

PROJECT SUMMARY

We propose to continue the project, "Long-term Ecological Research at Hubbard Brook Experimental Forest" in an effort to improve general understanding of the mutual influences of environment, disturbance, biological activity and the flows of energy and materials in forest landscapes. Our integrated program of long-term monitoring and process-level studies at HBR and a series of other regional sites addresses a series of hypotheses in three thematic categories: biogeochemistry, vegetation dynamics and primary productivity, and heterotroph population dynamics. Our biogeochemical studies focus upon the cycles of C, N, Ca and S and build especially upon our 30+ year record of fluxes from the HBR experimental watersheds to address several striking and surprising observations about element cycling in the northeastern forest. We propose to expand our investigations of vegetation and primary productivity at the landscape scale, focusing upon the interactions between tree spatial distributions, soil and glacial till properties, and nitrogen cycling and nutrition. Our heterotroph population studies focus on passerine birds, the food web interactions that govern their temporal abundance patterns and forest habitat relationships at larger scales. Our research will be synthesized and integrated using simulation models and in the form of monographic overviews of elemental cycles.

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1.0 - RESULTS FROM PRIOR NSF SUPPORT

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NSF Awards: 9211768; \$3,500,000; 1 Oct 92 - 30 Sept 98.

Title: Long-Term Ecological Research (LTER) at the Hubbard Brook Experimental Forest (HBEF)

Summary: The overall goal of the LTER study at the HBEF is to develop a better understanding of the responses of northern hardwood ecosystems to natural and anthropogenic disturbances. We have been conducting research on sites within and nearby the HBEF with contrasting histories of disturbance, as well as continuing the collection and analysis of long-term data sets. Our strategy has been to build upon previous and ongoing work at the HBEF through the use of long-term records and manipulated watersheds. Thus, we have used LTER funds to help support monitoring activities, initiate process-level research projects, and improve data management to facilitate integration of past and current research at the HBEF. A few of our recent initiatives include:

Response of Forest Ecosystem to Changes in Atmospheric Deposition. Long-term measurements of precipitation and stream chemistry at Hubbard Brook have demonstrated the linkage between atmospheric emissions of materials, atmospheric deposition and the biogeochemistry of forest watersheds. Atmospheric emissions of sulfur dioxide (SO_2) in the U.S. peaked in 1970 and have declined following the 1970 Amendments to the Clean Air Act. At Hubbard Brook changes in annual volume-weighted concentrations of SO_4^{2-} in precipitation and streamwater have closely corresponded with these changes in SO_2 emissions (Driscoll et al. 1992, 1998). Watershed mass balance calculations, however, indicate that stream losses of SO_4^{2-} exceed atmospheric deposition of S from bulk deposition and estimates of dry deposition using either inferential or net throughfall approaches (Lovett et al 1992). We applied a simulation model to assess the discrepancy in S mass balance from watersheds at Hubbard Brook and regionally across the Northeast. Model calculations suggest that the discrepancy in watershed S budgets cannot be explained by desorption of soil SO_4^{2-} , but rather is due to either a large underestimate in measured values of dry deposition and/or an internal source of S such as mineralization of soil organic S pools or weathering of S minerals (Driscoll et al. 1998).

Biogeochemistry of Basic Cations: Ca and K. Synthesis and integration of biogeochemical cycles at Hubbard Brook has provided insights into the mechanisms causing long-term changes, landscape-level patterns and responses to disturbance. Efforts in the past five years have focused on Ca and K (Likens et al. 1994; Likens et al. 1996 ; Likens et al. 1998). The combination of naturally base-poor soils, high deposition of anthropogenically-derived strong acids and periodically accelerated removal of bases associated with forest harvest would be expected to make the Hubbard Brook ecosystem susceptible to excessive depletion of soil base cations, especially Ca. In fact, a quantitative interpretation of our records of precipitation, soil and streamwater chemistry strongly suggests that ecosystem response to decreases in acidic deposition may be delayed significantly. Reductions in emissions of SO_2 and consequent decreases in deposition of

strong acids followed the passage of the Clean Air Act in 1970, but at the HBEF these reductions have been accompanied by declining deposition of basic cations (C_B), especially Ca. Coincident reductions in streamwater concentrations of strong acids and C_B since 1970 have limited the response of pH and acid neutralizing capacity of surface waters across the Northeast.

The Biogeochemistry of Nitrogen. Investigations have been conducted on the biogeochemistry of nitrogen at Hubbard Brook and throughout the Northeast region, from upstate New York to Maine. A spatial model of atmospheric deposition was developed for the Northeast based on empirical relationships for major solutes in precipitation from the National Atmospheric Deposition Program/National Trends Network, and particle and gas concentrations from the National Dry Deposition Network (Ollinger et al. 1993). The results demonstrate a marked spatial gradient of nitrogen from high values above 10 kg N/ha-yr in the Adirondack and Catskill mountains of New York to below 4 kg N/ha-yr in Maine. Using a chronosequence of cut-watersheds at and near the HBEF we have evaluated effects of land-use and cutting history on dissolved inorganic nitrogen (DIN) loss from the northern hardwood forest (Pardo et al. 1995, Aber and Driscoll 1997). Retention of DIN was high in recently cut watersheds and decreased with increasing stand age. However, there was considerable year-to-year variation in loss of DIN for a given watershed. Some of this variability in watershed loss of DIN may be due to climatic factors and events. For example, Mitchell et al. (1996) reported synchronous loss of NO_3^- in forested watersheds across the Northeast, including the HBEF, in the late 1980s and early 1990s in response to a soil freezing event. We have developed the simulation model PnET-CN as a research and management tool to assess the response of the nitrogen cycle in forest watersheds to disturbance, including changes in atmospheric deposition of nitrogen, climate and land-use (Aber et al. 1997, Aber and Driscoll 1997; [http:// pyramid.sr.unh.edu/csdc/aber/pnetweb](http://pyramid.sr.unh.edu/csdc/aber/pnetweb)).

Changes in Lead Biogeochemistry. In the 1970s the U.S. restricted sale of gasoline with ethyl-lead additives. Since that time the amount of lead consumed in gasoline has sharply declined, resulting in lower rates of atmospheric deposition of lead. At the HBEF the input of lead in precipitation has declined over 97% since 1976 (Johnson et al. 1995). Despite decreases in atmospheric deposition, lead continues to accumulate in the forest ecosystem. Between 1977 and 1987 the lead content of the forest floor decreased by 29%, but lead now appears to be accumulating in the mineral soil.

