successional process. Some of these postulates have been supported, a few refuted, and many have defied direct test. In a more detailed analysis of nutrient cycling attributes, Gorham et al. (1979) proposed a paradigm for the regulation of element budgets during ecosystem succession. Again, direct tests have been difficult, but it seems clear that overall patterns of ecosystem development are closely coupled to the key element cycles. Due to the difficulty in establishing adequate replication and control in chronosequence studies, it may be preferable to make long-term measurements of element influx/efflux, changes in pool sizes and changes in key ecosystem processes to test this important paradigm. Although the focus of ecosystem studies has shifted from the development of input/output budgets and quantifying pool sizes to basic process-level research, there is much to be gained from an integration of process studies with information on long-term changes in element pools and mass-balance calculations.

The theme of the proposed HBES LTER program is ecosystem response and ecological succession in northern hardwood-conifer watersheds following large-scale disturbance.

The overall goal of the study is to improve our understanding of mechanisms whereby ecosystem energy and element budgets change in response to disturbance.

We propose an integrated set of experiments and material balance studies to achieve this goal. These studies are designed to address the five core research topics identified in the NSF-LTER Announcement of Competition (Table I.1) and will couple detailed examination of critical ecological processes with continued precise monitoring of watershed inputs/outputs and measurements of major energy and element storage pools. This combination of approaches will allow us to explore the regulation of ecosystem function within the framework of precise budgetary studies and will provide bench marks for comparison with flux estimates derived from process-level studies.

Our proposed LTER program would pursue the goal of understanding the response of the northern hardwood-conifer ecosystem to disturbance through four major research components: (a) vegetation structure, composition and productivity; (B) dynamics of dead organic matter; (C) atmospheric-terrestrial-aquatic linkages; and (D) heterotroph population dynamics (Table I.1). Within each major component, experimental, survey and monitoring studies are proposed to provide the detailed information necessary for understanding ecosystem response to disturbance. The research components will be carefully integrated to provide critical information at a variety of levels of ecosystem organization and at a series of points along pathways of energy and element transfer. Studies of element transfer within ecosystems have often been limited by the failure of researchers to couple element cycles. To overcome this deficiency, the H^+ budget approach will be used as a tool to characterize and summarize ecosystem function, its response to disturbance, and changes during succession (van Breemen et al. 1983).

Forest ecosystems are seldom exposed to a single disturbance but rather a complex mixture of chronic and random stresses. For example, an important question concerning the northeastern U.S. is how continued exposure of ecosystems to a variety of air pollutants, coupled with increased harvesting of hardwood and conifer forests, effect vegetation, soil and water quality. This question is closely linked to critical environmental issues such as the effects of atmospheric inputs of strong acids, oxidants and trace metals, forest decline and surface water acidification. Assessments of the response of terrestrial and aquatic ecosystems to a given stress cannot ignore the cumulative effects of multiple disturbances to these systems. Effects of disturbance can only be addressed through integrated study.

Critical questions associated with ecosystem response/succession following disturbance must also consider delayed impacts which may not be apparent for a number of years. Changes in age-structure, growth and mortality of forests following natural and anthropogenic disturbance occur over long time periods. Response of biomass, forest-floor, soil, decaying wood and various element pools to disturbance may be obscured in the short term due to relatively slow rates of organic matter decomposition, soil development, and vegetation regrowth. Seasonal and year-to-year variations in climate, biomass accumulation, precipitatio inputs, hydrologic discharge, and element transfer complicate interpretation of long-term trends. Therefore, the study of ecosystem response and succession following disturbance can only be obtained through long-term research. While this is a time consuming, expensive process, alternative research approaches are not likely to provide the accurate quantitative information needed for environmental policy decisions. The end result of long-term research is cost-effective when one considers the social and economic consequence of ecological disasters to society. As we continue to improve our understanding of natural ecosystems and their response to disturbances, we will be better able to apply that knowledge to assess the effects of management and policy on the ecological integrity of forest ecosystems.

I.B. Statistical Considerations

We recognize in the LTER program the opportunity to provide more powerful tests of ecological patterns and processes during vegetation succession following large-scale disturbance. A wide array of experimental designs and statistical tests will be utilized within the HBES-LTER. Because of space limitations in this proposal we cannot provide detailed descriptions of statistical approaches for testing our hypotheses. Moreover, many of the hypotheses are descriptive in nature rather than directly testable.

Our research may be broadly classified into monitoring and survey studies, quantitative and conceptual modelling and budgetary analyses, and experimental studies. For the monitoring and survey work, randomization of permanent plots and careful duplication of sampling and analytical methods are most critical to avoid bias, both temporal and spatial. We are cognizant of this and great effort has been expended to avoid such problems in the HBES. We recognize the problems inherent in chronosequence studies with regard to replication and initial conditions, but owing to the great expense of setting up large-scale forest treatments we are compelled to make some use of experiments set up in the past. Moreover, because of the nature of LTER, we expect to be able to validate our chronosequence conclusions by directly following permanent plots and gaged watersheds through successional time.

One of the principal goals of the HBES-LTER is a better understanding of changes in biogeochemical behavior during succession following large-scale disturbance, a goal which we hope to pursue in part through a combination of conceptual and quantitative modelling approaches. The construction of internal ionic flux budgets for whole watersheds depends upon quantifying a large number of highly variable processes using a combination of many sampling and regression methods. Thus, statistical analysis of the resulting budgets is difficult and results are indicative rather than conclusive. However, independent tests of certain components of the budgets are possible, and the indicative results are valuable for improving our comprehension of complex biogeochemical interactions.

Finally, our experimental studies will follow carefully prescribed experimental designs to provide rigorous tests of specific hypotheses using standard methods of statistical analysis. Each of the parent institutions will provide expert statistical consulting services to the individual investigators through their biometric and statistical centers. We will utilize these services, when appropriate, for setting up experimental studies, optimizing sampling strategies and analyzing research results.

II.A RESEARCH COMPONENT A: VEGETATION STRUCTURE AND PRODUCTION

The northern hardwood-conifer forest exerts primary control over energy and nutrient flow in the watershed ecosystems at HBEF. A major component of the HBES has been the development of a conceptual and quantitative understanding of the factors influencing forest composition and structure. Both qualitative (Bormann and Likens 1979) and quantitative (Botkin et al. 1972, Aber and Melillo 1982) models have been developed for this site. The goal of this component of the proposed HBES-LTER Program is a better understanding of the dynamics of forest regeneration and growth on northern hardwood-conifer watersheds ranging in successional age from 0 to over 300 years. The detailed, long-term data sets on vegetation composition, structure, biomass and chemistry for several watersheds will be the basis for continued refinement and verification/validation of these models.

We seek to integrate traditionally separate levels of ecological organization by linking studies of mechanisms acting at the individual, population, and community levels with our whole watershed analysis of ecosystem attributes. Because our proposed research program relies upon repeated measurements of permanent plots to detect the slow changes in forest vegetation, long-term research support is essential to its success. The vegetation research component is designed to approach our goals by accomplishing three primary objectives:

Objective A.1. To explain the composition and age/size structure of early and late successional and old-growth stands on the basis of species-specific demographics and thereby refine the existing model of forest growth and composition for HBEF.

Objective A.2. To quantify the suppression of tree growth, reproduction and survival owing to neighborhood competition and initiate development of a spatial model of resource availability and tree growth and mortality.

Objective A.3. To quantify the effect of temporary elimination of regrowth, and consequent disruption of certain regeneration mechanisms, on long-term patterns of biomass and nutrient accumulation following large-scale disturbance (whole watershed deforestation).

II.A.1 Population Demography and Forest Growth and Disturbance

Objective: To explain the composition and age/size structure of early and late successional and old-growth stands on the basis of species-specific demographics and thereby refine the existing model of forest growth and composition.

Background, Hypotheses, and Research Approach

The dynamics of forest development at HBEF are now described quantitatively by an adaptation of a forest growth simulator (Botkin et al. 1972) which includes detailed predictions of nutrient (nitrogen) availability (Aber and Melillo 1982). Considerable refinement and extension of forest simulators has been accomplished in recent years (e.g., Shugart 1984), but these have not yet been incorporated into the HBEF simulations. We propose to incorporate additional detail into these simulators using information gathered from recently cut-over, late-successional, and old-growth northern hardwood-conifer watersheds at HBEF and nearby sites. Most critical in this regard is additional information on maximum biomass and leaf area, stress-induced mortality, and recruitment success in mature and old-growth stands.

Hypothesis A.1.1. Two major intervals of leaf area and living biomass decline (resulting from partial canopy break up) occur during succession following large-scale disturbance, one accompanying the onset of stress due to intraspecific competition among the pioneer trees and the other from interspecific competition in even-aged northern hardwood-conifer forests.

Bormann and Likens (1979) suggested that oscillations in forest biomass might occur following the "reorganization" and "recovery" phases of ecosystem development following large-scale disturbance. Chronosequence evidence for this phenomenon exists (Covington 1976), but interpretation of this evidence is fraught with problems. We propose to provide evidence for this supposition by long-term resurvey of permanent plots in W4 (15 yr old), W5 (3 yr old), W6 (75 yr old) and the Bowl (old-growth; > 300 yr old) including collection of leaf fall to estimate leaf biomass in these predominantly deciduous stands (pin cherry and maple-beech-birch). Our current evidence, based on resurveys from age 55 to 70, suggests rather constant mortality, slowly accumulating total biomass and steady leaf biomass (Siccama and Bormann, unpublished; Hughes and Fahey, unpublished). These stands will approach the maximum biomass of old-growth northern hardwoods (Martin 1977) during the next 2-3 decades, but a major decline in overstory stem density will occur first. Thus, we would expect two distinct waves of overstory mortality centered around age 30 and age 100.

Hypothesis A.1.2. The proportion of area in gaps is similar in 70- to 90-yr-old and old-growth hardwood-conifer stands, but the largest gaps in the old-growth forest are larger and permit the establishment and reproduction of pioneer species.

Hypothesis A.1.3. Canopy gaps in young stands (< 40 yr old) are filled by ingrowth of neighboring stems and only that regeneration (seeds, sprouts, advanced) recruited in the first 2 years following disturbance is significant in forming the overstory (initial floristics) until after the proposed 2nd phase of canopy break-up.

Using the methods of Runkle (1981, 1982) and Brokaw (1982), gap frequency and size will be measured at three-year intervals on randomly-placed, permanent belt transects in the 75-year-old reference area at Hubbard Brook, in 15-year-old W4 and in the old-growth northern hardwood-conifer forest at the Bowl (Martin 1977), located 26km from Hubbard Brook (see Appendix I, site descriptions). Gaps will be mapped and stems tagged in belt transects running north-south through gap centers and extending into the surrounding canopy. We will follow growth and survival within and around the gaps annually after the initial survey in 1988. These measurements will also contribute to the studies of neighborhood competition (section A.2, below) but will include a much larger area of survey.

Future Research and Collaboration

We anticipate the initiation of the USFS/EPA Eastern Hardwood Forest Cooperative at this site in the coming year. Approval of full funding for this embryonic program is currently under legislative review. It is likely that this program will utilize HBEF as one of its intensive sites (D. Burns, Director, NEFES; pers. commun.), and we expect to take advantage of this opportunity to expand our permanent plot studies to include complete mapping, tree-ring coring, environmental measurements (forest floor, soil, microtopography, etc.), and survey of pest and disease organisms. Colleagues at Cornell University (D. Weinstein, S. Riha) will be consulted in efforts to improve the performance of the gap models for HBEF.

An ancillary proposal currently is being prepared for submission to NSF to seek support for additional research on microenvironment and gap processes. The proposed project would build upon the mapping and demography effort described herein by applying gap treatments of different scales in the reference 75-year-old forest. Resource availability, both above and below ground would be monitored and alleviation of resource scarcity would be accomplished in a factorial experiment.

A.2 Neighborhood competition and tree growth and survival

Objective: To quantify the suppression of tree growth, reproduction and survival owing to neighborhood competition and to initiate development of a spatial model of resource availability and tree growth and mortality.

Hypotheses and Research Approach

Harper (1982, 1984) has argued convincingly for the study of individual plants to explain population structure and dynamics, and local competition models have been applied successfully to tree populations (e.g. Weiner 1984). In herbaceous systems these mechanisms, acting at the population level, have proven useful for exploring community patterns (e.g., Peart 1985). To accomplish a similar integration for forest communities long-term study is needed. Ideally, such an analysis might actually incorporate characterization of resource availability and microenvironment and concomitant effects on physiological responses of individuals. This type of integration rarely has been attempted, but recent modelling efforts of Sharpe and colleagues (Sharpe et al. 1986) represent an initial attempt.

By definition, growth of each individual canopy tree is depressed by interference from other trees within the individual's "neighborhood" — the zone of direct inference. In forests, the size of the neighborhood is difficult to define because competition for soil resources is intense and tree root systems extend far beyond the canopy perimeter. Nevertheless, Weiner (1984) found that up to 50% of the variation in individual tree growth (*Pinus rigida*) could be explained by the sizes and distances of immediate neighbors.

Hypothesis A.2.1. In northern hardwood-conifer forests the effective "neighborhood" of an individual overstory tree is best defined as including those individuals in direct canopy contact.

Hypothesis A.2.2. The "neighborhood" of overstory species with highly dispersed root systems (e.g., yellow birch) is more inclusive than that of species with more restricted root distribution (e.g., sugar maple).

Hypothesis A.2.3. Under closed canopy sapling growth is correlated with light penetration to the understory and with neighborhood suppression amongst saplings. The analagous corollary also holds for seedling growth.

We propose to begin testing these hypotheses by establishing permanent plots of mapped and tagged overstory trees, saplings and seedlings in the late-successional reference area and in 20-year-old W2, and by continuing our ongoing analysis of established plots in 3-

year-old W5. Square plots (25 x 25m) with a grid coordinate system were established in W5 and currently are censused annually (see A.3, below). A similar array will be established in the other forests, allowing the treatment of nearly all mapped plants as "focal" individuals whose neighborhoods are measured in detail. The correlation between growth of "focal" individuals and size and distance to nearby trees will be used as a measure of the neighborhood dimensions.

To test hypothesis A.2.2 we require detailed information on the distribution of root systems in surface soils, a feature which rarely has been measured for trees. To avoid disturbance to the mapped plots we will accomplish this task by examining root distribution for trees, saplings/shrubs, and seedlings/herbs on nearby plots. The extent, branching and density of surface woody roots (to 15 cm soil depth) of yellow birch and sugar maple will be examined by excavation of three random octants radiating from the base of individuals of different age, size and growth rate. This information will be used to help define the neighborhood of focal individuals within the mapped plots. For the mature trees these measurements will be labor intensive and will be carried out gradually over several years of the study.

Growth of mature trees will be quantified with band dendrometers and application of newly-revised allometric equations for the major species (Whittaker et al. 1974; Siccama, unpublished data). For seedlings and saplings annual measurements of diameter growth, shoot extension and maximum leaf number will be made.

Finally, we propose to adapt the spatial modelling approach of Sharpe and colleagues (Sharpe et al. 1986) for application to early- and late-successional northern hardwood-conifer forests. This modelling approach is a powerful tool for describing the interactions of physiological, population and community ecology. Sharpe (personal commun.) anticipates that the computer code for the general model will be complete and error-free before the beginning of our proposed LTER Program and is willing to provide advice and assistance in adapting it to the HBEF situation.

Future Research and Collaboration

Obviously, Objective A.2 is an ambitious undertaking, and we expect only to set up the framework for testing the hypotheses 1-3 under funding through the LTER Program. The establishment of permanent mapped plots on W5 has been accomplished through NSF funding (BSR-8316950 to Johnson and Fahey). As described above, we will submit an ancillary proposal to NSF and/or USDA to provide funding for characterization of microenvironment, resource availability, and physiological responses in the gap and neighborhood analyses.

Within the framework of that proposal we will develop the detail for a collaborative effort with P. Sharpe to adapt the Texas A&M Systems Group modelling approach to the northern hardwood-conifer ecosystem. Finally, the anticipated establishment of permanent plot studies at HBEF by the USFS/EPA Eastern Hardwood Forest Cooperative will be incorporated into this research effort (see A.1, above).

A.3 Herbicide effects on succession and biomass and nutrient accumulation

Objective: To quantify the effect of temporary elimination of regrowth, and consequent disruption of certain regeneration mechanisms, on long-term patterns of biomass and nutrient accumulation following large-scale disturbance.

Hypotheses and Research Approach

Forest vegetation recovery following large-scale disturbance can be accomplished by a variety of regeneration mechanisms including advanced regeneration, vegetative reproduction, germination from the seed bank and from newly-dispersed seeds. The diversity, concentration of dominance and productivity in both the initial and later stages of vegetation succession following large-scale disturbance depend upon the particular combination of regeneration strategies which prevails on a site (Whittaker 1974). Because the initial rate of biomass and nutrient accumulation strongly regulates nutrient retention on disturbed sites as well as the ultimate composition and structure of the forest, the early revegetation process is most critical to the long-term dynamics of forest watersheds and needs to be more clearly understood.

Recovery of vegetation following large-scale disturbance in temperate zone forests often is characterized by high concentration of dominance in one or a few plant species. At HBEF the buried-seed species, pin cherry (Prunus pensylvanica), fills this role and exerts a strong influence over the ecosystem recovery process (Marks 1974) probably in part because of the earlier, large-scale disturbance history (timber cutting) at this site. However, great spatial variation in the abundance of pin cherry often corresponds with landscape positions in the watersheds, and each of several regeneration strategies becomes dominant under certain conditions (Hughes and Fahey, unpublished).

In the W2 experiment (Bormann et al. 1974), repeated herbicide application for three years following the clear felling resulted in the partial exhaustion of the pin cherry seed bank and decisively lowered the concentration of dominance when regrowth began (Reiners, unpublished data). Three major modes of regeneration were either eliminated (advanced regeneration) or curtailed (vegetative sprouting, buried seeds) on this site. Of course, this treatment also led to very high initial nutrient losses (esp. N) from this site. In contrast, in the W5 experiment (whole-tree harvest), all the important modes of regeneration were fully operative and nutrient loss via leaching was much lower (Likens et al., unpublished data).

We propose to utilize these contrasting treatments to test a set of basic hypotheses regarding the control of vegetation succession and biomass accumulation across complex landscapes following large-scale disturbance.

Hypothesis A.3.1. The combination of high initial nutrient losses and elimination or curtailment of certain regeneration mechanisms resulted in lower biomass and nutrient accumulation in vegetation for the W2 than the W5 experiment.

Hypothesis A.3.2. Differences in biomass and nutrient accumulation between W2 and W5 are greatest on rich sites where elimination or curtailment of buried seed, sprouting, and advance regeneration are relatively greatest; and on very poor, ridgetop sites where erosion and nutrient loss in the absence of vegetation are most severe.