The Effects of Whole-Tree Clear-Cutting on Soil Processes. Whole-tree clear-cutting represents a severe ecosystem disturbance, and leads to leaching losses of nutrients from the soil profile, increased acidification, and elevated concentrations of Al in soil solutions and streamwater (Dahlgren and Driscoll 1994). The process of nitrification, resulting in the production of nitric acid in both the forest floor and mineral soil horizons, was the principal mechanism driving these changes immediately after clear-cutting. The acidity generated through nitrification was largely neutralized by release and leaching of basic cations and inorganic monomeric Al. The major source of nutrient loss was from the forest floor. Basic cations lost from the forest floor and decaying roots were mostly retained on mineral soil cation exchange sites (Johnson et al. 1997). The consequent short-term increase in the base status of the mineral soil has been followed by

elevated leaching losses of Ca^{2+} and K^{+} in streamwater for several decades following cutting (Likens et al. 1994 1998; Romanowicz et al. 1996).

Forest Response to Fertilization. We altered soil resource availability during the early stages of stand development after clear-cutting of northern hardwood forests to generate empirical evidence for physiological, morphological, allocational and architectural factors regulating plant competition (Fahey et al. 1998). We expected the competitive ability of the extreme pioneer species, pin cherry, to be enhanced by increased nutrient supply, with consequent effects at the community and ecosystem level of organization. Nutrient availability was increased by about 3-fold by monthly fertilization for six yr in nine even-aged northern hardwood stands dominated by pin cherry, three each of three ages (6, 12 and 18 yr at initiation of the experiment). Measurements in the control plots indicated that the interval of stand development from age 6 to 23 yr was marked by a peak in basal area and leaf area of pin cherry at about age 17 yr followed by a steady decline in its dominance thereafter. Fertilization increased and prolonged the dominance of pin cherry indicating that nutrient limitation accelerates the demise of this species during the 2nd and 3rd decade of stand development. Thus, the competitive ability of pin cherry was improved by the removal of apparent nutrient limitations on its physiological performance, canopy growth and ability to compete for light.

Leaf area index of the fertilized plots was only slightly higher than the control plots, and the same was true for stand basal area. The removal of nutrient limitation increased the intensity of one-sided competition for light by concentrating the dominance among the largest trees; consequently, very high mortality of suppressed stems of all species occurred. The increased dominance of the fast-growing pin cherry contributed to increases in aboveground net primary productivity (ANPP) in the fertilized plots. Some of this ANPP response probably was associated with reduced C allocation to roots in some of the fertilized plots, but this pattern was not consistent across all the stands. The results indicate that the outcome of inter-specific competition in mesic forests, where co-limitation by light and soil resources prevails, depends upon the effect of site quality upon the relative intensity of one-sided competition (for light).

Fine Root Dynamics in Northern Hardwood Forests. Limited understanding of the dynamics of fine roots constrains our ability to accurately characterize the structure and function of terrestrial ecosystems and to predict their responses to natural and human-accelerated environmental changes. However, recent methodological advances, especially the minirhizotron (MR) technique may provide the means to improve estimates of fine root production and turnover and their response to environmental perturbations. Comparisons between MR and soil cores indicate that depth distributions of fine roots are altered by MR access tubes; however, the MR technique could still provide valid estimates of fine root production if the longevity of roots growing along tubes is not different from that in soil. We compared MR measurements of the longevity of fine roots growing in forest floor horizons with measurements obtained using *in situ* root screens (Fahey and Hughes 1994) to improve confidence in fine root production estimates by MR. Patterns of fine root longevity were very similar for these two methods. Moreover, these estimates of fine root production concurred with independent estimates of the forest floor carbon balance (Fahey and

Tierney, submitted). These results strongly suggest that MR access tubes do not significantly alter the longevity of fine roots in forest floor of northern hardwood forests.

Microbial Dynamics. In the last cycle of LTER funding, we initiated an effort to build a long-term data base to understand the factors that regulate microbial biomass and activity and to understand the role that microbes play in regulating biogeochemical fluxes in the northern hardwood forest. The effort was designed to complement existing long-term monitoring efforts of litter, soil solution chemistry and stream chemistry and to provide a background for more detailed studies of microbial processes. A paper on spatial, seasonal and annual variation in microbial biomass and activity, with analysis of relationships between microbial parameters and litter quality and soil solution chemistry is "in preparation". Two more detailed studies, funded by other sources, have been initiated; a manipulative study of "snow depth, soil frost and nutrient loss" (funded by the interagency program on Terrestrial Ecosystems and Global Change (TECO) and a study examining relationships between gross rates of N transformations and N gas fluxes (funded by a USDA NRICGP grant).

Population Dynamics of Birds and Insects, and Tree Growth Patterns. Monitoring of bird populations at Hubbard Brook, begun in 1969, continued to show declines in some species, increases in others and stable patterns in yet a third group (Holmes and Sherry, in prep.). Most species exhibited similar trends on three replicate plots, suggesting regional synchrony and the effects of environmental factors acting at large scales. The finding that different species exhibit different trends within the same sites, however, indicates that the factors and processes affecting these populations are diverse and their effects species-specific (Sherry and Holmes 1996, Rodenhouse et al. 1997, Holmes and Sherry in prep.). Process studies indicate that habitat quality differs among species, some responding to factors such as shrub density (Holmes et al. 1996) while others are affected by changes in overall forest structure (and presumably food resources) over successional gradients (Hunt 1996, 1998). Monitoring of defoliating Lepidoptera between 1991-1997 showed no irruptions or major changes in abundance at Hubbard Brook or in the three replicate sites in the southern parts of the White Mountain National Forest.

To test the hypothesis that birds indirectly influence tree growth through their consumption of leaf-chewing insects, we measured the growth responses (e.g., shoot extension, leaf biomass) of sugar maples (*Acer saccharum*) 1) from which birds were denied access through the use of exclosures, 2) from which all herbivores had been removed by application of a biodegradable insecticide, 3) on which herbivores were augmented by the addition of caterpillars, and 4) on controls. Preliminary results indicate that birds significantly reduced insect herbivores outside the exclosures compared to inside, confirming an earlier finding at Hubbard Brook (Holmes et al. 1979), but more importantly, those trees from which birds had been excluded exhibited increased shoot extension in the following season. However, leaf biomass did not differ significantly, despite greater shoot masses in exclosure and insecticide treatments (Strong et al., in prep.). These findings extend our long-term studies of the ecological role of birds in northern hardwood ecosystems (Holmes and Sherry 1997).

The Transport and Fate of CFC Replacement Chemicals. The phase out of chlorofluorocarbons (CFCs) has resulted in the use of hydrochlorofluorocarbons and

hydrofluorocarbons as environmentally acceptable alternative chemicals. Trifluoroacetate (TFA) has been identified as a byproduct of these CFC replacement chemicals, which following production in the atmosphere largely returns to the Earth's surface via precipitation. Little is known about the ecological fate of TFA. Two investigations were initiated to assess the transport and fate of TFA in the environment. A cross-site study of LTER sites was conducted to investigate soil adsorption of TFA (Richey et al. 1997a,b). Batch adsorption studies using soils from LTER sites indicated a wide range of TFA adsorption. TFA adsorption was most strongly related to soil organic matter. TFA adsorption increased with decreasing soil pH and competing anions influenced the extent of adsorption. A field manipulation study was also conducted at the HBEF to investigate the fate of added TFA to upland soils and a wetland. These results showed limited retention of TFA in upland soil plots. In contrast there was considerable retention of added TFA on soil and by vegetation in the wetland (Likens et al. 1997).

Controls on Water Quality of the Merrimack River Basin. We have been investigating spatial and temporal patterns in the water quality of the Pemigewassett-Merrimack River basin which drains most of New Hampshire. Hubbard Brook is a headwater tributary to the Pemigewassett-Merrimack River. Fifty-two water quality stations have been established along the basin and have been sampled for 16 months. Water samples were analyzed for all major solutes. Using water chemistry and U.S. Geological Survey discharge information mass fluxes for these solutes have been determined. This initiative has also involved the development of a geographic information system for the basin, including a digital elevation model, land-use, population density, soils, hydrography, and precipitation quantity and chemistry. This information will be used to assess the role of land-use in regulating water quality in the basin. These current data will be compared to historical data from the early 1970's to evaluate causes of water quality changes over the last 25 years.

Data and Information Management. During this funding cycle we have modified and upgraded the data and information management system from the original direct-dial, computer bulletin board, "The Source of the Brook" (SOTB; Veen et al. 1994). We have developed a Hubbard Brook Ecosystem Study (HBES) home page (<http://www.hbrook.sr.unh.edu>) to replace the SOTB. The home page is maintained by the USDA Forest Service data manager, who coordinates the data and information management efforts of all the HBES cooperators by uploading and connecting data sets, either on this "umbrella" site or at the major nodes that are linked to this site. Components of the HBES homepage include: an overview of the HBES research history and results and HBEF site description; long-term data sets (meteorological, hydrologic, chemical, biological); a bibliography of all HBES publications; resumes of HBES investigators; a list of organisms of the HBEF; GIS coverages; information of sample and document archives; current research initiatives; protocols for research involvement; and Hubbard Brook Research Foundation activities.

PUBLICATIONS

I. Journal articles

1993

Aber, J. D., C. T. Driscoll, C. A. Federer, R. Lathrop, G. M. Lovett, J. M. Melillo, P. Steudler and J. Vogelmann. 1993. A strategy for the regional analysis of the effects of physical and chemical climate change on biogeochemical cycles in northeastern (U.S.) forests. *Ecol. Modelling* 67:37-47.

Arthur, M. A., L. M. Tritton and T. J. Fahey. 1993. Dead bole mass and nutrients remaining 23 years after clearfelling of a northern hardwood forest. *Can. J. For. Res.* 23:1298-1305.

Bormann, B. T., F. H. Bormann, W. B. Bowden, R. S. Pierce, S. P. Hamburg, D. Wang, M. C. Snyder, C. Y. Li and R. C. Ingersoll. 1993. Rapid N₂ fixation in pines, alder and locust: evidence from the sandbox ecosystem study. *Ecology* 74(2):583-598.

Browne, B. A. and C. T. Driscoll. 1993. pH-dependent binding of aluminum by a fulvic acid. *Environ. Sci. Technol.* 27:915-922.

Bukaveckas, P. A., G. E. Likens, D. C. Buso and T. C. Winter. 1993. Hydrologic controls of chemical flux rates in the Mirror Lake watershed. *Verh. Internat. Verein. Limnol.* 25(1):419-422.

Findlay, S., K. Howe and D. Fontvieille. 1993. Bacterial-algal relationships in streams of the Hubbard Brook Experimental Forest. *Ecology* 74(8):2326-2336.

Findlay, S.E.G., G. E. Likens, L. Hedin, S. G. Fisher and W. H. McDowell. 1997. Organic matter dynamics in Bear Brook, Hubbard Brook Experimental Forest, New Hampshire, USA. In: J. R. Webster and J. L. Meyer (eds.). *Stream Organic Matter Budgets*. J. North Amer. Benthol. Soc. 16(1). pp. 43-46.

Gavin, D. and D. R. Peart. 1995. Effects of beech bark disease on growth of American beech (*Fagus grandifolia*). *Can. J. For. Res.* 23:1566-1575.

Ollinger, S. V., J. D. Aber, G. M. Lovett, S. E. Millham, R. G. Lathrop and J. M. Ellis. 1993. A spatial model of atmospheric deposition for the northeastern U.S. *Ecological Applications* 3:459-472.

Pardo, L. H. and C. T. Driscoll. 1993. A critical review of methods for calculating critical loads of nitrogen for forest ecosystems. *Environ. Reviews* 1:145-156.

Poage, N. J. and D. R. Peart. 1993. The radial growth response of American beech (*Fagus grandifolia*) to small canopy gaps in a northern hardwood forest. *Bull. Torrey Botanical Club* 120(1):45-48.

Pu Mou and T. J. Fahey. 1993. REGROW: a computer model simulating the early successional process of a disturbed northern hardwood ecosystem. *J. Appl. Ecology* 30:676-688.

Pu Mou, T. J. Fahey and J. W. Hughes. 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem. *J. Appl. Ecol.* 30:661-675.

Smith, W. H., R. C. Hale, J. Greaves and R. J. Huggett. 1993. Trace organochlorine contamination of the forest floor of the White Mountain National Forest, New Hampshire. *Environ. Sci. Technol.* 27(10):2244-2246.

1994

Dahlgren, R. A. and C. T. Driscoll. 1994. The effects of whole-tree clear-cutting on soil processes at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Plant Soil* 158:239-262.

Fahey, T. J. and M. A. Arthur. 1994. Further studies of root decomposition following harvest of northern hardwoods forest. *Forest Science* 40(4):618-629.

Fahey, T. J. and J. W. Hughes. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *J. Ecology* 82:533-548.

Hughes, J. W. and T. J. Fahey. 1994. Litterfall dynamics and ecosystem recovery during forest development. *For. Ecol. Manage.* 63:181-198.

Likens, G. E., C. T. Driscoll, D. C. Buso, T. G. Siccama, C. E. Johnson, D. F. Ryan, G. M. Lovett, T. Fahey and W. A. Reiners. 1994. The biogeochemistry of potassium at Hubbard Brook. *Biogeochemistry* 25:61-125.

Shabel, A. B. and D. R. Peart. 1994. Effects of competition, herbivory and substrate disturbance on growth and size structure of pin cherry (*Prunus pensylvanica* L.) seedlings. *Oecologia* 98:150-158.

Siccama, T. G., S. P. Hamburg, M. A. Arthur, R. D. Yanai, F. H. Bormann and G. E. Likens. 1994. Corrections to allometric equations and plant tissue chemistry for Hubbard Brook Experimental Forest. *Ecology* 75(1):246-248.

Veen, C., D. C. Buso, C. A. Federer and T. G. Siccama. 1994. Structure and function of the Hubbard Brook Data Management System. *Bull. Ecol Soc. Amer.* 75(1):45-48.