Hypothesis A.3.3. On rich sites, most of the differences above are accounted for by lower rates of site occupancy (i.e., development of maximum leaf and fine root biomass) owing to lower plant density and more of the slower growing species, rather than by lower growth rates owing to nutrient stress.

Hypothesis A.3.4. The initial trajectory of biomass and nutrient accumulation carries into later stages of succession so that the maximum "steady-state" biomass and nutrient accumulation is higher on W5 than W2. Moreover, the differences are largest on rich and very poor landscape sites.

Vegetation composition and biomass on W2 were sampled with a stratified-random array of seventy 10 x 10 m permanent plots (Fig. A.1). Sampling was done in the 1st,

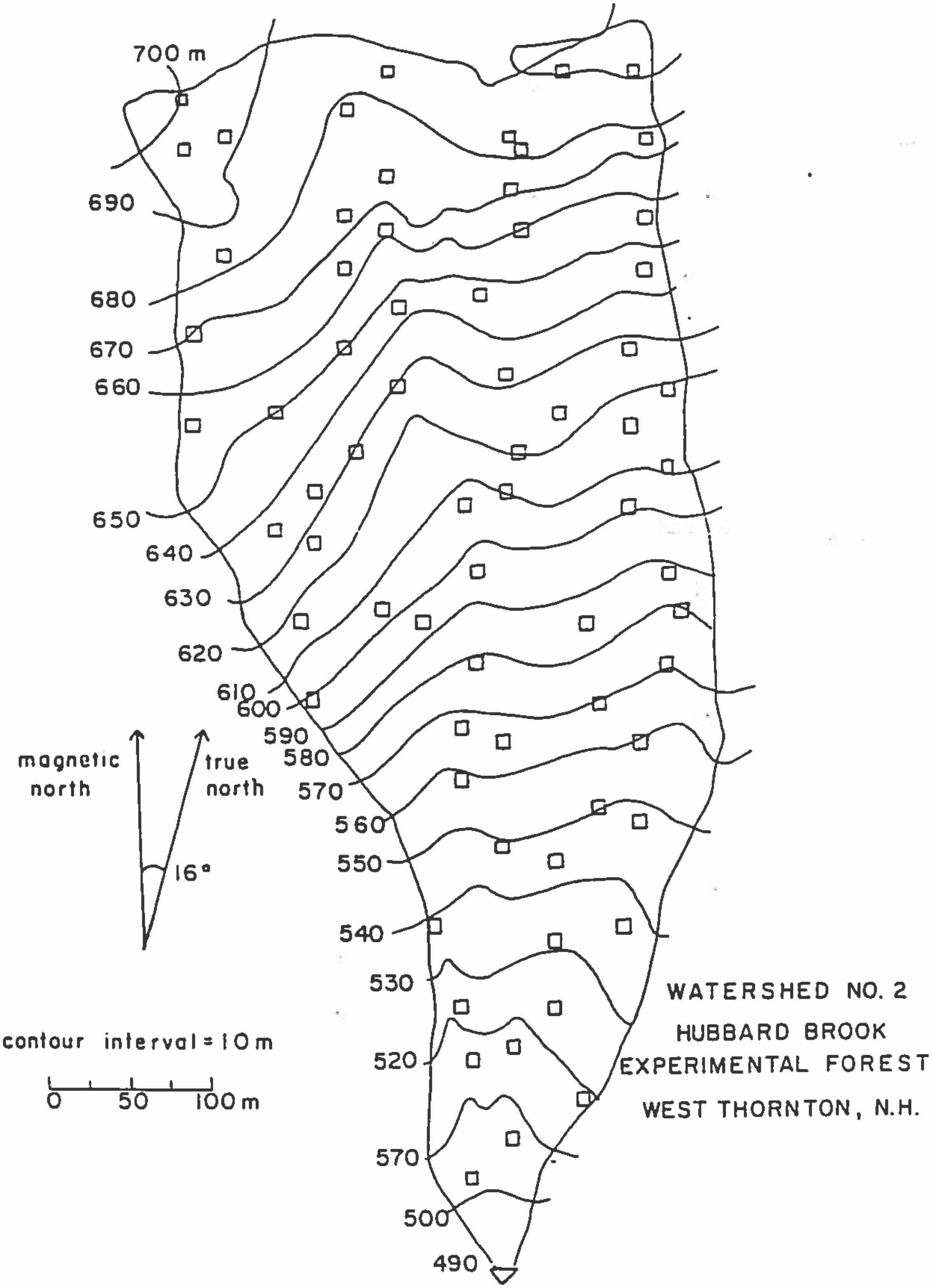


FIGURE A.1 Array of permanent plots (10x10m) established on W2 in 1969.

2nd, 3rd, 5th and 11th year of regrowth after cessation of the herbicide treatment. Aboveground biomass and nutrient content of 33 herb species, 13 shrubs, and 6 tree saplings were determined in each year using a variety of allometric and direct sampling methods. Data for years 1, 2, 3 and 5 have been summarized (Fig. A.2) and a portion was presented in Likens et al. (1978). Data from year 11 are complete but have not been worked up.

A similar array of 330 5x5 m permanent plots was established in W5 and has been sampled in years 1, 2, and 3 since harvest. The next re-sampling is scheduled for year 5 (1988). Aboveground and belowground biomass and nutrient content are determined using a variety of direct and allometric regression methods for 8 major herbs and 16 woody species in a manner similar to that used for W2. Thus, a stratified comparison of composition, biomass and nutrient accumulation will be possible by classifying quadrats in both watersheds according to landscape positions. Thus, we will be analyzing an unbalanced, random design with the caution that the study sites may have differed in important ways at the initiation of the treatments.

Future Research and Collaboration

The permanent plots on W5 were established with NSF funding to Johnson and Fahey (BSR-8316950). Additional experimental and survey studies of vegetation were initiated at the time of harvest of W5 including surveys of seed rain, experiments on regeneration mechanisms and competition, surveys and experiments on demography and life history of important species. We hope to continue these related studies through renewed funding for our W5 whole-tree harvest project. In this proposal we seek funding for the periodic resurvey of the permanent plots in W5 in year 5 of regrowth (1988) and in W2 in year 20 of regrowth (1988). Funding by the LTER program will permit only the field surveys. Our renewal proposal will request funding for chemical analysis and data synthesis. In addition, we will propose surveys of nutrient availability and soil organic matter quality to extend studies undertaken in the mature forest, W5, and W4. Information gathered in this part of the project could act as a valuable validation data set for both the gap models and any newly-developed

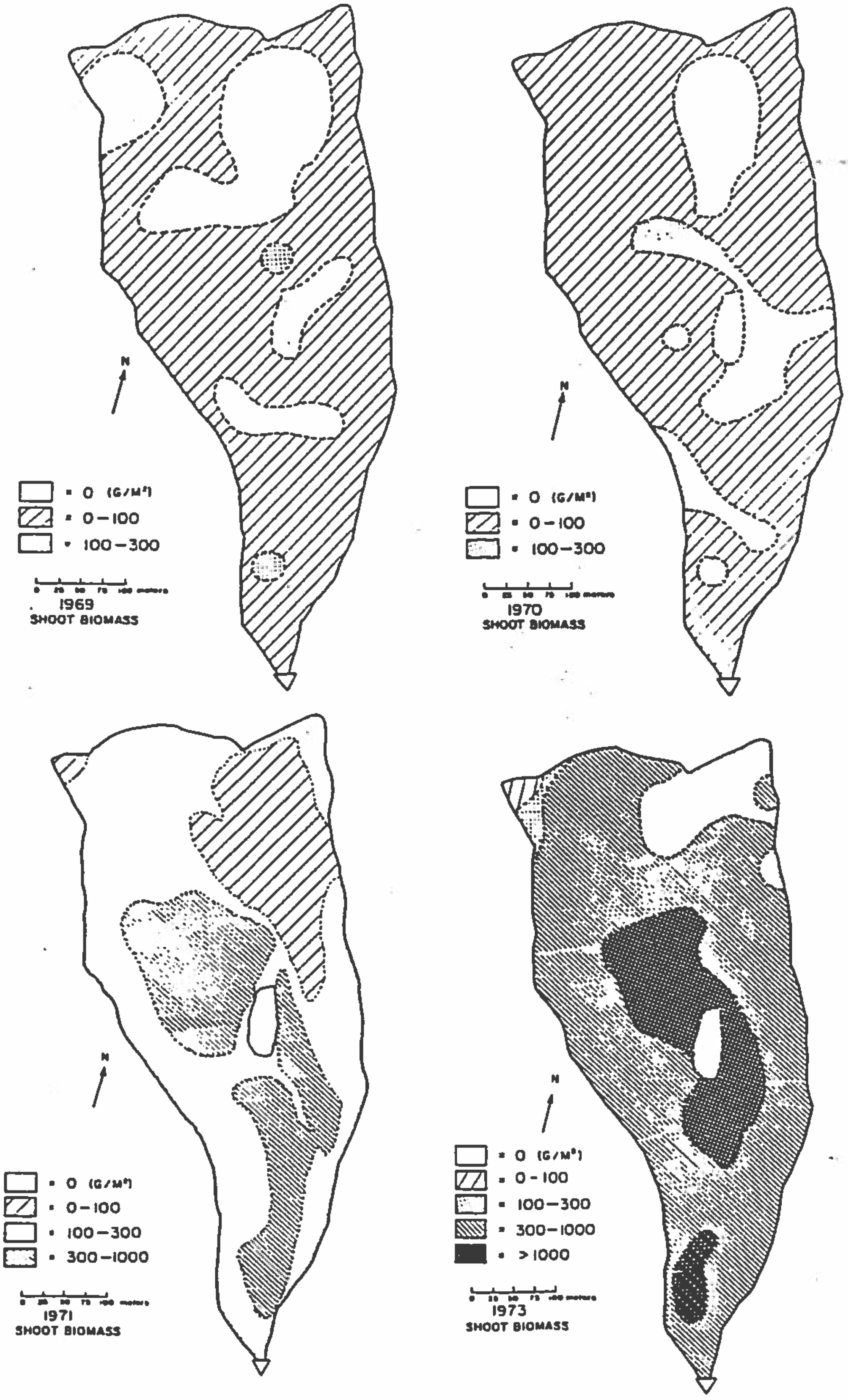


FIGURE A.2 Biomass accumulation on W2 at HBEF during years 1,2, 3 and 5 of regrowth after deforestation and three years of herbicide treatment.

models in the HBES. Finally, coordination of these efforts with the USFS/EPA Eastern Hardwood Forest Cooperative is anticipated.

II.B RESEARCH COMPONENT B: DYNAMICS OF DETRITUS

In its roles as the principal energy source for aquatic food chains and as the rooting medium for trees, detrital organic matter is critical to the overall functioning of many forested watersheds. Moreover, coarse woody detritus acts as a critical habitat for organisms, a slowly-available source of plant nutrients and energy, and the key substrate for debris dams which control the structure of headwater stream ecosystems. The second major component of the proposed LTER for HBEF is to quantify the changing patterns of production, utilization, and dissipation of plant detritus following large-scale disturbance of the watershed ecosystem. As for the vegetation studies we will combine information from past studies, ongoing research, and new initiatives to meet a series of objectives within the arena of organic matter dynamics:

Objective B.1: To quantify changes in aquatic food chains and efficiency of detrital processing in streams following overstory removal.

Objective B.2: To quantify the accumulation and dissipation of forest floor organic matter and the fates of detrital C, N and P during 20+ years following forest harvest.

Objective B.3: To quantify the supply, mineralization and leaching of large, woody debris.

Objective B.4: To determine the patterns of formation and disruption of organic debris dams in first- and second-order streams.

II.B.1 Organic matter processing in streams

Objective: To quantify changes in aquatic food chains and efficiency of detrital processing in streams following forest harvest.

Background, Hypotheses and Research Approach

Circumstantial evidence suggests that the trophic transfer efficiency is greater in autotrophic than detritus-based streams. Grazing aquatic insects have been shown to deplete algal standing stocks and compete strongly for access to algal food (McAuliffe 1984, Hart 1985) implying that consumption by invertebrates may be a significant fate of algal production. Also, seston export from autotrophic stream channels was not significantly different in the presence of grazers (Mulholland et al. 1985). On the other hand, leaf-shredding detritivores seem to have an abundance of food available and might be more influenced by changes that occur during early stages of decomposition (Cummins and Klug 1979, Sinsabaugh et al. 1985, Findlay et al. 1984a, 1986). Given the apparent inefficiency of microbial growth on leaf litter (Findlay and Meyer 1984) and the potentially large losses of organic matter to downstream transport (Bilby and Likens 1980, Webster 1983), one would expect that the losses of detritus would be large compared to the amount incorporated into consumer biomass. At HBEF only a small fraction of the detritus input is used by macroconsumers (Fisher and Likens 1973). These points argue that the transfer of algal biomass to invertebrate biomass is relatively more efficient than the transfer of detrital organic carbon to invertebrate biomass. These observations lead to the following hypotheses:

Hypothesis B.1.1. A unit of algal primary production will support more secondary production than a unit of detritus input.

Hypothesis B.2.1. Realized secondary production in algal-based and detritus-based streams may be comparable due to the larger magnitude of detritus inputs.

The manipulated watersheds at HBEF provide an ideal situation to test hypotheses about how different organic carbon sources fuel stream ecosystems. Obviously, long-term research is needed to quantify the changes in organic matter processing in streams as the surrounding forest develops, and so there are no data on patterns of trophic level transfer efficiencies or secondary productivity in streams during terrestrial succession. We propose to follow the rates of supply of detritus and the resulting biological standing stocks in the autotrophic clear-cut stream (WS 5) and the undisturbed detritus-based Bear Brook. In conjunction with the algal biomass estimates of T.M. Burton, these measures will document the potential availability of the two organic carbon sources. In initial work, we will measure rates of bacterial production, and standing stock of bacteria, fungi and invertebrates to begin to assess the heterotrophic biomass supported by the two carbon sources. Ideally, we would measure production of all heterotrophic organisms but this task is clearly beyond the scope of this proposal. The logic behind concentrating on bacterial production is that bacteria are expected to be closely coupled in time and space to changes in organic carbon supply. Also, data for a headwater stream at the Coweeta Hydrologic Lab in NC, show bacterial production (20 mg C m^{-2} d^{-1}) to be much greater than production of the dominant shredder (Peltoperla 0.7 mg C m^{-2} d^{-1}, O'Hop et al. (1984)). We feel that bacterial production measures, together with standing stocks of other groups, will provide adequate information to begin to test the hypotheses. All sampling will be habitat-specific using a stratified-random design. The area of habitats will be mapped so that we can calculate bacterial biomass per unit area of stream, knowing the proportional area of each habitat type. Detrital inputs will be measured with leaf fall and blow-in traps. The standing stock of benthic organic matter will be followed using Surber samplers. Decomposition rates will be determined for individually tagged, weighed leaves. We propose to use the most abundant leaves from traps to represent actual leaf inputs. Nutrient content of decomposing leaves will be determined as for terrestrial litter. Aquatic insects will be sampled with Surber samplers and/or cores, depending on substrate type. Insects will be identified to the lowest feasible taxonomic level and assigned to a functional group (Cummins 1973). A functional group assignment is only an approximation of the actual food resources being used and a subsequent proposal will be necessary to directly determine consumption of algae and detritus and production supported by these foods. Finally, bacterial and fungal biomass will be determined using epifluorescent direct counts, and bacterial production as the rate of incorporation of tritiated thymidine into DNA (Findlay et al. 1984b).

Future Research and Collaboration

It will not be possible to obtain unequivocal tests of the hypotheses early in the proposed research. A separate proposal will be submitted during Year 3 to request support for invertebrate production and feeding studies. Additional heterotroph populations also will be examined in those studies. Comparison with ongoing research at LTER sites at Coweeta Hydrologic Laboratory, Andrews Experimental Forest and Konza Prairie also will be pursued to provide a more general understanding of controls on aquatic food chains in stream ecosystems. Finally, we hope to identify parallels between organic matter processing in stream and terrestrial systems during vegetation recovery following large-scale disturbance.

B.2 Forest floor accumulation and dissipation

Objective: To quantify the accumulation and dissipation of forest floor organic matter and the fates of detrital C, N and P during 20+ years following forest harvest.

Background, Hypotheses and Research Approach

Using a chronosequence approach, Covington (1981) demonstrated that the mass and nutrient content of forest floor horizons in northern hardwood-conifer ecosystems declines following forest harvest to about 40% of pre-cut levels after about 10-15 years before returning slowly to "steady-state." Because of the typically short-term nature of ecological studies, direct tests of this post-cut, forest floor dissipation model and mechanistic explanation of the phenomenon have not been undertaken. Moreover, the occurrence and nature of the forest floor "steady-state" also have not been critically evaluated. The importance of these patterns cannot be overstated as the forest floor horizons are the principal root zone of the trees in these ecosystems (Wood et al. 1984). Problems of closure in the N budgets of HBEF following forest harvest may result from our inability to quantify the fates of the N lost and the accuracy of this model. For example, Ryan and Huntington (1986) suggest that significant quantities of N are mechanically mixed with mineral soil during a typical harvest operation. Management implications must also be stressed, as Aber and Melillo (1978) have adapted the Covington model to judge the long-term effects of forest harvest on nutrient availability in northern hardwood ecosystems.

We are currently using an integrated set of studies to evaluate the quantity and mechanisms of C and nutrient loss from forest floor horizons following forest harvest at HBEF. Studies in progress are summarized in Table B.1. These studies are designed to improve our understanding of the process of formation of the organic horizons in northern hardwood-conifer ecosystems, as represented by formulations such as those of Aber and Melillo (1980), which provide a valuable conceptualization of this critical ecosystem process.

We propose to continue and to expand these efforts and seek support in this proposal for measurements which are particularly long-term in nature: (1) periodic remeasurement of forest floor mass and chemistry in reference watershed area; (2) continued maintenance and

Table B.1 Summary of measurements of terrestrial detritus at HBEF.