Zak, D. R., D. Tilman, R. R. Parmenter, C. W. Rice, F. M. Fisher, J. Vose, D. Milchunas and C. W. Martin. 1994. Plant production and soil microorganisms in late-successional ecosystems: a continental-scale study. *Ecology* 75(8):2333-2347.

1995

Aber, J. D., S. V. Ollinger, C. A. Federer, P. B. Reich, M. L. Goulden, D. W. Kicklighter, J. M. Melillo and R. G. Lathrop, Jr. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research* 5:207-222.

Christ, M., Y. Zhang, G. E. Likens and C. T. Driscoll. 1995. Nitrogen retention capacity of a northern hardwood forest soil under ammonium sulfate additions. *Ecol. Appl.* 5(3):802-812.

Johnson, C. E. 1995. Soil nitrogen status eight years after whole-tree clear-cutting. *Can. J. For. Res.* 25:1346-1355.

Johnson, C. E., T. G. Siccama, C. T. Driscoll, G. E. Likens and R. E. Moeller. 1995. Changes in forest lead cycling in response to decreasing atmospheric inputs. *Ecol. Appl.* 5(3):813-822.

Lovette, I. J. and R. T. Holmes. 1995. Foraging behavior of American Redstarts (*Setophaga ruticilla*) in summer and winter: an assessment of relative food availability. *The Condor* 97:782-791.

Ollinger, S. V., J. D. Aber, C. A. Federer, G. M. Lovett and J. M. Ellis. 1995. Modeling physical and chemical climatic variables across the northeastern U.S. for a geographic information system. *USDA Forest Service General Technical Report NE-191*. 30 pp.

Pardo, L. H., C. T. Driscoll and G. E. Likens. 1995. Patterns of nitrate loss from a chronosequence of clear-cut watersheds. *Water, Air, and Soil Pollution* 85:1659-1664.

Postek, K. M., C. T. Driscoll, J. D. Aber and R. C. Santore. 1995. Application of PnET-CN/CHESS to a spruce stand in Solling, Germany. *Ecol. Modelling* 83:163-172.

1996

Bailey, S. W., J. W. Hornbeck, C. T. Driscoll and H. E. Gaudette. 1996. Calcium inputs and transport in a base-poor forest ecosystem as interpreted by Sr isotopes. *Water Resour. Res.* 32(3):707-719.

Battles, J. J. and T. J. Fahey. 1996. Spruce decline as a disturbance event in the subalpine forest of the northeastern United States. *Can. J. For. Res.* 26:408-421.

Battles, J. J., T. J. Fahey and E.M.B. Harney. 1996. Spatial patterning in the canopy gap regime of a subalpine *Abies-Icea* forest. *J. Veg. Sci.* 6:807-814.

Battles, J. J., J. Dushoff and T. J. Fahey. 1996. Line intersect sampling of forest gaps. *Forest Science* 42:131-138.

Goodbred, C. O. and R. T. Holmes. 1996. Factors affecting food provisioning of nestling Black-throated Blue Warblers. *Wilson Bulletin* 108:467-479.

Holmes, R. T., P. P. Marra and T. W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *J. Animal Ecology* 65:183-195.

Hunt, P. D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwoods forest: evaluation of habitat quality. *The Auk* 113:875-888.

Likens, G. E. 1996. Air pollution and forest health. *Environmental Review* 3(8):1-6.

Likens, G. E., C. T. Driscoll and D. C. Buso. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* 272:244-246.

Likens, G. E., C. T. Driscoll and D. C. Buso. 1996. Acid rain revisited? [Letter in response to C. R. Frink and to J. W. Kirchner]. *Science* 273:294-295.

Lovett, G. M., S. S. Nolan, C. T. Driscoll and T. J. Fahey. 1996. Factors regulating throughfall flux in a New Hampshire forested landscape. *Can. J. For. Res.* 26:2134-2144.

Mitchell, M. J., C. T. Driscoll, J. S. Kahl, G. E. Likens, P. S. Murdoch and L. H. Pardo. 1996. Climatic control of nitrate loss from forested watersheds in the Northeast United States. *Environ. Sci. Technol.* 30(8):2609-2612.

Pardo, L. H. and C. T. Driscoll. 1996. Critical loads for nitrogen deposition: case studies of two northern hardwood forests. *Water, Air, and Soil Pollution* 89:105-128.

Romanowicz, R. B., C. T. Driscoll, T. J. Fahey, C. E. Johnson, G. E. Likens and T. G. Siccama. 1996. Changes in the biogeochemistry of potassium following a whole-tree harvest. *Soil Sci. Soc. Amer. J.* 60:1664-1674.

1997

Aber, J. D. and C. T. Driscoll. 1997. Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests. *Global Biogeochemical Cycles* 11:639-648.

Aber, J. D., S. V. Ollinger, C. A. Federer and C. T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecol. Modelling* 101:61-78.

Berger, T. W., S. L. Tartowski and G. E. Likens. 1997. Trifluoroacetate retention in a northern hardwood forest soil. *Environ. Sci. Technol.* 31(7):1916-1921.

Hornbeck, J. W., S. W. Bailey, D. C. Buso and J. B. Shanley. 1997. Streamwater chemistry and nutrient budgets for forested watersheds in New England: variability and management implications. *Forest Ecology and Management* 93:73-89.

Likens, G. E., S. L. Tartowski, T. W. Berer, D. G. Richey, C. T. Driscoll, H. G. Frank and A. Klein. 1997. Transport and fate of trifluoroacetate in upland forest and wetland ecosystems. *Proc. Nat. Acad. Sci. USA* 94:4499-4503.

Lovett, G. M., J. J. Bowser and E. S. Edgerton. 1997. Atmospheric deposition to watersheds in complex terrain. *Hydrological Processes* 11:645-654.

Richey, D. G., C. T. Driscoll and G. E. Likens. 1997. Soil retention of trifluoroacetate. *Environ. Sci. Technol.* 31(6):1723-1727.

Rodenhouse, N. L., T. W. Sherry and R. T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78(7):2025-2042.

Currie, W. S. and J. D. Aber. 1997. Modeling leaching as a decomposition process in humid, montane forests. *Ecology (In Press)*

1998

Driscoll, C. T., G. E. Likens, D. C. Buso and M. R. Church. 1998. Recovery of soil and surface waters in the northeastern U.S. from decreases in atmospheric deposition of sulfur. *[BIOGEMON Conf.] Water Air Soil Pollut. (In Press)*

Fahey, T.J., J.J. Battles, and G.F. Wilson. 1998. Response of early successional northern hardwood forests to changes in nutrient availability. *Ecol. Monogr. (In Press)*.