Researchers	Description	Frequency of measurement	Next measure
Ryan/Huntington	Burial of forest floor during forest harvest operations	—	—
Siccama	Forest floor mass and chemistry on 60 random plots in a reference area	1977, 1982	1987, 1992
Fahey/Hughes	Mass and nutrient changes of intact forest floor blocks on W5	1985, 1986	1987, 1989
Fahey/Hughes	Forest floor leaching on plots adjacent to intact blocks	event basis	1987, 1989
Fahey/Hughes	Forest floor CO_2 evolution on plots adjacent to intact blocks	monthly	1987, 1989
Bowden/Bormann	Gaseous N efflux from forest floor	n/a	----
Fahey/Hughes	Litterfall (including deadwood) in W5 , W101 (11 years old), and reference area	biennial collection	1987
Fahey/Hughes	Leaf litter and slash decay in W5, W101 (including deadwood), and reference area	biennial collection	1987
Fahey/Hughes	_In situ_ N mineralization in forest floor and spodic horizons	biannual (1984, 1986)	1988
Fahey/Hughes	Isolation _in situ_ of annual litterfall in W101 and reference area	annual	1987

collection of intact forest floor blocks in W5 including organic C, N, and P leaching and CO_2 evolution; (3) establishment of a network of forest floor blocks in W4 (15 years since cutting) similar to that in W5; (4) measurement of decay constants and tissue chemistry changes in leaf litter of different decay states (time since leaf fall) in reference area and 3 to 15-year old stands.

Our integrated, long-term program of studies of organic matter is designed to test the following hypotheses:

Hypothesis B.2.1. Forest floor biomass and nutrient content attain steady-state within 80 years after harvest of northern hardwood forest.

No significant change was detected in forest floor mass and chemistry on a reference area adjacent to W6 between 1977 and 1982, despite intensive, stratified random sampling (60 samples) and careful replication of methodology. Comparison with 1970 measurements of Gosz et al. (1976) has not been achieved because of problems of replicating methods, but corrections for non-volatile matter may permit such a comparison, which will be attempted during this funding cycle (sub-samples of Gosz' forest floor collections have been retained). We propose to resample again in 1987 (support from Likens et al., BSR 8406632 is available) and in 1992 (support sought in this proposal) to better quantify the development of steady-state conditions within the forest floor. In conjunction with this monitoring program, we are isolating annual litterfall in the reference watershed area to permit in situ analysis of physical and chemical changes over the long-term (see below).

Hypothesis B.2.2. A large proportion (over 30%) of the organic matter and N and P lost from the forest floor following harvest actually is retained in the mineral soil, arriving there as a result of mechanical mixing and by leaching and subsequent precipitation of organic compounds in mineral soil.

Our initial data indicate that large amounts of organic C, N and P are leached from forest floor horizons in the first 2 years following harvest, but little DOC or N appears in Bs horizon lysimeters. Moreover, we have estimated that a significant proportion of the forest floor C and N is mechanically mixed into mineral soil horizons (Ryan and Huntington 1986). Thus, significant amounts of the forest floor nutrients which appear to be lost following harvest are actually retained in the mineral soil. Accurate estimation of the former transfer process requires continued monitoring of leaching from our permanent installations. We propose to continue this monitoring in conjunction with measurement of mass and chemical changes and CO_2 evolution from intact forest floor blocks on W5. To extend these estimates to later stages in succession we propose to initiate a parallel study in W4 which was harvested 14 years ago. Thus, at the end of the first interval of LTER funding we would have a continuous record of changes in forest floor dissipation through the period of Covington's chronosequence observation of forest floor decline. In conjunction with our ongoing studies of litter production, leaf and woody litter decay, fine root production and turnover, and our proposed study of decay of old, dated detritus (see below, Hypothesis B.2.3), this work will give us a clearer picture of the controls and pathways of forest floor dissipation following harvest. The insights gained from this research should be of general value to understanding the development of humus layers in northern forests.

Hypothesis B.2.3. During the later stages of decay, weight loss from leaf litter follows an exponential model and the efficiency of decomposers in converting residual carbon to new microbial biomass increases. Decay constants for highly-decayed material are not significantly different for pin cherry and northern hardwood-derived litter materials.

Although a variety of models has been proposed to explain litter decay (Wieder and Lang 1982) and microbial utilization of substrates (Bosatta and Agren 1985), these models rarely have been adequately tested for any but the early stages of decay (up to ca. 40% weight loss). To permit long-term estimates of decay model parameters we have isolated annual litter fall in reference areas (70 year-old forest) and 15 year-old pin cherry dominated stands at HBEF by placing coarse-mesh nylon screening below and over the annual litterfall. At the initiation of our proposed LTER (fall, 1987) we will have isolated litter layers 4, 3 and 2 years old. We propose short-term (less than one year) incubations of 4, 3, and 2 year-old litter beginning in fall, 1987. Decomposing materials will be placed in mesh bags at about the depth of collection, with samples retrieved in early spring, early summer and late summer the following year. For each date complete chemical analysis, including organic fractionations (Kedrowski 1983, Yavitt and Fahey 1986a) and lignin oxidation products (Ziegler et al. 1986) will be performed, and estimates of microbial biomass C and N will be obtained by a combination of chloroform fumigation

(Jenkinson and Powlson 1976, Voroney and Paul 1984) and direct counting and hand-sorting of macrofungi. We propose to repeat this study on 6-, 5-, and 4-year-old material beginning in fall 1989 as well as in the second interval of LTER funding. This information will be integrated with the studies of development of steady-state forest floor conditions to obtain a better understanding of the dynamics of these organic horizons.

Future Research and Collaboration

We plan to seek ancillary funding for related studies which will capitalize on the experiments initiated under this component: (i) radiotracer and ^{15}N labelling of detritus (pin cherry leaves), and (ii) studies of detrital food webs using selective biocides. Although no experts in these areas currently are working on the HBES, we expect colleagues from IES, Cornell, and the University of New Hampshire to be involved in these ancillary proposals. Related studies of decomposition of roots are funded by NSF through BSR-8316950. These efforts will contribute to our understanding of nutrient availability at different stages in succession, critical for beginning to test hypotheses under research component A.2. (above).

B.3 Dead wood supply, mineralization and leaching

Objective: To quantify the supply, mineralization and leaching of large, woody debris.

Background, Hypotheses and Research Approach

The importance of coarse woody debris (CWD) to the structure and function of temperate forest ecosystems has been summarized recently by Harmon et al. (1986) who noted that: "CWD is abundant in many natural forest and stream ecosystems, forming major structural features with many crucial ecological functions as habitat for organisms, in energy flow and nutrient cycling, and by influencing soil and sediment transport and storage" (p. 134).

Because of the contrasting anatomy and chemistry of the major tree species, HBEF is ideally suited for a detailed, long-term examination of CWD for purposes of understanding the decay process and its role in ecosystem structure and function. Studies of CWD in northeastern hardwood-conifer forests have been limited to branch and twig decay (Gosz et al. 1983), overall wood disappearance rates (Tritton 1980) and slash decay (Spaulding and Hansbrough 1944) and a few estimates of CWD mass (Gore and Patterson 1986) and chemistry

(Lang and Forman (1978). Moreover, few studies in other upland eastern forests have been done (e.g., Mattson et al. 1986). We propose an integrated set of long-term studies to parallel the ongoing work at Andrews Experimental Forest in Oregon (Harmon and Franklin 1986 and personal communication).

Recent reports of increased tree mortality in many eastern hardwood forests, resulting from introduced and native pests and unexplained "declines", indicate the potential for large additions of bole wood to the surface soils of these ecosystems in coming decades. We are routinely monitoring tree mortality in reference areas of HBEF as well as several other northern hardwood and subalpine forests in the region (Siccama and Tritton, unpublished). These monitoring programs allow us to evaluate rates of input to the decaying wood pool in these successional stands. Although the first wave of attack from the beech bark disease (Twery and Patterson 1983) and the highly-publicized spruce decline probably have resulted in some increases in dead wood, our data suggest that at HBEF the proportion of standing dead has remained constant at about 15% for the past 8 years. By continuing our studies of mortality and monitoring the timing of tree falls in the reference watershed we will be able to document the rates and conditions of woody debris input to the soils at HBEF, essential information for evaluating its overall role in ecosystem function.

Our principal hypotheses with regard to bole wood decay parallel those of Harmon and Franklin (1986) for Andrews EF and will provide a valuable test of the general applicability of a model of the regulation of wood decay across contrasting environments and forest types.

Hypothesis B.3.1: Initial decay rate is controlled by colonization of wood by insects and fungi, a feature which is dependent upon characteristics of bark. Thus, initial decay rate of maple and beech (thin bark) is more rapid than for yellow birch, red spruce and balsam fir (thick bark).

Hypothesis B.3.2: Over the long-term the hardwoods decay more rapidly than the conifers, in part because of higher amounts of extractives (polyphenols and other wood decay inhibitors) in the latter group.

Hypothesis B.3.3: Long-term decay of yellow birch (persistent bark) exceeds that of maple and beech (ephemeral bark) because bark retains moisture in the decaying logs. Alternatively, thick bark causes excessive moisture retention with consequent depression of heterotrophic activity.

Hypothesis B.3.4: Relative weight loss from whole logs increases with diameter from small branches (<5 cm) to small boles (>30 cm) because of increasing wood:bark ratios, but wood decay alone follows the reverse pattern because of delayed fungal colonization.

To facilitate statistical comparisons and the development of general models, our experimental design will parallel that of Andrews EF. The study will be established in a reference area within HBEF (west of W6) and will consist of a main study to test hypotheses 1-3 and a secondary study to test hypothesis 4. Three dicotyledonous trees (*Acer saccharum*, *Betula allegheniensis* ssp, *Fagus grandifolia*) and two gymnosperms (*Picea rubens*, *Abies balsamea*) will be used in the main study, and only *Acer* and *Betula*, in the secondary study. Several mature and healthy trees of each species will be felled in an area adjacent to the study site for field incubations.

For the main study a total of 72 sections of each species, within the diameter range from about 25 to 35 cm and about 2 m long each, will be randomly assigned to each of three treatments: (control, bark removal, insect exclosure) and four blocks (location). Samples will be placed on large-mesh nylon netting in contact with the forest floor. For the bark removal treatment, samples will be mechanically debarked on site. Tents of fine mesh nylon netting will discourage colonization by insects in the exclosure treatment for five years following initiation of the study. All samples will be tagged and a detailed map of sample placement will be drawn. Samples will be weighed (moist) in the field with sections taken for determination of initial moisture, chemistry, density and wood:bark ratio. Samples will be collected after 2, 3, 5, 10, 15, and 25 years of decay, with one replicate of each species and treatment collected in each block at each sampling time.

For the secondary study, samples of three additional size classes (3-5 cm, 8-12 cm, 15-20 cm diameter) of birch and maple will be incubated in the four blocks for comparison with the larger bole samples. Experimental design will be as above for the main study.

At several times during each year of study and at the time of collection, bole and branch samples will be carefully censused for insect colonization and fungal fruiting bodies. The extent of hyphal growth will be examined by sectioning samples, and relations between fungal infection and localized wood density and chemistry changes will be quantified.

The final component of our analysis of the long-term dynamics of decaying wood at HBEF will be to examine leaching by melting snow and summer rain. Dead wood forms discrete layers in the organic horizons of most northern forests and infiltrating water is altered chemically during passage through these layers (Yavitt and Fahey 1986b). High concentrations of organic acids in this percolating water may contribute to eluviation in surface mineral horizons (Cromack, personal communication). Although leaching contributes little to C and mineral nutrient release in the early stages of wood decay (Mattson et al. 1986), high DOC and N concentrations in later stages suggest that its long-term role may be significant (Yavitt and Fahey 1986). This process apparently never has been studied in eastern hardwood forests. This highly decayed wood also acts as an important rooting medium for trees, but its quality as a rooting substrate rarely has been examined.

Hypothesis B.3.5: Leaching of C and mineral nutrients from decaying wood increases rapidly as boles become flattened and woody tissue structure is lost. Differences between dicot tree species are not significant, and all species are heavily invaded by plant roots at this time.

Hypothesis B.3.6: Long-term leaching of strong organic acids from highly-decayed wood increases the extent and thickness of the eluviated and illuvial horizons in the Spodosols at Hubbard Brook.

Five plate tension lysimeters (scintered glass) will be positioned beneath random decaying boles of sugar maple, beech, and yellow birch on W2. This site was clear-cut and boles left in place twenty years ago. Many of the large logs on this site remain relatively intact, and lysimeters will be positioned with minimal disturbance to the wood by excavating from the side. Percolating water will be collected under tension (10 kPa) during major snowmelt intervals in spring and occasionally during large rain events in the snow-free period. Sampling will continue for at least 10 years during which boles will be changing from moderate to advanced decay class (Harmon et al. 1986). The lysimeter plate will be covered with polyester fiber to prevent blocking of pores by fine colloidal materials. Subsamples from nearby sections of the boles will be collected at about 3-5 year intervals during the study and analyzed for specific gravity and chemical changes to allow the development of a simple model for the relationship between bole leaching and decomposition for these three major species. In addition, visual observations of depth and thickness of E horizon will be made beneath boles and in adjacent areas.

Future Research and Collaboration

We anticipate expanding the funding for these studies through grant proposals to USDA Competitive Research Grants Program, NSF, or USFS. Such expansion will likely include: (1) dead wood exchange with Andrews EF and perhaps other LTER sites; (2) role of deadwood as nurse sites for tree seedlings in mature and early-successional, cut-over stands; (3) effect of dead wood removal on long-term nutrient availability in northern hardwood-conifer forests (the W5, whole-tree harvest experiment will be compared with conventional (W4) and no removal (W2) treatments); (4) reconstruction of dead wood patterns in old-growth northern hardwood-conifer forests using dendrochronologic methods on tree scars.

B.4 Organic Debris Dams

Objective: To quantify the patterns of formation and disruption of organic debris dams in first- and second-order streams.

Background, Hypotheses and Research Approach

Organic debris dams serve a variety of important roles in forested watersheds including: regulation of export of organic and inorganic sediments (Bilby and Likens 1980, Bilby 1981); erodibility and channel morphology of streams (Swanson et al. 1982); and control of aquatic habitat structure (MacDonald and Keller 1983). Despite their obvious importance, the patterns and controls of dam formation and disruption rarely have been determined (Swanson et al. 1984). In the HBES we are taking advantage the whole-watershed manipulations to examine the effects of deforestation on the abundance and function of organic debris dams. We seek an understanding of the immediate response of dams to deforestation and to quantify changes occurring during long-term succession of the surrounding forest.

Our results to date show a large, however somewhat delayed, effect of deforestation on the density (i.e., #/stream length) of organic debris dams. Densities in a first-order stream did not change significantly during the first two years following deforestation (13 dams/100 m), but a sharp decline occurred in the third year (9 dams/ 100m). A reference stream showed little change during the same period. Also, densities in a stream draining a watershed cut over 20 years ago were considerably lower (3 dams/100m) (Hedin et al. 1986).

We propose a long-term model describing the abundance and function of debris dams in northern hardwood-conifer watersheds during succession following large-scale disturbance:

Hypothesis B.4.1: Following deforestation organic debris dams are depleted on 1st and 2nd order streams because of continued dam destruction concurrent with an abrupt decline of input of CWD. A delay in this depletion is stochastic in nature, depending upon the occurrence of large storm-flow events.

Hypothesis B.4.2: The number of debris dams continues to decline until a major pulse of woody debris input occurs during the break up of the canopy of the pioneer forest stand.

Hypothesis B.4.3. Moderate (e.g. 20 year) floods significantly deplete organic debris dams on 1st and 2nd order streams, but because they also cause export of large amounts of erodible sediments, particulate losses in subsequent years (i.e., dam-depleted streams) is not unusually high.

Because of the slow changes expected and the low frequency of catastrophic events (i.e., floods), long-term measurements are required to quantify the dynamics and functions of debris dams. We propose to test our model by resurvey of organic debris dams on W6, W5, and W2 at 1- to 2-year intervals, with contingencies for extreme weather events. Sediment export and hydrologic discharge from the watersheds are measured by the USFS as a component of the monitoring program. Statistical correlations will be determined between time since deforestation, forest canopy break-up and debris input, major discharge events, sediment export, and debris dam density.

Future Research and Collaboration

If time and expenses permit, we expect to initiate a study of decay of CWD in debris dams to parallel our work on log decay in the terrestrial system. These studies would be aimed at quantifying differences in decay processes between terrestrial and aquatic environments and the state of decay at which major structural supports in dams lose their integrity. In addition, we hope to compare decay rates and detrital pathways for woody and non-woody detritus of different species (see section B.1). Finally, we hope to examine the effect on chemical export of modifications in debris dam density at different stages in ecosystem development following deforestation. Additional funding for these studies will be sought in conjunction with colleagues at IES.

II.C RESEARCH COMPONENT C: ATMOSPHERE-TERRESTRIAL-AQUATIC LINKAGES

Studies of hydrologic-element cycling interactions have long been a focus of research at the HBES. We have relied heavily on the small watershed approach, by comparing bulk precipitation inputs with stream outflow as well as internal inputs from weathering and element accumulation/loss from vegetation and soil to better understand element cycles. While this approach has yielded a wealth of information on the biogeochemistry of forested ecosystems (e.g. Likens et al. 1977; Likens 1985), important complexities of element transfer across the landscape, between ridgetops, down upland and slope segments, through riparian source areas and downstream must also be considered. Clearly the level of our understanding is limited by a lack of detailed information on material transfer to, within and from ecosystems. Although the small watershed approach has proved valuable to characterize input/output budgets and will remain essential for verification purposes, we propose that great advances are needed in our understanding of specific pathways and mechanisms of material transport within small watersheds to evaluate response to disturbance. We believe that the integration of geomorphic and ecosystem studies should be an area of fruitful research in coming years, and we propose that the linkage between the small watershed approach and plot studies of geological and ecological processes will provide a valuable method for forging this integration. Research objectives to enhance our current understanding of atmospheric-terrestrial-aquatic linkages at the HBEF are as follows:

C.1 to continue long-term characterization of precipitation inputs and stream outputs,

C.2 to determine the magnitude and seasonal characteristics of nitrogen, sulfur and basic cation inputs by dry deposition,

C.4 to modify the hydrologic model, BROOK, to facilitate solute transport calculations within soil and ultimately for solute transport modeling,

C.4 to better understand the hydrologic and element linkages between uplands, source areas and stream flow, and

C.5 to use the H^+ budget approach to integrate studies of element cycles and facilitate our understanding of the response of hardwood-conifer watersheds to disturbance.

II.C.1. Long-term Trends in Precipitation and Streamwater Chemistry

Objective: To continue to characterize long-term trends in the chemistry of precipitation inputs and stream outputs at the HBEF.

Background, Hypotheses and Research Approach

We have established long-term records of climate and hydrology since 1956, and precipitation and streamwater chemistry, since 1963 on reference and experimentally manipulated watershed-ecosystems at the HBEF (Likens et al. 1977; 1984; Likens 1985). These records show that short-term data are often misleading and that decades of monitoring may be required to detect real changes in complex ecosystems.

Long-term data are necessary to test hypotheses which address the successional development of northern hardwood-conifer ecosystems and effects of disturbance. Moreover, they are essential to identify and evaluate unusual or extreme events. Unfortunately, most ecological studies are forced by financial or other considerations to be short-term (i.e. less than 5 years) and may result in inaccurate or unrepresentative conclusions regarding long-term trends.