Johnson, D. W. and M. J. Mitchell. 1997. Responses of forest ecosystems to changing sulfur inputs. In: D. Maynard (ed.). *Sulfur in the Environment. (In Press)*

Likens, G. E., C. T. Driscoll, D. C. Buso, T. G. Siccama, C. E. Johnson, G. M. Lovett, T. J. Fahey, W. A. Reiners, D. F. Ryan, C. W. Martin and S. W. Bailey. 1998. The biogeochemistry of calcium at Hubbard Brook. *Biogeochemistry (In Press)*

Yimin Zhang, M. J. Mitchell, M. Christ, G. E. Likens and H. R. Krouse. 1998. Stable sulfur isotopic biogeochemistry of the Hubbard Brook Experimental Forest, New Hampshire. *Biogeochemistry (In Press)*

II. Books and Book Chapters

Martin, C. W. 1993. Hubbard Brook Experimental Forest, New Hampshire. p. 27. *In: M. Peale, R. Kavanagh, D. Taylor and C. Slaughter (eds.). Proc. of Chena Hot Springs Workshop, Strategies for Sustained Monitoring in Arctic and Subarctic National Park Service Units and Researched Areas. 24-27 January 1989. Fairbanks, Alaska. Natural Resour. Rep. NPS/AR/NRR-93-20, Anchorage.*

Sherry, T. W. and R. T. Holmes. 1993. Are populations of Neotropical migrant birds limited in summer or winter? Implications for management. pp. 47-57. *In: D. M. Finch and P. W. Stangel (eds.). Status and Management of Neotropical Migratory Birds. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO. General Tech. Report RM-229.*

Dahlgren, R. A. and C. T. Driscoll. 1994. The effects of whole-tree clear-cutting on soil processes at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Plant Soil* 158:239-262.

Driscoll, C. T. and G. E. Likens. 1994. Transport and fate of trifluoroacetate in the terrestrial environment. *In: Alternative Fluorocarbons Environmental Acceptability Workshop on Decomposition of TFA in the Environment, Washington, D.C. 13 pp.*

Johnson, C. E., M. I. Litaor, M. F. Bittlett and O. P. Bricker. 1994. Chemical weathering in small catchments: climatic and anthropogenic influences. pp. 323-341. *In: B. Moldan and J. Cerny (eds.). Biogeochemistry of Small Catchments: A Tool for Environmental Research. SCOPE. J. Wiley & Sons, Chichester, England.*

Swank, W. T. and C. E. Johnson. 1994. Small catchment research in the evaluation and development of forest management practices. pp. 383-408. *In: B. Moldan and J. Cerny (eds.). Biogeochemistry of Small Catchments: A Tool for Environmental Research. SCOPE. J. Wiley and Sons, Chichester, England.*

Driscoll, C. T. and K. M. Postek. 1995. The chemistry of aluminum in surface waters. pp. 363-418. *In: G. Sposito (ed.). The Environmental Chemistry of Aluminum. Lewis Publishers, Chelsea, MI.*

Johnson, C. E., C. T. Driscoll, T. J. Fahey, T. G. Siccama and J. W. Hughes. 1995. Carbon dynamics following clear-cutting of a northern hardwood forest ecosystem. pp. 463-488. *In: J. M. Kelly and W. W. McFee (eds.). Carbon: Forms and Functions in Forest Soils. American Society of Agronomy, Madison, WI.*

Likens, G. E. 1995. Sustained ecological research and the protection of ecosystems. pp. 13-21. *In: T. Herman, S. Bondrup-Nielsen, J.H.M. Willison and N.W.P. Munro (eds.). Ecosystem Monitoring and Protected Areas. Proc. Internat. Conf. on Science and the Management of Protected Areas. Wolfville, Nova Scotia, Canada.*

Santore, R. C. and C. T. Driscoll. 1995. The CHESS model for calculations equilibria in soils and solutions. pp. 357-375. *In: R. Loeppert, A. P. Schwab and S. Goldberg (eds.). Chemical Equilibrium and Reaction Models. Soil Sci. Soc. Am., Special Publication 42. Madison, Wisconsin.*

Schecher, W. D. and C. T. Driscoll. 1995. ALCHEMI: A chemical equilibrium model to assess the acid-base chemistry and speciation of aluminum in dilute solutions. pp. 325-351. *In: R. Loeppert, A. P. Schwab and S. Goldberg (eds.). Chemical Equilibrium and Reaction Models. Soil Sci. Soc. Am., Special Publication 42. Madison, Wisconsin.*

Sherry, T. W. and R. T. Holmes. 1995. Summer versus winter limitation of populations: conceptual issues and evidence. pp. 85-120. *In: T. E. Martin and D. M. Finch (eds.). Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues. Oxford University Press, New York.*

Likens, G. E. and F. H. Bormann. 1995. Biogeochemistry of a Forested Ecosystem. *Second Edition, Springer-Verlag New York Inc. 159 pp.*

USDA Forest Service, Northeastern Forest Experiment Station. 1996. Hubbard Brook Ecosystem Study. Site Description and Research Activities. *USDA Forest Service, NE-INF-96-96R. Second Edition. 53 pp.*

Findlay, S., G. E. Likens, L. Hedin, S. G. Fisher and W. H. McDowell. 1997. Organic matter dynamics in Bear Brook, Hubbard Brook Experimental Forest, New Hampshire, USA. pp. 43-46. *In: J. R. Webster and J. L. Meyer (eds.). Stream Organic Matter Budgets. J. North Amer. Benthol. Soc. 16(1).*

Holmes, R. T. and G. E. Likens. 1997. A checklist of organisms of the Hubbard Brook watershed-ecysystems, including Mirror Lake. *Unpublished Manuscript, Second Edition. August 1997, Unpublished Manuscript, Second Edition. 54 pp.*

Bledsoe, C.S., T.J. Fahey, F.P. Day and R. Reuss. Measurement of static root parameters — biomass, length, distribution. *In: Standard Soil Methods for Long-Term Ecological Research (G.P. Robertson, C.S. Bledsoe, D.C. Coleman and P. Sollins, editors). Oxford University Press, New York. In press.*

Bledsoe, C.S., T.J. Fahey, F.P. Day and R. Reuss. Measurement of static root parameters — biomass, length, distribution. *In: Standard Soil Methods for Long-Term Ecological Research (G.P. Robertson, C.S. Bledsoe, D.C. Coleman and P. Sollins, editors). Oxford University Press, New York. In press.*

Fahey, T.J., C.S. Bledsoe, F.W. Day, R. Reuss and A. Smucker. Fine root dynamics. *In*: Groffman, P.M., E. Holland, D. D. Myrold, G.P. Robertson and X. Zou. Denitrification. *In* Standard Soil Methods for Long Term Ecological Research (G.P. Robertson, C.S. Bledsoe, D.C. Coleman and P. Sollins, editors). Oxford University Press, New York. In press.

Holland, E.A., R. Boone, J. Greenberg, P.M. Groffman and G.P. Robertson. Measurement of Soil CO₂, N₂O and CH₄ exchange. *In* Standard Soil Methods for Long Term Ecological Research (G.P. Robertson, C.S. Bledsoe, D.C. Coleman and P. Sollins, editors). Oxford University Press, New York. In press.