Since the initiation of the HBES in 1963, special care has been taken to maintain the integrity of the long-term data base (see Likens et al. 1984). Necessary changes in sampling and analytical procedures have only been implemented after systematic comparison of methods has guaranteed that inconsistencies have not been introduced. Our sampling locations and methods for the collection of bulk precipitation (see Appendices A.1-A.3) have essentially not changed since the beginning of the study. Specific uses of precipitation and streamwater chemistry include:

1. the development of element input/output budgets to supplement process-level studies of mechanisms regulating element retention/loss in forested ecosystems,
2. quantifying the temporal and spatial variability of cosystem inputs/outputs,
3. quantifying element-element and element-biota interactions,
4. providing reference data for evaluation of whole-ecosystem experiments, and
5. comparison with national monitoring networks such as MAP3S, NTN and the USGS.

In addition, major questions of local, regional and national significance have been addressed with these data. For example, the pH of precipitation samples (rain and snow) has been monitored continuously at the HBEF since 1964. Our continuous record of precipitation chemistry is the longest in North America. Two recent reports by the National Academy of Sciences have relied heavily on precipitation chemistry data from the HBEF in addressing the issue of acidic precipitation (Calvert 1983, Gibson 1986).

Our continuous record (1963-1982) of weekly, bulk precipitation chemistry at the HBEF shows no statistically-significant trend in annual, volume-weighted concentration of H^+ and NO_3^-, but a 34% decrease in SO_4^{2-}, a 34% decrease in NH_4^+, a 63% decrease in Cl^-, a 79% decrease in Mg^{2+} and an 86% decrease in Ca^{2+} during this period (Likens et al. 1984). Nitrate concentrations increased from 1964 to 1971 and H^+ concentrations decreased after 1970 (Figure II.C.1). These "short-term trends" were apparent within the overall record in each case.

The explanation for the marked decline in Ca^{2+} and Mg^{2+} concentrations is not clear. However, it is noteworthy that emissions of total suspended particulate matter to the atmosphere in the U.S. decreased by 46% between 1970 and 1978 (Council of Environmental Quality 1980). The significant decline in annual, volume-weighted SO_4^{2-} concentrations is correlated with a similar decline (% basis) in SO_2 emissions for the surrounding region during this period (Calvert 1983, Likens et al. 1984).

Concentrations of Pb in bulk precipitation at Hubbard Brook have been highly variable, but on the average, have decreased by more than 70% since 1975 (Figure II.C.2). This reduction coincides with a period of regulation on the use of leaded gasoline by motor vehicles. Elevated pools of Pb have accumulated in the forest floor at the HBEF, presumably from atmospheric inputs, and as a result of this adsorption/filtering action, streamwater concentrations of Pb are low (about 1 $\mu g \cdot l^{-1}$; Smith and Siccama 1981).

It is particularly difficult to assess long-term trends in stream chemistry. For example, although the long-term seasonal pattern for NO_3^- in stream water and in precipitation is consistent (Figure II.C.3), the annual volume-weighted concentrations of total inorganic nitrogen in precipitation and stream water have been unpredictable (Figure II.C.4). From 1964-65 to 1968-69, streamwater concentrations were less than in precipitation. However from 1969-70 to 1976-77, except for 1972-73), average streamwater concentrations increased by about 3- to 4-fold and exceeded precipitation. After 1976-77 precipitation inputs of inorganic N again exceeded streamwater concentrations. Fragmentary portions of this record (e.g., 1 to 5 years) yield highly variable results regarding

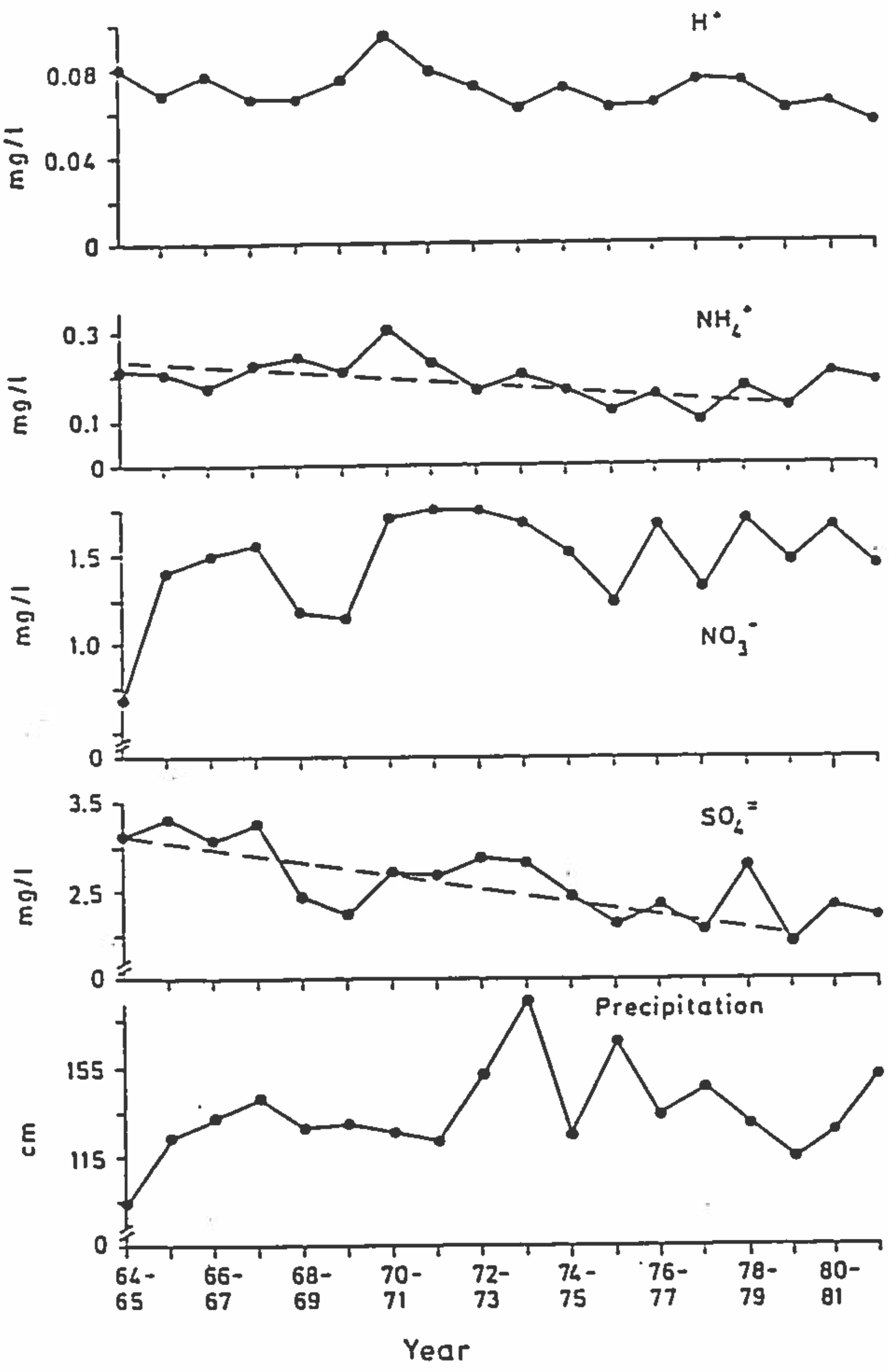
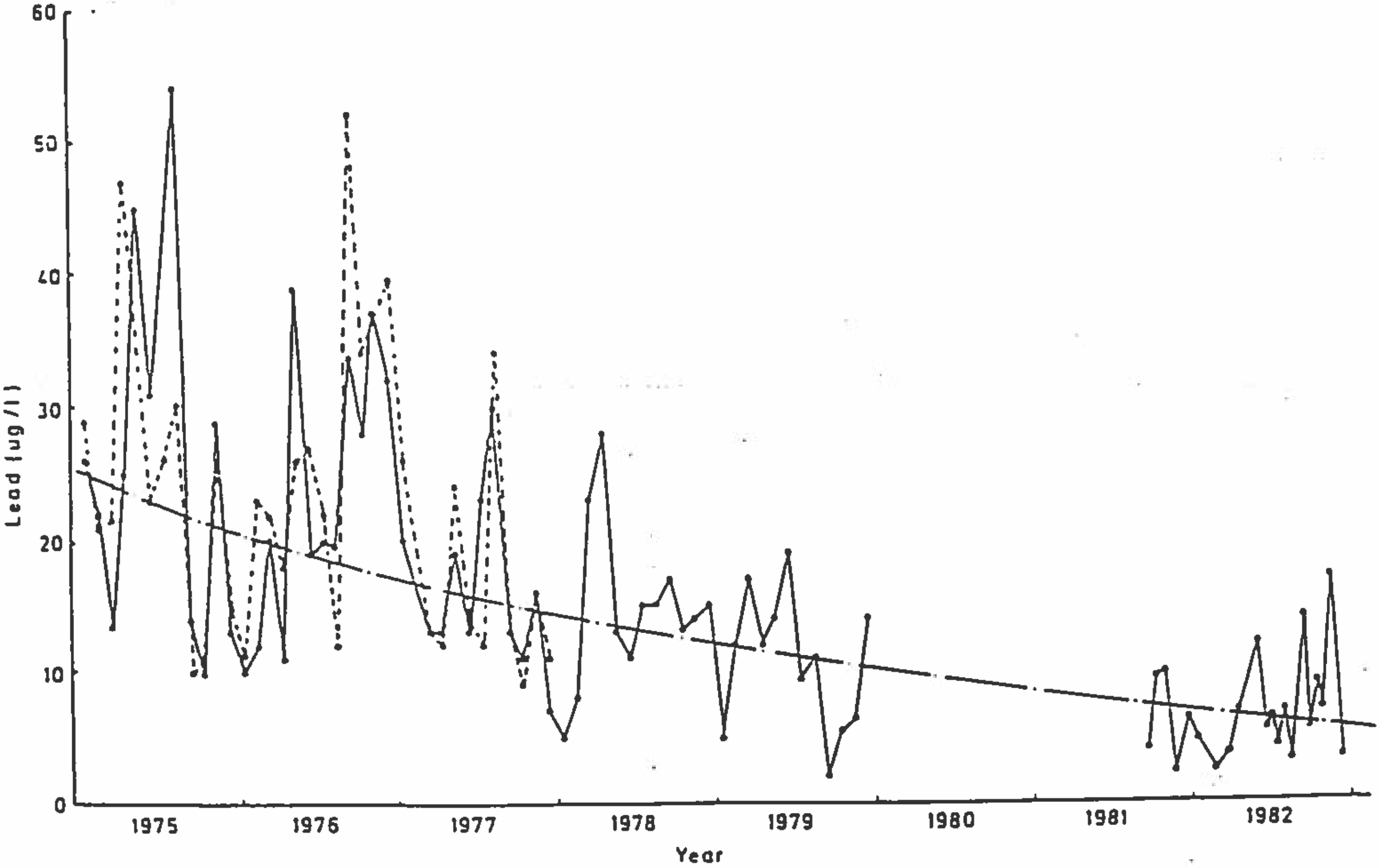


Figure II.C.1. Annual volume-weighted concentrations and amount of precipitation for the HBEF during 1964 - 1982. The dashed lines represent linear regressions significant at $p < 0.05$. Correlation coefficients (r) are $H^{+} = -0.69$, $NH_4^{+} = -0.51$, $SO_4^{=} = -0.77$ and $Cl^{-} = -0.56$.


60
50
40
30
20
10
0
Lead (μg/l)
1975
1976
1977
1978
1979
1980
1981
1982
Year

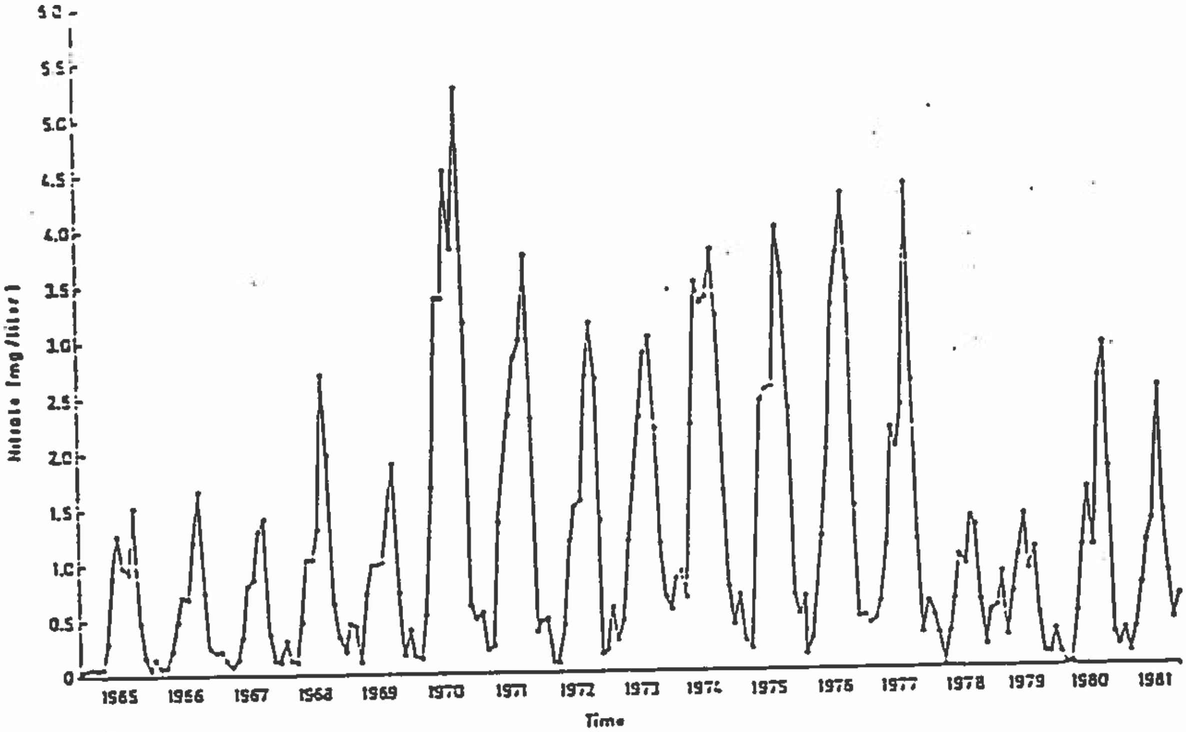


Figure II.C.3. Volume-weighted monthly concentrations of NO_3^- in streamwater from W6 at the HBEF (after Likens 1984).

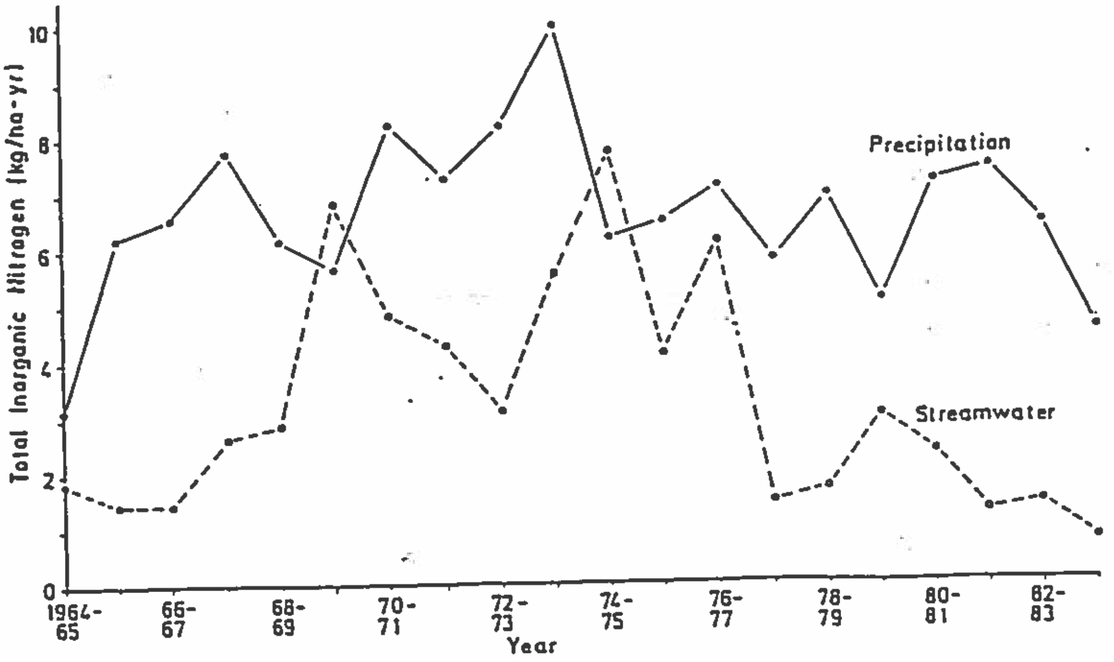


Figure II.C.4. Annual volume-weighted concentrations of total inorganic nitrogen ($NH_4^+ + NO_3^-$) in precipitation and streamwater for W6 at the HBEF (after Likens 1984).

input/output budgets. Without knowledge of this variability, inaccurate conclusions regarding element cycling and ecosystem processes could easily be made.

Long-term monitoring of manipulated ecosystems has also resulted in important information regarding element transfer and drainage water chemistry (Figure II.C.5). In 1965 all trees in W2 were felled, left in place and herbicides were applied to prevent regrowth (Likens et al. 1970, Likens et al. 1978). This treatment was used to separate the effects of vegetation uptake from decomposition on the transport of elements through drainage water. A large release of NO_3^-, H^+, basic cations and Al were evident in streamwater during and immediately following deforestation and herbicide treatment (1966-1968 The initial period of element loss was followed by a dramatic decline in stream NO_3^- and H^+ (increase in pH) during vegetation recovery, relative to the reference watershed. These observations suggest that during early regrowth the forest ecosystem effectively retained NO_3^-, which resulted in alkalination of stream waters. After longer periods of regrowth (e.g., $\approx$ 75 years for the HBEF) the ecosystem is less efficient in retaining NO_3^- (Vitousek and Reiners 1975) and coincident with lower pH in streamwater.

Decreases in streamwater pH during devegetation and increases in streamwater pH during regrowth coincided with retention and release of SO_4^{2-}, respectively, relative to the reference watershed (Figure II.C.5). These observations have lead us to hypothesize that SO_4^{2-} in stream and mineral soil solutions is regulated by pH-dependent adsorption on free Fe and Al surfaces within soil (Nodvin et al. 1987; Fuller et al. 1987). Acidifiction of drainage water protonates these variable charge surfaces facilitating SO_4^{2-} retention, whereas increases in soil solution pH due to alkalination reduces anion adsorption resulting in SO_4^{2-} desorption and increases in drainage water concentrations.