Johnson, D. W. and M. J. Mitchell. 1997. Responses of forest ecosystems to changing sulfur inputs. *In*: D. Maynard (ed.). *Sulfur in the Environment*. (In Press)

Mitchell, M. J. 1997. Sulfur transformations and fluxes. *In*: C. W. Finkl (ed.). *The Encyclopedia of Soil Science and Technology*. Van Nostrand Reinhold Co., New York. (In Press)

Mitchell, M. J., C. R. Krouse, A. C. Stam and Y. Zhang. 1996. Use of stable sulfur isotopes in evaluating biogeochemistry of forest ecosystems. *In*: J. McDonnell and C. Kendall (eds.). *Isotope Tracers in Catchment Hydrology*. Elsevier, The Netherlands. (In Press)

Robertson, G.P., D. Wedin, P.M. Groffman, J.M. Blair, E.A. Holland, K.J. Nadelhoffer and D. Harris. Soil carbon and nitrogen availability: Nitrogen mineralization, nitrification and carbon turnover. *In* Standard Soil Methods for Long Term Ecological Research (G.P. Robertson, C.S. Bledsoe, D.C. Coleman and P. Sollins, editors). Oxford University Press, New York. In press.

III. Dissertations and Theses

1993

Christ, M. 1993. Investigating the role of base cation and ammonium deposition in soil and soil-water acidification at the Hubbard Brook Experimental Forest, New Hampshire. *Ph.D. Thesis, Rutgers University*. 222 pp.

1994

Bailey, S. W. 1994. Biogeochemistry of aluminum and calcium in a linked forest-aquatic ecosystem. *Ph.D. Thesis, Syracuse University, Syracuse, NY*. 75 pp.

Letvin, E. 1994. Adsorption of trifluoroacetate, chloride and bromide on a mineral soil of a forest spodosol. *M.S. Thesis, Syracuse University*. 101 pp.

Romanowicz, R. 1994. Changes in soil exchangeable cation pools and concentrations 8 years after whole-tree harvesting. *M.S. Thesis, Syracuse University*.

1995

Hunt, P. D. 1995. Habitat selection in the American Redstart (Setophaga ruticilla). The importance of early successional habitat and the role of landscape change in population declines. *Ph.D. Thesis, Dartmouth College. 152 pp.*

1996

Aloi, M. A. 1996. Aluminum and proton binding characteristics of a forest floor organic horizon leachate. *M.S. Thesis, Syracuse University. 142 pp.*

Arp, J. T. 1996. Ecological factors influencing habitat selection by foliage-gleaning birds along a vegetation gradient in a northern hardwoods forest ecosystem. *M.S. Thesis Tulane University. 94 pp.*

Schad, D. E. 1996. The biogeochemistry of silicon and sodium at the Hubbard Brook Experimental Forest. *M.S. Thesis, Syracuse University. 124 pp.*

1997

Fujikawa, W. 1997. A reconstruction of the presettlement forest in the White Mountains of New Hampshire. *Honors Thesis, Center for Environmental Science, Brown University.*

Taylor, L. A. 1997. An assessment of microbial biomass across a northern hardwood forest successional sequence. *M.S. Thesis, University of Kentucky. 85 pp.*

2.0 - Long-term Ecological Research at Hubbard Brook Experimental Forest

1. INTRODUCTION

In our continuing effort to comprehend the ecological patterns and processes characterizing the northeastern forest landscape, long-term measurements in and around the Hubbard Brook Experimental Forest (HBEF) repeatedly provide surprises and insights that both question our previous understanding and challenge us to improve our conceptualization of forest ecosystem structure and function:

- Forest biomass on the reference watershed (W6) at HBEF leveled off at a stand age 65 yr, much earlier than projected by earlier models of forest production and C balance. What factors govern the spatio-temporal patterns of C flux in the northeastern forest?
- Despite the reduction in biomass accumulation, N is strongly retained in the HBEF watersheds even in this region of high N deposition; in fact, preliminary studies suggest that productivity of stream biota is primarily N limited. What explains spatio-temporal patterns of N retention and flux in the northeastern forest?
- Long-term changes in the acid-base balance of the forest and linked aquatic ecosystems indicate that recovery from reductions in strong-acid loading will be slow and that ecological disruptions owing to soil Ca depletion may occur in some landscapes. How can spatio-temporal patterns in acid-base balance of forest watersheds be explained?
- Despite careful, long-term accounting of S inputs and outputs, the magnitude and dynamics of some important S sources remain highly uncertain. What are the important S sources in the HBEF forest and in other regional ecosystems?
- Varying temporal patterns of abundance within the passerine bird assemblage in the HBEF illustrate the complex food web interactions that control population sizes of the diverse heterotrophic community. What explains the spatio-temporal variations in population size of various nesting birds in the HBEF?
- During the second week of January, 1998 the HBEF and Northeast region was devastated by an extraordinarily severe ice storm. What determined the spatial patterns of its impacts and what will be the ecosystem responses to this intense, diffuse disturbance event?

The program of monitoring, experimentation and quantitative modeling in the HBR-LTER is designed to address these and related questions about forest ecosystem dynamics. As a central element of the Hubbard Brook Ecosystem Study (HBES), the LTER program provides both an intellectual core and a funding base from which we examine our theme — controls of the structure and function of the northern hardwood ecosystem. Our principal goal is to improve general understanding of the mutual influences of environment, disturbance, biological activity and the fluxes of energy and materials in the forest landscape. Our overarching research hypothesis is that biological activity (especially species distribution and abundance) is the mediator of the influence of environmental conditions and disturbance on biogeochemical cycling and energy flow. The context for this influence includes the complex food web of the northern hardwood forest; and we regard the biogeochemical (Fig. 1) and food web (Fig. 2) diagrams of the forest as the conceptual basis from which our research program is derived. By clarifying and quantifying the linkages within and among these conceptual models we are providing basic knowledge about ecosystem dynamics, as well as information that will help to inform policy-makers addressing difficult

environmental management problems such as changes in land-use, air and water pollution control, human settlement, exotic species invasions and pathogen outbreaks, and global climate change (Aber et al. 1997). Our participation in the larger LTER network provides both the opportunity and the responsibility for the HBES, in concert with the other sites, to continue to advance ecological science on regional, national and global scales.

Our proposed program of experimental and process research, monitoring, and simulation modeling is designed to address a series of objectives and specific hypotheses that expand upon the observations noted above. Although the focus of most of the research is the Hubbard Brook Valley and especially the experimental watersheds therein, our research program addresses ecological problems at a variety of scales. We regard the combination of precise, long-term measurements of environment and biota, and the experimental unit of the small watershed, as an ideal basis for improving understanding of ecosystem dynamics in these forest landscapes. However, we recognize and stress the need to analyze the catchment at finer resolution and also to expand the scales of measurement and modeling to encompass the broad region which the HBEF partially represents.