Our long-term monitoring of bulk precipitation and streamwater chemistry have lead us to the following hypotheses:

Hypothesis C.1.1 Concentrations of SO_4^{2-} in precipitation will continue to decrease coinciding with projected declines in SO_4^{2-} emissions in the northeastern U.S.

Hypothesis C.1.2 Concentrations of Pb in precipitation will continue to decline in response to recent federal legislation regulating Pb in gasoline.

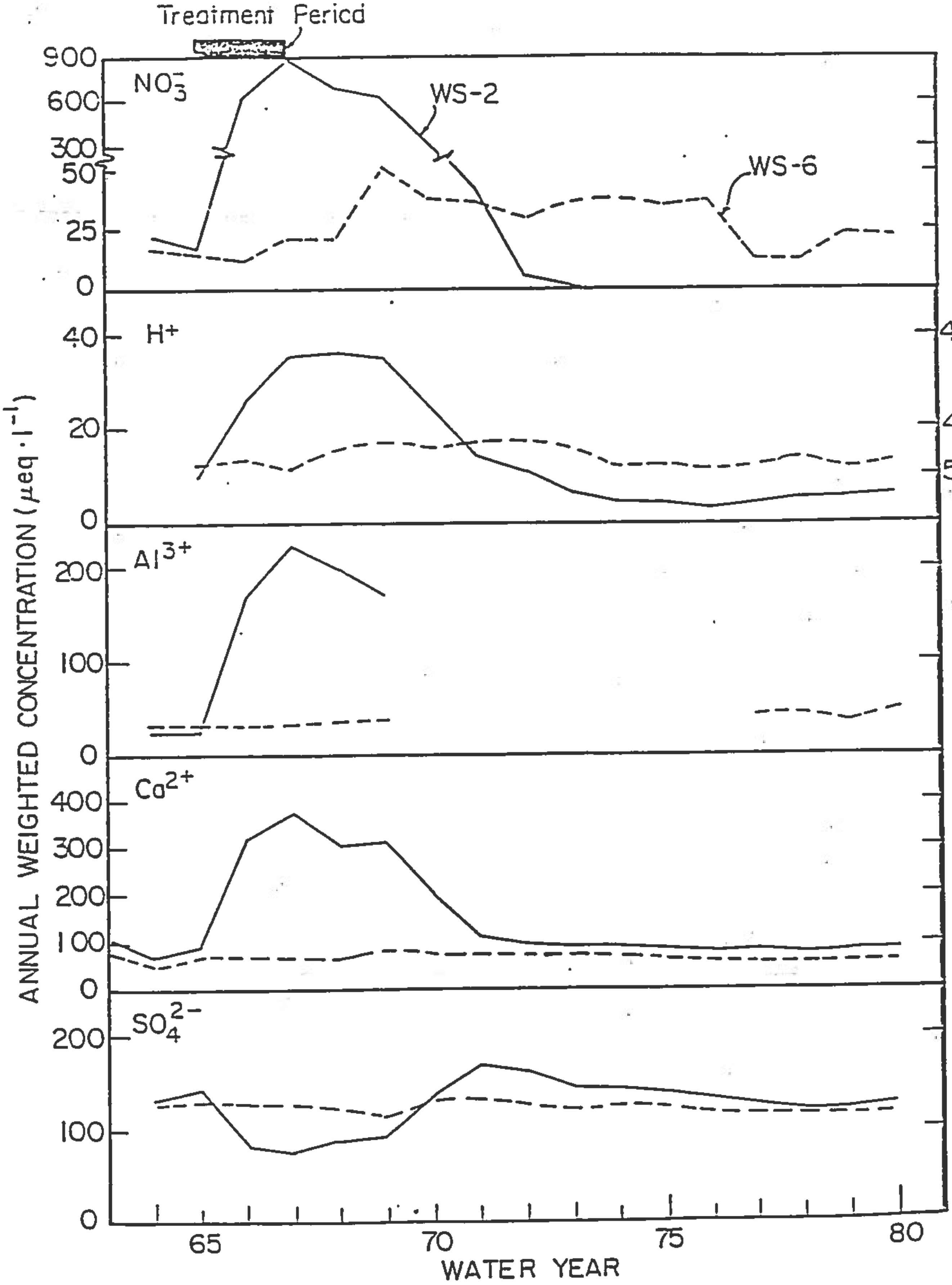


Figure II.C.5. Annual weighted stream concentrations of selected water chemistry parameters in the treated (W2 devegetation and herbicide application) and reference (W6) watersheds. Note that analysis of Al was discontinued in 1969 and resumed in W6 in 1977.

Hypothesis C.1.3 Although long-term trends in precipitation SO_4^{2-} are evident, no consistent temporal patterns in stream SO_4^{2-} will be evident due to year-to-year variations in precipitation loading, climate and the soil buffering of SO_4^{2-}.

Hypothesis C.1.4 The extent of element loss from watersheds through drainage water is closely linked to disturbance and patterns of forest growth.

To test these hypotheses element budget studies will be continued on seven watersheds (W1,W2,W3,W4,W5,W6,W101). Statistical analyses have shown that weekly sampling of precipitation and streamwater are adequate for all elements except P, C and Fe, whose concentrations are strongly related to discharge (e.g. Johnson et al. 1969). Measurements of total P and DOC, however, will be continued on streamwater and precipitation samples. Analysis of streamwater and discharge data will be conducted to refine concentration-discharge relationships and improve mass balance calculations for these elements. Element balance studies will include the collection of particulate matter output from W5 and W6, particularly that material collected in ponding basins at the gauging weirs. These data will also support the organic debris dam studies discussed previously (see Section II.B.4).

Trace metal studies will also continue on W6 and W5. These data will be used to further our understanding of trace metal flux and cycling in undisturbed forests and to study the effect of deforestation on trace metal relationships established for forested ecosystems (Simone et al. 1987).

In addition, analyses of long-term trends in precipitation and streamwater chemistry will continue so that the effects of changes in atmospheric emissions (e.g. SO_4^{2-}, Pb) on precipitation loading and the biogeochemistry of northern hardwood-conifer ecosystems can be evaluated. These analyses may serve as an early warning system to forecast changes in the biogeochemistry of forested ecosystems in the northeastern U.S.

Finally, data obtained from the monitoring of precipitation and streamwater chemistry will be coupled with studies of element transfer associated with soil processes, decomposition and vegetation uptake to assess mechanisms regulating element transfer/concentration, element-element linkages and the effects of disturbance and succession on the biogeochemistry of a northern hardwood-conifer ecosystem (discussed in section II.C.5).

II.C.2 Dry Deposition Inputs and Chemistry

Objective: To determine the seasonal characteristics of nitrogen, sulfur, and basic cation inputs by dry deposition to the HBEF.

Background, Hypotheses and Research Approach

Recent evidence suggests that dry deposition is an important component of the total atmospheric inputs of nitrogen and sulfur to ecosystems (Mayer and Ulrich 1978, Sehmel 1980, Huebert and Robert 1985, Lindberg et al. 1986). Quantifying dry deposition is, therefore, very important for the development of ecosystem element budgets and for questions concerning linkages between forest health and atmospheric deposition of acids.

For example, the most recent published nitrogen budget for the HBEF suggests that in the 75+ year-old forest, nitrogen accumulation in forest biomass and export in stream water exceeds that entering the forest in bulk precipitation (Bormann et al. 1977). This pattern appears to be a common conclusion from whole ecosystem studies. At the HBEF, nitrogen fixation in undisturbed areas (i.e. not W2, W5, W101) does not seem to account for the discrepancy (Roskoski 1977, Homann et al. unpublished ms). A portion of this nitrogen input may be obtained from deep soil horizons that were previously thought not to interact effectively with the vegetation (i.e. soil "mining", see for example Melillo 1981). Research currently under way at the HBEF (Appendix II.B) is designed to investigate this component.

Dry deposition of nitrogen gases and particulates could also explain a portion of this discrepancy (Sehmel 1980, Huebert and Robert 1985, MacRae and Russell 1984). Various inputs include NH_4^+ and NO_3^- bearing particulates, nitric oxide and nitrogen dioxide (commonly referred to as NO_x), and nitric acid vapor (HNO_3).

There are few data to substantiate the importance of nitrogen deposition to hardwood forests. One approach to quantify the magnitude of nitrogen dry deposition is to estimate the difference between bulk (wet) deposition and throughfall deposition. Unlike the basic cations, which often leach from vegetation, nitrogen is conserved by vegetation and may even be assimilated (Parker 1984). Thus, measurements of throughfall less bulk precipitation may well be an underestimate of dry deposition inputs. Lovett (1983) has made one estimate based on throughfall and bulk precipitation data at the HBEF (Eaton et al. 1973) and concluded that the dry deposition inputs could be 6.6 kg N ha^{-1} during the growing season alone. The magnitude of this dry deposition estimate is comparable to the long-term average annual precipitation input at the HBEF (6.5 kg N ha^{-1} yr^{-1}) and would supply 42% of the unexplained accumulation of nitrogen in living and dead biomass. Using a more rigorous approach, Lovett and Lindberg (1986) determined that dry deposition of NO_3^- alone was about 4.8 kg N ha^{-1} yr^{-1} or 50% of the total wet plus dry deposition at Walker Branch at Oak Ridge, Tennessee. There is, therefore, substantial evidence to suggest that this vector of input is important to the nitrogen budget at the HBEF.

The current HBEF budget for sulfur indicates that precipitation inputs are 12.7 $kg \cdot ha^{-1} \cdot yr^{-1}$ while dry deposition is 6.1 $kg \cdot ha^{-1} \cdot yr^{-1}$ and weathering inputs are 0.8 $Kg \cdot ha^{-1} \cdot yr^{-1}$ (Likens et al 1977). While wet deposition appears to be accurate, estimates of dry deposition and weathering inputs are considerably more tentative and could be greatly improved through more rigorous determination of dry deposition inputs. Accurate inputs of sulfur loading through dry deposition are critical to the development of H^+ budgets and assessments of processes contributing to the acidification of soil and drainage waters (see II.C.5 Effects of disturbance of the H^+ cycle).

There is abundant interest at present in the relationships between forest health and atmospheric inputs of nitrogen and sulfur. For example, Friedland et al. (1984) and Nihlgard (1985) have suggested that exogenous input of nitrogen to high-elevation forests may be so large that it interferes with physiological preparation of the trees for winter cold stress. Winter frost damage due to over-fertilization of nitrogen is one explanation that has been proposed for the large scale dieback of spruce in the U.S. and Europe (Friedland et al. 1984). Nitrogen inputs by all mechanisms, including dry deposition, would contribute to this problem.

Atmospheric inputs of nitrogen and sulfur are both significant sources of acidity to ecosystems. When oxidized, gases such as NO_x and SO_2 transfer acidity directly to forests as nitric and sulfuric acid. Canopy dynamics modify this acidity and are important in the regulation of throughfall chemistry (Lovett 1983). Strong acid inputs can also have indirect effects on the biogeochemistry of forested ecosystems through mobile anion leaching (Johnson 1984). Atmospheric deposition of NO_3^- and SO_4^{2-} not only contribute to the H^+ loading but facilitate the mobilization of basic cations and Al, resulting in elevated concentrations of these constituents in surface waters (Johnson et al. 1981). Dry deposition of nitrogen and sulfur represent a potentially important component of the biogeochemistry of the HBEF. Therefore, we have developed the following hypotheses concerning dry deposition inputs to the HBEF.

Hypothesis C.2.1 The deposition of NO_x and HNO_3 vapor in ambient air represent important atmospheric sources of nitrogen to the forest ecosystem.

Hypothesis C.2.2 Sulfur dioxide (SO_2), the dominant form of gaseous sulfur deposited on the canopy, is quantitatively an important source of sulfur to the ecosystem.

Hypotheses C.2.3 Deposition of particulate nitrogen and sulfur (as NH_4^+, NO_3^- and SO_4^{2-}) on leaf surfaces and are important inputs to the ecosystem.

We propose to measure the concentrations of gaseous NO_x, HNO_3 and SO_2 and particulate N and S at the HBES meteorological monitoring site (see Appendix I.B). Initially, we will estimate fluxes of gases to the forest canopy from literature values of deposition velocities. We will estimate the flux of particulate nitrogen, sulfur and basic cations based on a combination of air filtration and deposition to surrogate surfaces deployed in the forest canopy.

Specific methods - dry deposition

Gases: Methods exist to estimate the concentrations of each of the gases we propose to measure. However, several alternative methods exist and there is not yet a consensus on the best method for each component. As a consequence, we will need to do some developmental work to determine the methods most appropriate for our needs and logistical constraints. For reasons of consistency, we plan to maintain compatibility with the Mountain Cloud Chemistry Program site on Mt. Moosilauke, a regional network site that is adjacent to our site (see below).

We will measure the concentration of HNO_3 with a dual filter pack (Huebert and Robert 1985). In this technique, an inert (teflon) filter precedes a nylon filter in an inert (teflon) filter holder. The teflon filter retains particulates and passes HNO_3. The nylon filter quantitatively absorbs the HNO_3 gas. A pump and a mass flow monitor/controller are used to pump a known volume of gas through the filters. This system is "off-the-shelf" technology and will not require special development. The filters are then washed and desorbed in water (teflon filter) or 0.1 N NaOH (nylon filter) and the water analyzed for NO_3^- and NH_4^+. Given the nitrogen concentration in the wash solution and volume of air filtered, air concentrations of both particulates and HNO_3 can be calculated.

The dual filter-pack technique has been criticized because particulates on the forefilter may degas to the second filter, causing a sampling artifact (Appel et al. 1981). Since particles and gases have very different deposition velocities (Sehmel 1980) this artifact will overestimate deposition. Kelley et al. (1987) concluded that this artifact does not introduce significant errors. Since it is possible to remove the particulates prior to filtration with a "denuder", the potential for bias can be tested. This procedure will be incorporated into our QA/QC program.

We will test alternative methods to measure NO_x and SO_2. Sulfur dioxide may be collected on K_2SO_3 impregnated filters or by bubbling air through wet chemical traps in an impinger apparatus (Lindberg et al. 1986). Ideally we would develop a single sampling apparatus that allows for the collection of all of the gaseous components of interest under field conditions. If we find that this approach is not a practical solution, we will use commercially available NO_x and SO_2 monitors. The disadvantage of these instruments is that instantaneous data would be provided, rather than preferred time-averaged concentrations.

<u>Particles</u>: We suspect that particle deposition may be important for some elements. Small particles (<2 μm diameter) are efficiently collected by the teflon pre-filter in the filter pack apparatus described above. The filters will be extracted in water and concentration of ions in the extractant solution will be used to calculate atmospheric concentrations of nitrogen and sulfur in small particles. We will use literature values of deposition velocities for small particles to determine deposition fluxes.

Larger particles are inefficiently collected by standard air filtration techniques but their deposition to artificial surfaces can be assessed directly (Lindberg and Lovett 1985). We will expose polycarbonate petri dishes above the canopy during dry periods and extract the collected particles in water. These artificial surfaces collect primarily sedimenting particles (those that fall onto the surface by gravity) which are generally greater than 3 μm in diameter. We will use the "calcium scaling" technique (Lovett and Lindberg 1986) to convert large particle collection rates on these surfaces to large particle deposition rates for the entire canopy.

We are aware that there may be a certain amount of overlap between the size ranges of particles collected by air filtration and by artificial surfaces. The two techniques together will overestimate total particle deposition to the canopy if there is substantial overlap. Nevertheless, these are the most appropriate methods available to us for field use. In addition, they provide estimates of particle deposition rates that can be easily updated when better data are available on the potential overlap in size range collection.

Future Research and Collaboration

The research described in this section is part of a larger effort to quantify the importance of atmospheric deposition at an ecosystem and ultimately landscape level.

Our initial efforts will be to create the capability to measure the concentrations of nitrogen and sulfur compounds in the atmosphere that we believe are important in dry deposition and to make indirect estimates of their flux rates to the forest canopy based on literature values of deposition velocities.

Fluxes estimated in this way will provide an adequate estimate of the importance of dry deposition relative to other element inputs to the HBEF. However, deposition velocities to forest canopies for the compounds that are of interest to us are poorly quantified at present. In the future we plan to investigate alternative methods to measure gas and particle fluxes directly. Given the gas and particle concentration data we propose to collect here, future direct measurements of fluxes will allow us to more accurately calculate deposition velocities that are specific to the northern hardwood forest type.

We plan to submit a separate proposal to study relationships between measured dry deposition, precipitation and throughfall fluxes and various landscape characteristics. It is unreasonable to expect that a single dry deposition measurement station will be adequate to characterize whole-ecosystem or whole-landscape dynamics. However, it is prohibitively expensive to install many such stations in one study area. Building on information obtained form our LTER dry deposition research, we will propose separately to study methods to extrapolate that information to a landscape scale.

In addition, we plan to maintain compatibility with other regional deposition measurement networks so that our data may be regionalized. In particular, we will maintain close ties with the Mountain Cloud Chemistry Program (MCCP) on Mt. Moosilauke, immediately adjacent to our site (HBEF). The MCCP site is in a mid-elevation spruce-fir stand. We propose to install our station in a lower elevation, hardwood site so that comparison between these two sites can be used to assist in regionalization of deposition information.

Finally, the dry deposition measurement program we propose here will complement the intensive and long-term biogeochemical monitoring program that is already active at the HBEF. With the addition of this capability we will be able to compare wet deposition, dry deposition, throughfall, stream chemistry, forest growth, and as a consequence improve calculations of whole-ecosystem input/output budgets. In addition, estimates of dry deposition obtained in this study will be compared to values obtained by difference from throughfall and bulk (wet) deposition monitoring. Given the capabilities to calculate whole-ecosystem budgets and to measure several components of atmospheric deposition, both wet and dry, we believe that the HBEF would be an excellent site for a future, rigorous comparison of methods and mechanisms of atmospheric deposition.

II.C.3 Hydrologic Modeling

Objective: The objective of the proposed research in hydrologic modeling is to modify the hydrologic model, BROOK, to facilitate solute transport calculations within soil and to initiate development of a comprehensive solute transport model.

Success in improving physical aspects of the model should be achieved within the time frame of this study, but chemical modeling must be considered as continuing long-term research.

Background and Research Approach

In watershed research, hydrologic simulation models provide a quantitative summary of current knowledge, and allow extrapolation of results to other sites and to hypothetical situations. Simulation models separate watershed function into component processes and provide physically meaningful mathematical expressions for how each process works. Such models are widespread in physical hydrology and procedures for model development using water budgets are generally accepted (Proceedings 1982). Recently, mathematical representations of biogeochemical processes have been coupled to hydrologic models to simulate the chemistry of drainage waters within forested watersheds (ILWAS 1983).

The hydrologic model, BROOK, was developed for small, forested watersheds, and was based on research at the HBEF (Federer and Lash 1978). BROOK simulates daily streamflow and changes in soil and snow water from inputs of daily precipitation and temperature. It has been widely used for teaching and research in both eastern North American and Europe (e.g. McKenna 1981; Focazio 1984; Laudelout et al. 1984; Forster and Keller 1986). Although some attempts have been made through the HBES to incorporate element cycling and streamflow chemistry into BROOK, the results have not yet been satisfactory.

To successfully model the chemistry of drainage waters, subsurface saturated flow must be incorporated to account for spatial variation of soils. At present only saturated overland flow, unsaturated subsurface flow and groundwater flow are included in BROOK (terminology of Whipkey and Kirkby 1978). Hydrologic processes such as return flow and saturated subsurface flow need to be added, as well as the effects of macropore (pipe) and piston flow (Bevan and Germann 1982). Controversy exists over the specific definitions and relative importance of these various flow processes. These issues can only be resolved by a combination of modeling and field experiments. The field measurements described later in this proposal (II.C.4 Hillslope hydrology - Dynamics of source areas) will provide valuable information for model development. Additional research on source area mapping (Dr. A. Federer), extensive soil water monitoring by time-domain reflectometry (Dr. S. Hamburg) and flow in isolated soil blocks (Dr. R. Pierce) is currently underway at the HBEF. Information from this research will also be used to develop and calibrate the model.

Other components of the BROOK model will also be improved through research proposed here. Incorporation of a root zone layer will facilitate modeling chemical transformation and transport. The approach used will be similar to the transpiration model of Federer (1979) and estimates of soil water available for transpiration will also be improved. The BROOK availability constant, and the estimate of potential evapotranspiration will also be modified as described by Federer (1982). These changes will be made so that BROOK will remain comprehensible to other users, while still reflecting real hydrological processes. Parameters must remain physically meaningful and easily approximated. Continued documentation of BROOK for external users is essential.

As a long-term objective of this research, we will incorporate chemical submodels into the modified version of BROOK. Modeling efforts will try to avoid the complexity and unestimatable parameters of the ILWAS (1983) model, while attempting to accurately depict relevant processes. Considerable effort has been made in recent years in chemical process modeling at the HBEF. Fuller et al. (1987) have developed a kinetic model simulating S transfer between soil pools at the HBEF, while Schecher and Driscoll (1987) have developed a chemical equilibrium model which simulates the solubility and speciation of Al, as well as pH-dependent adsorption of SO_4^{2-} and F^-. Research is currently underway to develop models describing organic acid equilibria, organic-metal complexation and cation exchange processes. These submodels will be incorporated into BROOK as a first-step towards developing a comprehensive solute transport model. Parameter selection and model calibration will be developed both from long-term streamflow, soil solution and stream chemistry records and from the research on hillslope hydrology-dynamics of source areas (II.C.4 described latter). Modeling will begin with simplified systems such as soil blocks and individual lysimeter locations (profiles), and then be expanded to whole watersheds.

Both for physical and chemical aspects of BROOK, model calibration will utilize streamflow data from W3 and W6 prior to 1977, the same period used in earlier BROOK development. Verification will be done with later data and data from experimentally manipulated watersheds (Appendix I.A), using methods described by Federer and Lash (1978). Validation or acceptance of any new model must remain the province of others.

II.C.4 Hillslope hydrology - Dynamics of variable source areas

Objective: The objective of this research is to better understand the hydrologic linkages between uplands, source areas, and stream flow and the relationships of these linkages to element transport.

We propose to quantify changes in the extent and duration of source areas on first or second order streams over long-term, annual and storm-event time scales and to study linkages between hillslope hydrology and biogeochemistry with a hydrologic process model (BROOK).

Background, Hypotheses and Research Approach

Early models of water yield from watersheds considered hillslopes adjacent to streams as homogeneous source areas in three dimensions. Although adequate correlations may be made between basin size and various geomorphological and hydrologic properties of streams (Leopold et al. 1964), the assumption of watershed homogeneity is misleading for considerations of actual subsurface flow in forest soils and the biogeochemical processes that affect the chemical characteristics of drainage water.

More recent models of runoff generation such as variable source areas (Hewlett and Hibbert 1967), partial source areas (Dunne and Black 1970) and macropore flow (Mosley 1979) all acknowledge spatial variability in hillslope response to storm events. There is general consensus that streamflow in steep forested watersheds, typical of the HBEF, is largely derived from subsurface flow, or at least water that has initially infiltrated prior to becoming surface runoff (Pearce et al. 1986). There is less agreement on the relative importance of different subsurface flow mechanisms under varying flow conditions. Central to all current theories of runoff generation, however, is the concept of source areas which vary in size from storm to storm. These source areas directly contribute to surface runoff and are a function of storm intensity and duration, topography, soil characteristics and antecedent soil moisture conditions. The remainder of the watershed produces base flow which maintains the high water content of source areas.

It is evident that although the specific subsurface flowpaths of varying flow conditions have not been identified, changes in flowpaths can result in differential expression of watershed variability. Base flow through the lower mineral soil, for example, would be chemically different than interflow through a spodic horizon. Stream chemistry, therefore, reflects the spatial variation of watershed characteristics through temporal variations of processes which generate surface runoff.

Research on the linkage between subsurface flow dynamics and biogeochemical processes is still in preliminary stages. An understanding of this linkage, however, is necessary for our planned development of the process-oriented computer model BROOK (see section II.C.3 Hydrologic modeling) which will provide valuable insights into questions of ecosystem disturbance and recovery.

Our hydrologic and biogeochemical research at the HBEF have lead us to the following hypotheses concerning hillslope hydrology and dynamics of source areas:

Hypothesis C.4.1 The quantity and composition of streamflow at the HBEF is mediated by patterns of subsurface flow.

Hypothesis C.4.2 Temporal variations in subsurface flow patterns can be estimated from information on daily or weekly water budgets based on simple measurements of precipitation and temperature.

Hypothesis C.4.3 Temporal variations in stream chemistry are dependent upon watershed characteristics such as soil depth and chemistry within varying source areas.

To test these hypotheses, we will deploy a grid of piezometers and lysimeters to define the shape, position, depth and extent of the saturated zone that serves as a source area for an adjacent stream in an undisturbed hillslope, just west of the HBEF reference watershed (W6). Piezometers will be deployed in a grid whose shape, size and orientation will depend on the topography of the site selected. Our ideal design will be an 8 x 8 grid (i.e. 64 node points). Water level within piezometers will be monitored continuously using a data logger. Both tension and zero-tension lysimeters (Appendices I.B, I.C) will be installed below the Oa and within the Bs2 horizon along a transect at eight locations within the piezometer grid. Triplicate lysimeters will be installed at each lysimeter site for a total of 96 lysimeters. The two lysimeters types (tension and zero-tension) will be used to facilitate both integrated and event sampling and to allow comparisons since previous work has shown that these collectors sample different types of water with different chemical characteristics (Haines et al. 1982). Tension lysimeters sample under less than saturated conditions, while zero-tension lysimeters only sample under conditions of near saturation. Observations of water collection by piezometer/zero-tension lysimeters and tension lysimeters will provide qualitative information on the extent of source areas.

Soil samples will be collected during lysimeter installation and analyzed for a variety of hydrologic, physical and chemcial characteristics (Appendix I.C). Throughfall chemistry will be monitored beneath the canopy as part of the HBEF throughfall monitoring program (Appendices I.B, I.C). In addition, tipping bucket rain gauges will be installed with throughfall collectors and monitored by the data loggers to quantify inputs to the forest floor. Piezometer/lysimeter installations will be monitored on an event-basis during the period just prior to spring snowmelt until the onset of snowpack accumulation (typically early December) and occasionally during the winter. An event will be defined as any precipitation observed in collectors that exceeds the minimum volume necessary for chemical analysis (100 ml). If no such events occur over a prolonged period, we will sample every two weeks. Water levels will be recorded continuously in the piezometer with the aid of data loggers, while lysimeters will be collected during each sampling.

Samples will be collected and discharge estimated at three points in the stream that is influenced by the variable source study area. At each of the stream sites to be sampled (upstream, adjacent to and downstream of the source area) a Stevens Type F stage recorder and a Manning automatic collector will be installed. The automatic collector will be programmed with a data logger to initiate sampling on a 20 minute interval during the rising limb of the hydrograph and two hour intervals on the falling limb. Periodic discharge measurements will be related to stage measurements and combined with chemical measurements to estimate mass discharge for elements of interest. Water samples collected will be analyzed for all major solutes (Appendices I-B, I-C).

Through this research program we will monitor the expansion and contraction of the source area, and associated changes in the chemical composition of drainage water. Stream hydrographs during hydrologic events will be compared to data obtained from the piezometer field to assess the role of source areas in mediating streamflow. In addition, the chemical composition of streamwater will be compared to soil solution characteristics within the source area to better understand hydrologic flow paths and the processes regulating solute concentrations in streamwater. Ultimately, information resulting from this study will be used to improve the formulation of the hillslope hydrologic model, BROOK (see II.C.3 Hydrologic modeling). Continued monitoring of hydrologic flow paths will also be useful in evaluating soil development processes and changes in subsurface flow mechanisms through ecosystem disturbance and recovery.

II.C.5 Effects of disturbance on the H^+ cycle

Objective: The objective of this research is to use the H^+ budget approach to integrate studies of element cycling and facilitate an understanding of the response of hardwood-conifer watersheds to disturbance.

Background, Hypotheses and Research Approach

Integration of biogeochemical studies and assessments of ecosystem response to disturbance have long been hindered by failure of researchers to consider element-element interactions. Recently the H^+ budget approach has been developed as a tool to characterize ecosystem function. Virtually every pathway of element transfer is coupled to the H^+ cycle, including atmospheric deposition, weathering, protonation/deprotonation of organic and inorganic carbon, adsorption/desorption at soil surfaces, biomass assimilation/degradation as well as drainage of soil and streamflow (van Breemen et al. 1983; Table II.C.1). Thus H^+ budgets serve to couple element cycles through the stoichiometry of biogeochemical reactions.

Since the principles of cation/anion budgeting were first proposed by Pierre et al. (1971), several H^+ budgets have been developed for forested ecosystems (e.g. Sollins et al. 1980, Anderson et al. 1980, van Breemen et al. 1984). In a recent review of the principles and applications of the H^+ budget, Binkley and Richter (1986) concluded that this approach provides a stimulating direction for integrating ecosystem biogeochemistry. Precise characterization of these budgets may be limited by accurate documentation of several key processes; however, the wealth of data at the HBEF has greatly faciliated

Table II.C.1 Proton budget of the HBEF under current conditions (a) and shortly (0-3 years) after devegetation and herbicide treatment (b) (after van Breemen et al., 1984)

System	H^+ sources ($kmol \cdot ha^{-1} \cdot yr^{-1}$)						H^+ sinks ($kmol \cdot ha^{-1} \cdot yr^{-1}$)				
	atmos. inputs	N-transfer	acid deprot.	biomass	weathering	total sources	N-transf.	biomass	weathering	stream export	total sinks
a) Current HBEF	1.3	0.1	0.1	1.0	0.1	2.6	0.0	0.2	2.2	0.1	2.5
b) HBEF after devegetation	1.0	11.2	0.0	0.8	2.1	15.1	3.1	5.9	4.3	0.6	13.9

H^+ sources are tabulated as 1) atmospheric deposition of mineral acids, 2) nitrogen transformations, net ammonium accumulation less net nitrate loss, 3) deprotonation of H_2CO_3 and organic acids, 4) accretion of cations in vegetation and forest floor and 5) net weathering of anionic components. H^+ sinks include 1) nitrogen transformations, net nitrate accumulation less net ammonium loss, 2) accretion of anions in vegetation and the forest floor, 3) net weathering of cationic components in soil and 4) export of free protons from the ecosystem in drainage water.

Table II.C.2 General reactions that result in proton transfer

Proton Source	Reaction	Proton Sink
assimilation of cations	$M^{n+} + nR\text{-}OH \rightleftarrows (R\text{-}O)_nM + nH^+$	mineralization of cations
mineralization of anions	$nH_2O + Rn\text{-}A \rightleftarrows nR\text{-}OH + A^{n-} + nH^+$	assimilation of anions
dissociation of aqueous acids	$H_nA \rightleftarrows A^{n-} + nH^+$	protonation of aqueous anions
oxidation	$Red + O_2 + H_2O \rightleftarrows Ox + H^+$	reduction
formation of secondary cationic minerals	$M^{n+} + \frac{n}{2} H_2O \rightleftarrows \frac{n}{2} M_{2/n}\ O + nH^+$	weathering of metallic oxide components
weathering of anionic components	$H_nA \rightleftarrows A^{n-} + nH^+$	formation of secondary anionic minerals

where M^{n+} is a metallic cation, R- is an ionic functional group, A^- is an anion, Red is the reduced form of a substance, Ox is the oxidized form of a substance, $M_{2/n}\ O$ is a metallic component, and n is a stoichiometric coefficient.

the development of H^+ budgets. The use of this tool within the framework of long-term measurements at the HBES will be extremely valuable for interpreting biogeochemical changes following ecosystem disturbance and through ecosystem development.

We have recently summarized the processes which result in H^+ flux to ecosystems (Driscoll and Likens 1982; van Breemen et al. 1983; van Breemen et al. 1984). In this analysis, ecosystem H^+ sources and sinks are tabulated by mass-balance calculations. Important transformations which participate in the H^+ cycle of ecosystems are summarized in Table II.C.2.

The H^+ budget for an undisturbed watershed at the HBEF indicates that 49% of the total H^+ sources may be attributed to atmospheric inputs of acidic substances and elevated concentrations of free H^+ occur with the outflow of drainage water (Driscoll and Likens 1982, Table II.C.2). These calculations also suggest that net accumulation of forest biomass and forest floor results in net production of H^+. While acidic deposition appears to be a significant source of H^+ to the HBEF, land disturbance can also radically alter the H^+ cycle. The H^+ budget compiled for a three year period in W2, following devegetation and herbicide treatments (Table II.C.2) indicates that mineralization of the forest floor followed by nitrification resulted in substantial H^+ production (Figure II.C.5). This H^+ loading was largely neutralized by weathering, mineralization of cationic components in the forest floor and NO_3^- reduction. Unfortunately, we do not have the complete data necessary to compile a H^+ budget for the recovery period following the devegetation of W2. Indirect evidence of the effects of forest regrowth on the H^+ cycle, however, are available through stream chemistry data (Fig. II.C.5). The alkalinization of stream water (increase in pH) in W2 relative to W6 during the early period of regrowth appears to be largely due to the efficient retention of NO_3^-. Release of SO_4^{2-} in W2 from pH-dependent desorption of SO_4^{2-} serves to acidify the drainage water and restrict the extent of surface water alkalinization. Because release of basic cations is the dominant process neutralizing H^+ inputs, the long-term response of basic cation pools to deforestation disturbance is particularly relevant. Regrowing vegetation might serve to deplete the pocl of readily available basic cations on exchange sites resulting in the acidification of soil and drainage waters, and increasing ecosystem sensitivity to atmospheric deposition of strong acids. Alternatively the alkalinization of drainage waters by NO_3^- retention might increase cation exchange capacity as well as the affinity of basic cations for exchange sites within soil.

Although disturbances such as atmospheric deposition and deforestation have profound effects on the H^+ budget of forested ecosystems, little is known about the specific transformations involved in the response to these stresses. As a result, we have formulated a number of pertinent research hypotheses:

Hypotheses C.5.1 Long-term changes in atmospheric deposition and forest growth have had a marked effect on H^+ transfer within the HBEF.

Hypotheses C.5.2 Dry deposition represents an important pathway of external H^+ loading to the HBEF.

Hypothesis C.5.3 As drainage water is transported through the soil, a variety of hydrologic, biologic and chemical processes serve to modify its acid/base status.

Hypothesis C.5.4 Biological uptake of NO_3^- during vegetation regrowth causes an increase in drainage water pH and enhanced affinity of basic cations for cation exchange sites. These processes serve to mitigate soil and drainage water acidification associated with regrowth of forest ecosystems.

To test these hypotheses we will make use of the HBES data on precipitation inputs, stream water chemistry (II.C.1, Appendices I.B,I.C) soil and soil solution chemistry (Appendices I.B,I.C), element accumulation in vegetation (II.A.3, Appendices I.B,I.C), as well as proposed studies on dry deposition (II.C.2) and hydrologic flowpaths (II.C.3, II.C.4). To facilitate our evaluation of the effects of deforestation disturbance on the acid/base status of soil and drainage water we plan additional soil and soil solution monitoring of W2.

The response of the HBEF to long-term changes in atmospheric deposition will be assessed by formulating H^+ budgets for the reference watershed (W6) for the years 1966, 1977, 1982, 1987 and 1992. These years correspond with the long-term monitoring of biomass in W6 (Table II.C.3) and span a period of marked change in precipitation loading (see II.C.1 Long-term trends in precipitation and stream chemistry). The previous H^+ budget

Table II.C.3 Periods of Ongoing and Proposed LTER Element Cycle Monitoring for Reference (W6) and Deforested (W2,W5) Watersheds at the HBEF

Monitoring Program	W6 (reference)		W2 (devegetation and herbicide treatment 1966-1968)		W5 (whole tree harvest 1983)	
	ongoing	LTER	ongoing	LTER	ongoing	LTER
Precipitation Chemistry	1963-1988	1988-1992	1963-1988	1988-1992	1963-1988	1988-1992
Stream Chemistry	1963-1988	1988-1992	1963-1988	1988-1992	1963-1988	1988-1992
Soil Solution Chemistry	1983-1988	1988-1992	———	1988-1992	1983-1988	1988-1992
Biomass	1966,1977 1982,1987	1992	1966,1970 1971,1973 1979	1988	1983-1986	1989
Soil Chemistry	———	———	———	1989	1983,1986	1991

for the HBEF (Driscoll and Likens 1982) composited data collected over the period 1964 to 1974. A comparison of H^+ budgets over the period of long-term decline in atmospheric element loading (i.e. SO_4^{2-}, Cl^-, NH_4^+ and basic cations) should yield valuable information on ecosystem response to changes in acidic deposition. The H^+ budget for the HBEF reference watershed (in 1992) will be considerably more accurate than earlier representations due to the availability of detailed data on dry deposition. This analysis will allow for a precise assessment of the role of dry deposition in ecosystem acidification.