Research Themes. Three thematic categories underpin the research structure of this proposal: 1) biogeochemistry, 2) vegetation dynamics and primary production, and 3) heterotroph population studies. Although these categories are intimately interrelated in many respects, they do provide a convenient organizational structure. In the area of biogeochemistry our proposed work focuses upon C, N, S and Ca, and upon the acid-base, and microbially-mediated redox processes that largely determine their behavior. In addition to the studies described here, we recently submitted a proposal for separate NSF funding of a watershed-scale manipulation of soil Ca status through the application of a rapidly-weathering Ca-silicate mineral (wollastonite). Isotopic studies of the fate of the added Ca together with long-term, watershed mass-balance and plot-scale experiments on soil, microbial, vegetation and animal responses, will allow us to test a series of hypotheses about the role and mechanisms by which soil base status regulates ecosystem structure, function and composition. Our particular interest in the biogeochemical cycles of N and S builds upon past work, and is motivated by the recognition that important questions still remain to be answered regarding the behavior of these atmospherically derived nutrients and pollutants, as noted above.

At the scale of the experimental watersheds the dynamics of vegetation and primary productivity are well understood at HBEF. However, the analysis of vegetation patterns at both finer and coarser scales in the Hubbard Brook Valley (HBV) and the Northeast region suggests that variation at these scales could play an important role in determining the response of the forest to human-accelerated environmental change. For example, 1) unusual overstory mortality is observed only in certain landscape positions in the HBEF and this seems to be a region-wide phenomenon (Wilmot et al. 1995); and 2) the larger HBV is composed of a patchwork of stands that partly corresponds with patterns of topography and soils as influenced by bedrock and glacial deposits. Similar patch-scale variation in seedling and sapling recruitment and in net primary productivity, would emphasize the importance of understanding controls on the distribution and dynamics of these patches for predicting forest compositional change and emergent properties of the forest ecosystem.

We have focused our efforts in the area of heterotroph population dynamics on the diverse and complex assemblage of passerine birds. Although our general understanding of the processes regulating trends in abundance and distribution of birds in and around the HBEF is now well

developed, better quantification of certain crucial interactions is needed, especially the dependence of patterns of population abundances on 1) temporal variations in nest predation resulting from natural fluctuations in small mammal populations driven by masting cycles of trees; 2) temporal variations in food supply, especially phytophagous insects; and 3) spatial variations in habitat quality at the larger scale of the entire HBV. We propose to expand our investigations of heterotroph ecology by examining the role of moose in the structure and function of northern hardwood forest. This large mammal returned to the HBV in the last decade after a prolonged absence owing primarily to hunting pressure (Hicks 1986), and its effects on vegetation dynamics are already obvious.

In sum, our coordinated research program in the HBR-LTER is the logical outgrowth of previous studies that have provided a quantitative and integrative understanding of the composition, structure and function of northern hardwood forest ecosystems. We expect that the mutual influences of environment, disturbance, and biota in regulating nutrient cycles, energy flow and the composition of biological community will be clarified by these continuing studies and that as a result, predictions of responses to human-accelerated environmental change and the design of public policies will be improved.

Intensive Study Sites. Most of the research in the HBR-LTER project is concentrated at the HBEF in the White Mountains of central NH (Fig. 3). Because of space limitations we refer readers to detailed descriptions of the climate, soils, vegetation, and history of the HBEF at our WWW Homepage (<http://www.hbrook.sr.unh.edu>) or in Likens and Bormann (1995). At the HBEF we have been using the small watershed approach to quantify the response of forest and aquatic ecosystems to disturbance, and several experimental watersheds on the south-facing slope have been manipulated for this purpose (Table 1). Increasingly we have broadened the scope of our studies to encompass the wider HBV including north-facing experimental watersheds and additional landscape elements at HBEF. For example, Mirror Lake is a small (15 ha), clearwater lake near the mouth of the HBV. Extensive research has been done on the limnology, hydrology and paleoecology of the lake (Likens 1985; Bukaveckas et al. 1998a,b; Rosenberry et al 1998; Winter et al 1989). We have measured precipitation and the inlets and outlet for the lake since 1965, and propose to continue these measurements as part of this LTER. Detailed data on the inlets and outlet streamflow and groundwater flux for the lake are provided from the USGS.

The HBR-LTER also encompasses other regional forested sites that provide further context for studies at HBEF (Fig. 4). In particular, The Bowl Natural Area (BNA) is a nearby large watershed (206 ha) with no history of logging, human settlement or forest fire (Leak 1973), but in other respects closely resembles HBEF. The HBR-LTER supports periodic surveys of forest vegetation and element cycling at BNA that follow on earlier efforts (Martin 1979) and provide a comparative basis for interpreting temporal patterns at HBEF. Cone Pond Watershed (CPW) is a 53-ha catchment near HBEF that forms a regional "end-member" in terms of low soil base (fertility) status (Bailey et al. 1995, 1996; Hornbeck et al. 1997). The site experienced a major fire around 1820. The watershed is gauged and has been monitored for precipitation chemistry, throughfall chemistry, soil and soil solution chemistry, vegetation, hydrology and stream chemistry since 1988. We propose to continue these measurements of CPW as part of this LTER.

Study Regions. The HBR-LTER involves larger scale analyses of several relevant regions, including the northeastern U.S., the White Mountain Ecological Zone (WMEZ) and the Pemigewassett-Merrimack River (PMR) drainage basin (Fig. 4). The HBEF is part of the northeastern U.S., a region that is largely forested and contains abundant surface water resources (e.g., 7096 lakes >4 ha) that are characterized by low ionic strength and low acid neutralizing capacity (ANC). Across the Northeast we have analyzed the effects of atmospheric deposition on soil and surface water chemistry (Ollinger et al. 1993; Aber et al. 1997; Driscoll et al. 1998). Geographic information system (GIS) data layers for the Northeast region used in our analyses include a digital elevation model (DEM), precipitation, atmospheric deposition, vegetation, soil chemistry, and surface water chemistry. In this LTER proposal, we will examine factors regulating dissolved inorganic N (DIN) loss, controls of surface water SO_4^{2-} concentrations and soil Ca^{2+} depletion across the Northeast region and compare these results to patterns observed at the HBEF (see 2.2, 2.3, 2.4).

The HBEF is located in the southern part of the WMEZ. The White Mountains are over 90% forested with northern hardwood the predominant forest type, and conifers dominate in rocky and sandy habitats as well as above 775 m in elevation. Timber products and recreation dominate the economy, industries that are dependent on the ecological health of the region. GIS data layers for the WMEZ include a DEM, land-use, population density, roads, soils, hydrography, and precipitation quantity and chemistry. In 1995, as part of the current LTER, we conducted a survey of the water chemistry of the 130 ponded waters in the WMEZ. This survey will be repeated in 2000 as part of the proposed LTER.