The proposed hydrologic modeling should enable us to better understand element transfer and the role of processes contributing to the acidification/alkalinization of soil and drainage waters. We envision that a modified version of BROOK will enable us to estimate water movement through the soil profile, as well as through hydrologic units (i.e. uplands, source areas). These data coupled with soil solution chemistry (from the HBES soil solution monitoring program, Appendix I.B, or the proposed research on hillslope hydrology-dynamics of source areas, II.C.4) will be used to construct H^+ budgets. This analysis should provide considerable insight into element-element interactions within the soil environment.

Finally, we will use the H^+ budget approach as a tool to evaluate the effects of deforestation disturbance on the acid/base status of soil and drainage water. To accomplish this goal, we propose to expand our on-going studies of W2 and W5. Data are currently available for precipitation inputs, stream outputs and biomass accumulation in the HBEF reference watershed (W6), as well as two manipulated watersheds, W2 (devegetation and herbicide treatment 1966-1968, no removal of biomass) and W5 (whole tree harvest 1983; see Appendices I.A, I.B). In addition, soil and soil solution and soil chemistry is available for W5 (Table II.C.3). To facilitate our analysis, we plan to install lysimeters at three elevations in W2, similar to the ongoing monitoring program in W6 and W5 (at the high elevation ledge area ~ 750 m elevation, just below the ledge area ~ 730 m elevation and at a lower elevation ~ 650 m; Appendix I.B) Triplicate tension and zero tension lysimeters will be installed beneath the Oa and Bh, and within the Bs2 horizons. Soil solutions will be monitored at monthly intervals for major solutes (Appendices I.B, I.C).

To assess changes in soil pools due to deforestation, 60 quantitative soil pits will be excavated in W2 in 1989, 21 years after disturbance. In W5 60 quantitative soil pits were excavated prior to the whole-tree harvest in 1983. Quantitative soil pits (60) were also excavated in W5 three years after whole-tree harvesting (Appendix I.B), and through the LTER, soils in W5 will be quantitatively sampled in 1991. Changes in soil element pools will be determined by comparison to values obtained in 1983, for the three and six year periods following disturbance. Finally, through the LTER we will continue to monitor biomass and vegetation element composition in W6, W2 and W5 (see Table II.C.3).

Through this data collection program, H^+ budgets will be constructed for W2 for years 1,2,3,5,11 and 20 following devegetation and herbicide treatment and for W5 for years 1,2,3 and 5 following whole-tree harvesting. These budgets will be compared to those obtained for the reference watershed (W6) to assess changes in element transfer in response to deforestation disturbance. Evaluation of soil solution and soil data will enable us to further quantify the redistribution of elements following clearcutting. Comparison of results from W2 (no vegetation removed) and W5 (all vegetation of commercial value removed) should also provide valuable information on the effects of biomass export on the long-term depletion of elements from the watershed.

II.D RESEARCH COMPONENT D: LONG-TERM STUDIES OF HETEROTROPH POPULATIONS

In temperate forest ecosystems heterotrophs rarely form a major biomass or nutrient pool; however, the importance of heterotroph populations in ecosystem function often far exceeds their relative abundance and may involve both stable, chronic effects as well as infrequent acute effects. The former includes the processing of organic matter by such varied groups as soil microbes, invertebrate detritivores and phytophages and vertebrate herbivores. As a result of periodic population irruptions, some of these populations may act to disturb the ecosystem from its normal trajectory and to switch its structure and function. Long-term research programs are essential to improving our understanding of these dynamics.

The general features of energy flow for the HBEF and associated aquatic ecosystems have been examined and summarized (e.g., Gosz et al. 1978, Likens 1985). Also, the dynamics of certain heterotroph populations, and their role in ecosystem function, have been described (e.g., Holmes and Sturges 1975, Potter 1978, Pletscher 1982). We propose to build upon this background information and to expand some ongoing monitoring efforts to aid in quantifying the connection between population dynamics of several important heterotrophs, climatic variables, and the structure and composition of the primary producers. Our efforts will focus on four groups: breeding birds, phytophagous insects, large mammals, and a chronic and widespread fungal pathogen. We propose to accomplish four major objectives:

Objective D.1. To quantify long-term trends in population dynamics of breeding birds, the factors causing these trends, and the demographics of certain key bird populations.

Objective D.2. To quantify long-term patterns in populations of phytophagous insects in early- and late-successional stands and the effect of periodic irruptions on tree growth and breeding bird reproduction.

Objective D.3. To quantify the interactive effects of changes in forage quality and quantity and herbivory by mammals (white-tailed deer) during forest succession following large-scale disturbance.

Objective D.4. To quantify the relationships between the population size and genetic structure of an important and widespread root pathogen (Armillaria ssp.) and the age, vigor and composition of forest vegetation.

II.D.1. Population Dynamics of Breeding Birds.

Objective: To quantify long-term trends in population dynamics of breeding birds, the factors causing these trends, and the demographics of certain key bird populations.

Background, Hypotheses and Research Approach

Concern has developed recently that many bird populations in the eastern U.S. are declining (Morse 1980, Holmes et al. 1986), particularly for those species that winter in the neotropics (Terborgh 1980), and a linkage to tropical deforestation and other habitat modifications has been suggested (Terborgh 1980, Steinhart 1984). Other evidence, however, indicates that events in the temperate breeding grounds may be equally or even more important. Extensive fragmentation of temperate forests, affecting habitat-patch size and predation rates, has been strongly implicated (Whitcomb et al. 1981, Wilcove 1985).

Long-term studies of bird populations at Hubbard Brook also show declines in many species, including the neotropical migrants (Holmes et al. 1986). Correlative evidence, however, suggests that diverse factors are involved, including food limitation in the breeding season, climatic events, predation and other events that influence breeding productivity and recruitment, as well as over-wintering mortality. Actually, the current evidence for the latter applies to the north temperate resident species and the short-distance migrants, not those that winter in the neotropics (Holmes et al. 1986). It is not yet clear, however, the degree or extent to which bird populations are in fact declining or the factors causing the observed population changes.

Studies are currently underway 1) to monitor bird populations on replicate study sites within relatively homogeneous, undisturbed and unfragmented northern hardwoods forests at Hubbard Brook and nearby sections of the White Mountain National Forest;
2) to simultaneously monitor environmental factors (weather, predators, food) that will help explain long-term population trends and that will be used to develop alternative explanations concerning the factors causing population fluctuations; and 3) to conduct demographic and experimental studies of habitat saturation, food limitation and nest predation to test specific hypotheses concerning population abundance, dynamics, habitat selection, and the effect of other species on the distribution and abundance of certain migratory passerine bird populations.

These studies are currently funded by the National Science Foundation. A proposal for monitoring bird populations and environmental factors on replicate sites at Hubbard Brook and vicinity was funded 1 March 1986 for five years (BSR-8516838 to Holmes and others), while that for demographic and experimental studies was approved 1 July 1986 for three years (BSR-8604788 to Holmes and Sherry). No funding is sought for this work from this LTER proposal, but we consider this an important aspect of the proposed LTER program at HBEF. Moreover, we are seeking some support for more detailed surveys of Lepidopterans, an important food source of breeding birds (see below).

D.2. Population Dynamics of Phytophagous Insects

Objective: To quantify long-term patterns in populations of phytophagous insects in early- and late-successional stands and the effect of periodic irruptions on trees growth and breeding bird reproduction.

Background, Hypotheses and Research Approach

In terms of potential impacts on ecosystem structure and function, phytophagous insects are probably the most important group of heterotrophs (e.g., Lee and Inman 1975, Mattson and Addy 1975). In northern deciduous forests the defoliating Lepidopterans are of greatest importance. These herbivores typically consume only 1-10% of annual leaf production or about 1-4% of above ground net primary production in most years (Whittaker and Woodwell 1969, Carlisle et al. 1966, Bray 1964, Reichle et al. 1973, Phillipson and Thompson 1983). However, they do increase dramatically in abundance at periodic intervals, and at these times, they can remove a large proportion (up to 100%) of photosynthetic leaf tissue. The periodicity of these defoliator irruptions in northern hardwood-conifer forests and their effect on forest ecosystem dynamics have not been well studied. For temperate deciduous forests, there are very few long-term records of outbreak frequency or magnitude. From the few available (see Table D.1), it appears that irruptions occur on average about every 10 years, but the variability is high (5-15 years). Almost no information exists on the abundance of defoliating Lepidoptera between outbreaks, nor on the periodicity of outbreaks in any single forest ecosystem.

Since 1969 at HBEF, Holmes and associates have sampled defoliators with a variety of methods, including malaise traps, black lights, suction traps, frass collectors, and visual

TABLE D.1 **Examples of Irrupting Lepidoptera in North Temperate Deciduous Forests**

Species	Survey Period	Forest Type	Interval between Irruptions (Yrs) Range	Mean	Reference
Malacosoma disstria (Lasiocampidae)	1867-1960	Populus	6-14	10	Sippell 1962
Oporina & Operophthera (Geometridae)	1862-1968	Betula	5-15	9.4	Tenow 1972
Heterocampa guttivitta (Notodontidae)	1900-1983	Fagus Acer	10-13	10	Martinant 1984

counts of sedentary insects on leaves. Over this 18 yr period, only two major Lepidoptera irruptions have occurred (Fig. D.1), one of the saddled prominent (Heterocampa guttivita: Notodontidae) which peaked in midsummer of 1970 and one of an inchworm, Itame pustularia (Geometridae), which appeared in late May and early June of 1982 and 1983 (Holmes et al. 1986, Holmes 1987). In the periods between outbreaks, caterpillar densities have been extremely low (e.g., an average of 5.2 larvae/1000 leaves on beech) (Holmes 1987, Holmes and Schultz 1987).

We propose in this LTER to extend and expand our monitoring of defoliating Lepidoptera abundance in the Hubbard Brook forest. Until now, the data on defoliating insect abundance at Hubbard Brook have been collected when personnel and time permitted. Although the existing data are useful for indicating trends, they do not provide estimates of insect abundance on all major plant species, full seasonal coverage, or any indications how patterns may change with succession following large-scale disturbance.

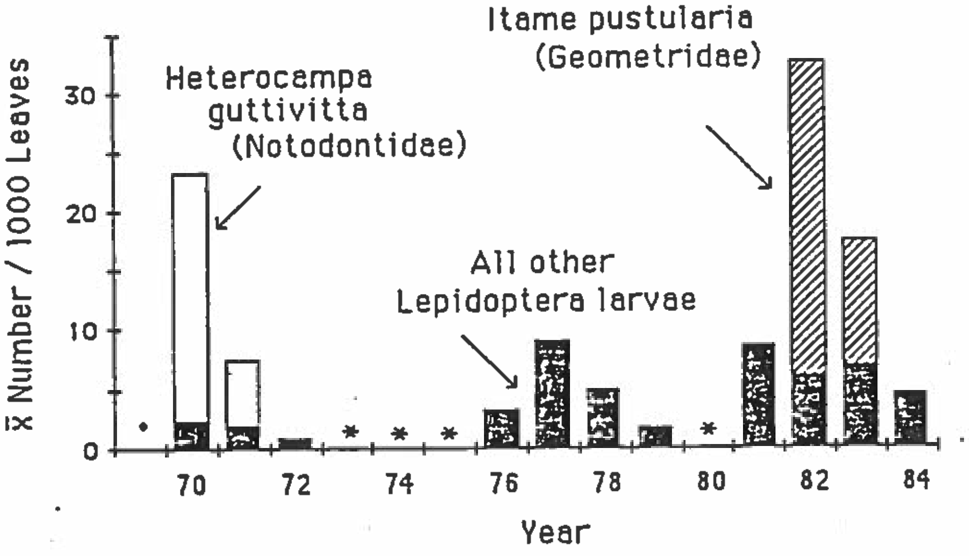
Based upon past trends (Fig. D.1), we hypothesize that a major irruption of the saddled prominent will occur during the first LTER funding cycle. Experience from past irruptions has indicated both local and regional patchiness in these populations (Collins 1926; Holmes and Sturges, pers. observ.) as well as significant damage to some forest stands (Grimble and Newell 1973). We propose to follow the expected irruption in some detail and to test the following hypotheses:

Hypothesis D.2.1. Local variation in saddled prominent populations during an irruption is related to density and vigor of preferred hosts (beech and sugar maple) and population densities are significantly higher in mature than in younger, successional stands.

Hypothesis D.2.2. A saddled prominent irruption results in stimulation of reproductive success in insect-feeding birds, and the numerical and functional responses carry over for several years following insect decline.

Our approach for phytophagous insect monitoring will include visual counts, frass collectors, and black lights, techniques which have been tested and used successfully at HBEF (Holmes et al. 1986). A reference collection of adult and larval Lepidoptera from HBEF is available at Dartmouth. Monitoring will be carried out during the in-leaf period of each year of the study with detailed sampling at 2-week intervals. Measurements within

Lepidoptera Larvae on Beech (Fagus grandifolia) Foliage at Hubbard Brook



* no quantitative samples taken

FIGURE D.1 Larvae of major lepidoptera on leaves of beech during 16 years of measurements (from Holmes 1987).

the permanent plots of component A-2 will permit detection of the effect of irruptions on tree growth. We also expect to make regional surveys of the irruption throughout the Northeast.

Future Research and Collaboration

In the initial year of a population irruption we will seek ancillary funding with colleagues from Cornell and/or Smithsonian to detail the life history dynamics of the irrupting populations and to identify the factors leading to the population decline. Associated studies on physiological effects on host trees also may be pursued. We will consult with these colleagues in identification of any obscure populations encountered and in identification of certain larval stages. Finally, we anticipate the involvement of the USDA/EPA Eastern Hardwood Forest Cooperative in these studies.

D.3 Forage quality and herbivory by white-tailed deer

Objective: To quantify the effects of changes in forage chemistry and quantity on herbivory by white-tailed deer during forest succession following large-scale disturbance.

Background, Hypotheses and Research Approach

The behavior and activity of free-ranging vertebrate herbivores can be explained largely on the basis of energetic limitations in natural environments (e.g., Moen 1973). Environmental changes may alter the energetics of these species in a number of ways but most commonly by altering food availability. Long-term increases in the proportion of forest cover in much of eastern North America (due to agricultural abandonment) have been paralleled by declines in population density of the white-tailed deer (*Odocoileus virginianus*), the most important and widespread vertebrate herbivore in the region (NY Bureau of Game 1953). However, recent increases in forest harvesting activity, as forests on abandoned land reach merchantable size, are promoting habitat heterogeneity and increased area in early successional stages, features which are known to favor deer and other wild mammals (Telfer 1972, Moen 1973, Peek et al. 1976). This attraction probably is related in part to food availability (Cooperrider and Behrend 1980). Thus, forest harvest activity is likely to lead to increased deer populations; moreover, increasing populations of deer can have important selective effects on tree regeneration because of their forage preferences (Marquis 1974).

Food availability to wildlife could be affected by forest harvest in a number of ways: (i) change in species composition (Boring et al. 1981); (ii) change in accessibility of preferred foods (Kelty and Nyland 1983); (iii) change in quantity of available forage (Behrend and Patric 1969); and (iv) changes in nutritional quality of forages. Surprisingly, despite the importance of food quality in controlling animal behavior and demography, the relationship between forest succession and the quality and availability of forage rarely has been examined. As part of our analysis of the W5 whole-tree harvest experiment we initiated such a study. The preliminary results of this analysis can be summarized as follows: (1) protein contents of forage species are 25-35% higher on W5 than for conspecifics in the contiguous mature forest; (2) high energy content, soluble carbohydrates are 20-30% higher; and (3) undigestible lignin fraction is 10-20% lower. Changes occurring after the first two years are not yet available, but the quantity and availability of preferred browse has continued to increase through the third year of succession. However, actual browsing as a percentage of total forage available peaked in the first year following harvest. Also, selection of the cut-over watershed for browsing activity was very strong, with little utilization of available browse species in the mature forest understory. Finally, in a common garden study we have observed strong browsing preference for paper birch (B. papyrifera) compared with closely related mountain birch (B. cordifolia), and we are investigating the biochemical explanations of this observation.

We propose to continue this analysis of browsing, forage chemistry and quantity to test the following hypotheses.

Hypothesis D.3.1. The quantity and quality of preferred deer forage and actual browsing increase to peak levels in the first 4-5 yr following large-scale disturbance; decline to very low levels until the break up of the pioneer forest canopy; and then increase to moderate values in maturing northern hardwood-conifer forest.

Hypothesis D.3.2. As succession proceeds, differential changes in tissue chemistry among pecies result in altered selection of browse species by deer.

Sixty permanent plots (each 5m x 25m) were established randomly after the harvest of 5, twenty in each of three elevational bands. A similar array was established in the ntiguous mature forest. We propose to establish another series of plots in the 15-year-d forest in contiguous W4 and to assess the availability, chemistry and herbivory of major forage species (Pletscher 1982) annually during the five-year LTER funding cycle. Each August we will enumerate browse twigs within 1.5m of the ground (Moen and Scholtz 1981), and the percentage of these twigs with evidence of deer browsing. Twig samples will be collected from random nested plots for chemical analysis, including protein, soluble carbohydrates, cellulose, lignin, hemi-celluloses (Van Soest 1983) and polyphenolics (Schultz et al. 1981, Martin and Martin 1982).

Future Research and Collaboration

Recent advances in forage fiber analysis (Van Soest 1983) and secondary chemistry of plants (Martin and Martin 1982) are indicators of our improved understanding of nutritional quality of animal food. Our tissue analysis has been performed in the laboratory of P. Van Soest at Cornell, incorporating new technical advances in the procedures. We hope to consult and compare results with F.S. Chapin and colleagues working on similar problems of wildlife/plant chemistry interactions in Alaskan ecosystems. Also at Cornell, A. Moen will be available for collaboration on patterns of deer utilization of browse, and we anticipate a future cooperative proposal on deer energetics at HBEF utilizing Moen's ecophysiological and energy budget approaches.

D.4 Population Dynamics of _Armillaria_

Objective: To quantify the relationships between population size and genetic structure of an important and widespread root pathogen (_Armillaria_ ssp.) and the age, vigor and composition of forest vegetation.

Background, Hypotheses and Research Approach

As suggested over 30 years ago by Woods (1953) our understanding of the autogenic component of succession (see component A) would be greatly improved if we could quantify the powerful influence of microbial pathogens. Species composition and vegetation structure of terrestrial ecosystems are strongly influenced by these organisms, and Dinoor and Eshed (1984) have emphasized their important role in species diversification.

Several basidiomycete fungi have evolved the specialized capacity to parasitize woody plant roots, and many (including _Phellinus weirii_, _Heterobasidian annosum_, and _Armillaria mellea_) are ubiquitous in the temperate zone and may cause extraordinary morbidity and mortality in managed (Shaw and Roth 1978) and unmanaged forests (Smith 1986). In particular, *Armillaria* is viewed as a secondary pathogen impacting trees stressed primarily by other biotic or abiotic factors (Wargo and Shaw 1985).

Rhizomorphs of *Armillaria* are generally abundant in the forest floor of northern hardwood-conifer ecosystems, but conventional wisdom suggests a positive correlation between rhizomorph abundance and such features as stand age, species composition and residual stumps or old trees. Weakened trees appear to be colonized by rhizomorphs growing from roots of infected trees or from quiescent lesions reactivated by stress. Thus, the *Armillaria* complex represents an interesting and important pathogenic system whose dynamics are likely related to ecosystem development following large-scale disturbance. Moreover, recent taxonomic and genetic investigations indicate high genetic diversity in the *Armillaria* genus (Wargo and Shaw 1985) and a relation to the diversity of the forest community seems possible.

Hypothesis D.4.1. Abundance of *Armillaria* rhizomorphs changes systematically during succession following large-scale disturbance in a pattern which is correlated with changes in forest structure and composition (i.e., density, diversity, mortality and composition).

Hypothesis D.4.2. Genetic diversity of *Armillaria* changes systematically along the successional gradient, with higher diversity in old-growth stages.

We will measure *Armillaria* abundance and genetic diversity on the same series of plots for which forest vegetation studies are proposed, including sites aged 4, 14, 18, 22, 75 and over 200 years. Sites of intermediate age (30-60 years) also will be located in nearby areas (cf. Covington 1975). Sampling will be stratified random along multiple contour intervals at each site, using quantitative extraction of surface soil horizons and visual examination for rhizomorph abundance (Carey et al. 1984; Wargo et al. 1986).

Biological species in *Armillaria* are defined as groups that are reproductively
solated and where intersterility between groups is absolute (Anderson et al. 1979). The
iological species of a diploid field isolate can be determined by pairing it with haploid
solates of each biological species group and observing a change corresponding to the
ller phenomenon (Korhonen 1978). In a compatible pairing of a diploid isolate with a
ploid tester, the appearance of the cottony haploid changes to the appearance of the
ustose diploid; in an incompatible pairing, the two isolates maintain their distinct

appearances (Kile 1983, Korhonen 1978). Genotypes within biological species can be determined by pairing diploid field isolates (Anderson et al. 1979, Kile 1983); a distinct demarcation line forms between dissimilar genotypes but not between similar ones. The occurrence of different biological species and of different genotypes within biological species will be determined using these pairing techniques.

III. PROGRAM MANAGEMENT

A. Administration of HBEF and LTER

Scientific management: Research activities of the HBES are coordinated by the Scientific Advisory Committee, consisting of F.H. Bormann, R.T. Holmes, G.E. Likens and R.S. Pierce. This committee screens and approves all projects, facilitates integration of new and on-going studies and suggests new initiatives while maintaining an ecosystems perspective in the overall program. The Committee meets semi-annually in a formal manner and at frequent intervals during the field season when all members are in residence at HBEF.

Under LTER the Scientific Advisory Committee would be augmented with two additional members, C.T. Driscoll and T.J. Fahey. The charge of the Committee will not be altered under LTER, but the importance and range of its activities will certainly be increased. The provision of two younger scientists will provide continuity to the Committee during the inevitable transitions which will occur in project personnel during the coming decade.

Driscoll and Fahey will act as primary representatives of the HBES to the overall LTER Program, providing communication with co-PIs, organizing coordinated cross-ecosystem comparisons, and attending administrative and organizational meetings and workshops. To provide broader representation, we anticipate that other key members of the proposed HBES-LTER also will be involved in these activities, particularly W.B. Bowden, C.A. Federer, and D.R. Peart. The participation of mostly permanent staff in the project will assure continuity to the proposed HBES LTER (Table III.1).

Table III.1 Major scientific personnel associated with the proposed HBES LTER program components and their employment status.

Research Component and Personnel	Specialty	Status[1]	Funding
Component A: Vegetation			
F. Bormann	Terrestrial ecology	T	Yale
T. Fahey	Forest ecosystems	T	Cornell
J. Hughes	Population ecology	N	Cornell-NSF
W. Martin	Forest ecology	T	USFS
D. Peart	Plant ecology	T	Dartmouth
W. Reiners	Terrestrial ecology	T	Wyoming
T. Siccama	Terrestrial ecology	N	Yale
Component B: Detritus			
T. Fahey	Forest ecosystems	T	Cornell
S. Findlay	Stream ecology	T	IES
G. Likens	Aquatic ecology	T	IES
T. Siccama	Terrestrial ecology	N	Yale
L. Tritton	Dead wood	T	USFS
Component C: Biogeochemistry and hydrology			
B. Bowden	Microbiology and hydrology	T	UNH
C. Driscoll	Environmental chemistry	T	Syracuse
J. Eaton	Forest ecology	T	IES
T. Federer	Forest hydrology	T	USFS
A. Johnson	Soil chemistry	T	Penn
G. Likens	Ecosystems	T	IES
G. Lovett	Dry deposition	T	IES
Component D: Heterotrophs			
T. Fahey	Forest ecosystems	T	Cornell
R. Holmes	Animal ecology	T	Dartmouth
J. Hughes	Population ecology	N	Cornell-NSF
T. Sherry	Animal ecology	N	Dartmouth-NSF
W. Smith	Forest pathology	T	Yale

[1] T = tenured or tenure-track
N = non-tenured

Site and Facilities Management: The HBES operates in the Hubbard Brook Experimental Forest with the support and cooperation of the U.S. Forest Service. Coordination is provided by the Site Management Committee consisting of R.S. Pierce (Site Coordinator) and C.W. Martin (Site Manager) for the USFS and J.J. Cole (Associate Site Coordinator) for the HBES. This group integrates new projects during the planning stages to avoid conflicts in site use and to coordinate activities within the HBEF. Communication among HBES collaborators is facilitated in this way, with Pierce providing a liaison between this Committee and the Scientific Advisory Committee.

Yale, Cornell, IES, and NSF have made large investments in purchasing and renovating dormitory facilities and building a new laboratory at the Pleasant View Farm complex. An independent, non-profit operating foundation (Hubbard Brook Research Foundation, Inc.) was recently established to administer research and facilities at this complex, with a Board of Directors consisting of senior administrators from Yale, Cornell, Dartmouth and IES. Day-to-day operation of the facilities is managed by the Facilities Committee, consisting of J.J. Cole (Associate Site Coordinator), W.B. Bowden (Research Coordinator), J.S. Eaton (Laboratory Manager) and J. Warner (Business Manager). Warner provides liaison between the Facilities Committee and the Foundation. The committee is responsible for allocation of laboratory and dormitory space, upkeep of facilities, and planning for long-term operation of the facilities.

Laboratory and dormitory space also is maintained at the USFS Hubbard Brook Research Station. This facility is managed by C.W. Martin in conjunction with the HBES and direct communication with the Facilities and Scientific Advisory Committee is maintained through R.S. Pierce.

National Advisory Committee (NAC): We have recruited three members for a prospective NAC for the proposed HBES LTER: C. Cronan (Biogeochemist, Univ. of Maine), K. Cummins (Aquatic Ecologist, Univ. of Maryland), and J. Franklin (Plant ecologist, USFS). Additional members in the areas of population ecology and hydrology will be recruited. The committee will attend the annual Hubbard Brook meetings and provide advice to the scientists on aspects of their expertise and on overall program synthesis and integration.

B. Data Management

Introduction and Recent Efforts

As a multi-Institutional research program, the HBES always has been confronted with an unusually difficult set of data management problems. For example, the standard long-term monitoring program has involved five separate institutions, and affiliations of PI's have changed since its inception. Moreover, in its early stages the HBES operated largely on the short-term, with 2-3 year funding cycles, and long-term continuity was not expected or assumed. Thus, each investigator was deemed responsible for careful maintenance of data records. This arrangement was suitable while the project remained small and rather personal, but the growing interest in ecological studies at HBEF during the past decade has strained this system of data management.

We view the LTER program as a valuable opportunity to improve the data management system of the HBES. Our initial plans for LTER data management have been conceived in consultation with other LTER projects (especially Andrews EF and North Inlet) and ongoing data management efforts in the Northeast (EDEX, see below; USFS, Spruce-fir and Eastern Hardwoods Cooperatives). During the first LTER funding cycle we hope to profit from additional consultation with other LTER sites.

Recently, great strides have been made towards improving data management of the HBES. Traditionally, long-term monitoring data have been maintained in the form of hard copies at USFS (meteorology, streamflow), Cornell-IES (solution chemistry), Yale (vegetation), and Dartmouth (heterotrophs). We are in the process of converting these and other long-term data sets to magnetic tape (9-track, 1600 bpi, EBCDIC, fixed record and block size), with careful editing during the conversion. Much of this initial job has been finished or is near completion (Table III.2). Also, we maintain a complete library of published and unpublished manuscripts from the HBES in a library at IES.

Recognizing the importance of accuracy and precision in identifying long-term trends, we have taken great pains to replicate and cross-check methodologies both as technology has advanced and as new laboratories have become involved in the HBES monitoring programs. Furthermore, we envision this aspect as an important goal in the LTER program, fostering

Table III.2 Current long-term monitoring data sets and their status.

Measurement	Institution	Status[1/]
I. Physical/hydrologic monitoring		
Instantaneous streamflow (n stations)	USFS	A,C
Daily streamflow (n stations)	USFS	A,C
Daily precipitation (n stations)	USFS	A,C
Daily temperature: mean, min, max	USFS	A,C
Daily solar radiation	USFS	B,D
Weekly snow depth on snow courses	USFS	B,D
Weekly soil temperature and moisture	USFS	B,D
Continuous air temperature, humidity, solar radiation, wind speed/direction, precipitation	USFS	E
II. Solution chemistry[2/]		
Weekly wetfall, bulk precipitation at n stations	IES	A,C
Weekly stream chemistry at weirs	IES	A,C
Monthly stream chemistry within W5, W6	Syracuse	A,C
Monthly soil solution chemistry W5, W6	Syracuse	A,C
Event basis throughfall chemistry: W5, W6	Syracuse	B,D
III. Organisms		
Bird and insect populations	Dartmouth	D
W2 Vegetation, biomass, chemistry	Wyoming	B,D
W4 Vegetation, biomass	USFS	D
W5 Vegetation, biomass, chemistry	Cornell/Yale	B,D
W6 Vegetation, biomass, chemistry	Yale	A,C
IV. Soils		
Forest floor mass, chemistry (5 yr intervals)	Yale	B,C
Morphology	Penn	C
Bulk density by horizon and depth	Penn	A,C
Rock mass, volume	Penn	A,C
Solid and adsorbed phase chemistry	Penn/Syracuse	B,D
V. Solid materials		
Herbarium specimens	USFS	C
Library	USFS/PVF/IES	C
Tree cores and cross sections	Yale	C
Forest floor	Yale/Cornell	G
Soils	Penn	C
Plant tissues	Yale/Penn	C

[1/] A – Magnetic tape, complete; B – Magnetic tape, in progress; C – Hard copy, available; D – Hard copy, in progress; E – Analog, available

[2/] see Appendix I.B for components measured more valid inter-site comparisons for the present and future, and we welcome the opportunity to be a leader in improving this aspect of the program.

During the planning and performance of our whole-tree harvest experiment (W5), the importance of integrated data management and planning was particularly evident. A series of data management/planning workshops is ongoing and will act as a model for improving the overall data management system for the HBES. These workshops have been instrumental in the development of our proposed data management plan, outlined below.

Another area of recent progress in data management has been organized storage of tissue and soil samples. With the development of new technology and changing research questions, the opportunity to re-sample biological tissues and soil samples of known origin may be very important; in fact, our recent experience has underscored this fact. Currently, we are depositing plant and soil samples at Yale and Penn with indexes and catalogs of sample collection and handling. We anticipate expanding this effort under LTER (see below).

Finally, in a cooperative effort with the Mellon Foundation, we are developing an ecological data exchange network (EDEX) to foster communication and cooperation among ecologists on a regional and national basis. The rationale and format for EDEX are presented as part of our LTER data management plan, below.

Proposed Data Management Plan for HBES-LTER

Our data management (DM) plan represents a compromise between the ideal (but difficult and expensive), all-encompassing centralized DM center and a more dispersed system. A DM Committee, consisting of the LTER representatives (Driscoll and Fahey) and the principal long-term data compilers (Eaton, Federer and Siccama) will be constituted to oversee the data management process.

We recognize two contrasting sets of data within the HBES: (1) long-term monitoring information, collected continuously or repeatedly by highly-standardized methods and generally of value to many or most HBES scientists; and (2) short-term, experimental information. We propose to include both sets within the DM Center of HBES but with different formats and protocols for entry and maintenance. We repeat that this compromise is necessitated by the dispersed, multi-institutional nature of the HBES, a feature which encourages a broad range of scientist involvement in the project but which hampers the achievement of truly centralized DM.

All the long-term data sets (see Table III.2) will be included in DM Centers at Yale, IES, and USFS in two forms: hard copies and magnetic tapes. Following approval by the DM Committee, formal requests for these data sets will be met by transferral to the appropriate form (hard copy or any of a variety of digital forms). Long-term monitoring data files will be updated annually to permit efficient dispersal of relevant information for analyzing experimental work and designing new studies. An annotated catalog will be maintained and additions or deletions and changes in methodology for specific monitoring efforts will be reviewed by the DM committee.

DM for short-term, experimental studies has been a problem at HBEF and other intensive research sites. All experimental studies at HBEF must be approved by the Scientific Advisory Committee (see section III.A); formal approval of projects will be made with the stipulation that data summaries (see below) be provided (hard copy and/or computer files) to the LTER DM Center at Yale at the completion of the study. Titles of data sets will be entered into the LTER DM catalog index and hard copies retained in the DM Center at Yale

The development of the HBES LTER DM catalog index and library will be carried out in conjunction with EDEX, the ecological data exchange network of T.G. Siccama and others (funded in part by the Mellon Foundation). EDEX was stimulated by a recognition of the need for better access to and higher visibility of historical ecological data sets. It recognizes the need for careful documentation of methods and site locations and is designed to stimulate communication among ecologists through advertising. Two initial steps in EDEX are unifying regional vegetation ecology data sets and organizing some of the back-log of experimental data sets from HBEF. Although the process will require the voluntary participation of individual scientists, initial reactions to the process appear favorable.

Data management efforts will be aided by the provision of personnel from the various parent institutions. A full-time data management and statistics specialist will be provided by Syracuse University to Driscoll's laboratory. Yale and Mellon Foundation support will provide a full-time data management specialist at that institution to augment the effort proposed under our LTER budget. Both the USFS and IES currently support data management work under the HBES, an arrangement which will continue during LTER. Finally, Cornell will provide a 50% time post-doctoral associate to assist Fahey in overall management of the research efforts under LTER. Through frequent meeting of the DM staff and DM committee we are confident of an efficient DM network for the HBES LTER.

In conclusion, we sincerely believe that the funding of an HBES LTER will greatly improve the data management capabilities at this site and contribute to better inter-site communication both within LTER and the rest of ecological community. We will welcome suggestions for improvements and adaptations to our proposed system from the other LTER DM programs.

C. Coordination with Other LTER Sites and Promotion of Site Use

The LTER program provides a forum for unusual integration of ecological ideas and measurements across the borders of ecosystem type and disciplinary specialties. The PI (T. Fahey) was highly impressed by the scientific interaction generated by the first LTER All-Scientist's Meeting, which he attended as an outside participant. We recognize great potential for the involvement of the HBES in coordinated activities within the LTER program, particularly in three areas: (i) workshops in empirical methodology and in development of general models; (ii) ecological data exchange and data management; and (iii) cooperative, cross-system scientific studies.

Several empirical methodologies have been widely used in recent years including *in situ* N mineralization; microbial biomass by fumigation and bacterial production by tritiated thymidine incorporation; selective biocides and detrital food chains; monitoring atmospheric chemistry and estimating dry deposition; and establishing experimental canopy gaps. However, site comparisons have been few and methodologies have not been adequately systematized. We would hope to contribute to LTER coordination by organizing workshops on these and other methodologic approaches to stimulate new thinking into the principles which cross the boundaries of ecosystem types. In conjunction with such methods-based workshops, we envision corresponding modeling efforts to provide linkages between parameter estimation and theoretical formulations of ecological processes and ecosystem behavior. In particular, workshops on modeling hydrologic-biogeochemical interactions across landscapes would be most valuable.

As indicated in our Data Management section (above) we recognize a weakness within the ecological community in the preservation, distribution and utilization of historical data sets. This problem has become most apparent during recent assessments of the ecological integrity of eastern forests and watersheds in the faces of high pollution loads. We hope to help foster within the LTER Program, carefully planned methods of data management and preservation and welcome the opportunity to profit from experience gained during the initial years of LTER. We also encourage the formulation of planning for these activities in the event of discontinuation of the LTER Program. Also, we hope to contribute to the Program our experience with the integrity of long-term records and the process of preventing temporal bias as new analytical methodologies are incorporated into research protocols.

Finally, we hope to become involved with and to initiate cooperative, cross-system scientific studies. We anticipate studies which include (i) comparison of log decay, dead wood leaching and organic debris dams among the forested sites; (ii) detrital accumulation and dissipation and food chains in both aquatic (stream and lake) and terrestrial sites; (iii) food chain and biogeochemical studies of lakes; (iv) long-term studies of population structure of breeding birds in contrasting habitats; and (v) experimental studies of canopy gaps, neighborhood competition and self-thinning in plant communities. We recognize great potential for combining studies at the individual, population, and community levels of organization in explaining phenomena at the ecosystem level for which the HBES is designed.

As indicated in Appendix II, site use at HBEF has been intense during the past decade. With the initiation of the proposed HBES LTER we envision continued increase in requests for site use. We plan to encourage activities which will contribute to the overall goals of the HBES. As indicated under Research Components, we expect to encourage the participation of other scientists at the parent institutions, colleagues from other LTER sites, and international cooperators to help us achieve the goal of gaining a better understanding of the dynamics of northern hardwood-conifer ecosystems.

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Curriculum Vitae

Principal Investigators

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a. William Breck Bowden (Terrestrial Microbiologist) - School of Forestry and Environmental Studies, Yale University, Greeley Memorial Laboratory, New Haven, CT 06511

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b. Ph.D. - University of Wisconsin, Madison, Forest Soils and Ecology (1957)

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a. William A. Reiners (Terrestrial Ecologist) - Department of Botany, University of Wyoming, Laramie, WY 82071.

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a. Thomas G. Siccama (Forest Ecologist) - School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511

b. Ph.D. - University of Vermont, Plant Ecology (1968)

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