Hubbard Brook is a headwater tributary to the PMR basin, and we have been investigating spatial and temporal patterns in the water quality of this 13,000 km² basin which drains from the White Mountains to the Atlantic Ocean. Land-use varies within the basin from largely forested wilderness areas in the north to increasingly residential and urban lands in the south. We have measured mass fluxes of major solutes for various sub-catchments of this basin, and we are currently synthesizing these results in conjunction with a GIS for the basin that includes a DEM, land-use, population density, soils, roads, political boundaries, industrial and municipal point sources, hydrography, and precipitation quantity and chemistry. This information is being used to assess the role of atmospheric deposition, and land-use and residential development in regulating water quality in the basin.

Description of Long-term Data Sets. A major element of the HBR-LTER is the development of long-term records for reference and experimentally manipulated watershed-ecosystems including: 1) meteorology and hydrology (since 1956); 2) precipitation and streamwater chemistry (1963); 3) forest vegetation (1965); and 4) forest floor mass and chemistry (1965) (Likens et al. 1977, 1984, 1985; Likens and Bormann 1995; Federer et al. 1990; Table 2). Annual quantitative surveys of bird and phytophagous insect populations within the forest have been conducted since 1969 (Holmes 1988). Largely through the HBR-LTER, long-term studies of air chemistry, throughfall, litterfall, fine root activity, microbial activity, soil water and soils have been initiated to develop a more comprehensive understanding of the ecology of the northern hardwood forest ecosystem. **The great value of these monitoring efforts is emphasized by the background they provide for quantifying responses to catastrophic events such as the January 1998 ice storm which will provide a natural experiment in coming years.**

Our long-term measurements have largely focused on the south-facing experimental watersheds (i.e., W1-6). As part of the proposed LTER, we plan to expand this effort to include north-facing experimental watersheds (Fig. 3). The north-facing watersheds at the HBEF are characterized by cooler climate, and a greater proportion of coniferous vegetation.

The routine measurement of precipitation and stream chemistry in 18 experimental watersheds is the backbone of the biogeochemical monitoring program (Fig. 5). All water samples are analyzed for all major solutes. The Hubbard Brook LTREB project "Hydrologic-element cycle interactions in small undisturbed and human-manipulated ecosystems" funded by the NSF, provides about 40% of the funding for the routine collection and analysis of precipitation and stream samples described above. We are requesting here funds to support about 60% of this critical monitoring. Thus, both of these funding sources are necessary to sustain the long-term records of biogeochemistry at HBEF.

Other ongoing monitoring programs (Table 2) are conducted at a number of sites within the HBEF. Complete forest surveys (all stems > 10 cm dbh) and forest floor collections are made every five years in W6. Atmospheric chemistry monitoring has continued since 1989 at two sites in the HBEF, and dry deposition is measured at W6 using three methods (inferential, throughfall, and watershed mass balance; Lovett et al. 1992). Litterfall, microbial activity and soil solution monitoring are conducted immediately west of W6 to minimize disturbance to this reference site. Fine roots are monitored using fine root coring, and observation of root growth and longevity using minirhizotrons. Bird and insect population monitoring is conducted in a large area west of W6.

Description of Models Used. We use models as research tools, to facilitate hypothesis testing and to integrate ecosystem studies. The hydrologic model, BROOK, was developed for small forest watersheds, and was based on research at the HBEF (Federer and Lash 1978). We have developed and linked two submodels to produce a comprehensive forest-soil-water model to simulate element cycling in forest and interconnected aquatic ecosystems. These submodels include: 1) PnET (Aber and Federer 1992; Aber et al. 1997; Aber and Driscoll 1997), a simple and well-validated model of monthly carbon, water and nutrient balances, which provides estimates of forest net primary productivity, nutrient uptake by vegetation and water balances; and 2) CHESS (CHEMical Equilibrium of Soils and Solutions; Santore and Driscoll 1995) a soil column model which simulates abiotic soil processes, such as cation exchange, weathering, adsorption and solution speciation. Separately or linked (PnET/CHESS), these models will be used to assess the effects of air pollution and land-use disturbance on the biogeochemistry of forest and aquatic ecosystems (e.g. Postek et al. 1995; Driscoll et al. 1998; see 2.2, 2.3, 2.4). Finally, we are using a nutrient uptake model (Yanai 1994) to simulate solute uptake at the root surface, and its dependence on solute movement to the root through the soil by mass flow and diffusion. The nutrient-uptake model will be used in a LTER cross-site study of root nutrient uptake in forest ecosystems (see 5.0).

Core Area Coverage. Because of space limitations we refer the reviewer to Table 3 for a summary of how this proposed research covers the LTER core areas.

2. BIOGEOCHEMICAL STUDIES

The biogeochemistry of forest watersheds in the northeastern U.S. is strongly regulated by natural factors and human disturbance. Cool, moist conditions limit the decomposition of organic matter and most elemental cycles are closely coupled with the dynamics of organic matter. Moreover, these watersheds are generally characterized by shallow deposits of surficial materials, soil minerals with slow rates of chemical weathering, and low concentrations and pools of exchangeable base cations in soil (April and Newton 1985; Driscoll 1991; Eilers and Selle 1991). These conditions result in low ionic strength, acidic drainage waters. Human disturbance alters the biogeochemistry of these watershed ecosystems. Atmospheric deposition of strong acids (H_2SO_4 , HNO_3) to forest watersheds accelerates the depletion of labile pools of nutrient cations from soil (Kirchner 1992; Likens et al. 1996, 1998; Bailey et al. 1996), the mobilization of Al from soil to drainage waters (Cronan and Schofield 1979, 1990) and the acidification of surface waters (Driscoll and Newton 1985). Elevated atmospheric deposition of N may result in nutrient imbalances in forest vegetation (Aber et al. 1995), soil and surface water acidification (Reuss and Johnson 1986; Schaefer et al. 1990), eutrophication of coastal waters (Fisher and Oppenheimer 1991) and changes in trace gas emissions (Steudler et al. 1989; Bowden et al. 1991). Clear-cutting results in marked increases in drainage losses of nutrients due to acidification of soil and drainage water associated with enhanced nitrification (Dahlgren and Driscoll 1994). Over the longer term, regrowing vegetation enhances nutrient retention (Pardo et al. 1995) and the redistribution of soil pools following clear-cutting alters stream nutrient loss (Romanowicz et al. 1996). Human settlement will enhance element losses in drainage water and result in a deterioration of water quality (Valiela et al. 1997).

Our general objective is to quantify spatial and temporal patterns of element concentrations and fluxes and to assess their response to natural factors such as climate, vegetation, geomorphology and bedrock geology and human disturbances such as air pollution, clear-cutting and human settlement. We will use our ongoing measurements of precipitation chemistry, litterfall, microbial biomass and transformations, vegetation uptake, soil, soil water and stream chemistry and model calculations to test hypotheses on the biogeochemical response of forest watersheds to environmental conditions and human disturbance. Results of site specific observations will be extrapolated to the northeastern region, the WMEZ, and the PMR basin regions using GIS and model calculations.

OBJECTIVE 2.1. To evaluate the factors controlling organic carbon concentrations in soil and drainage water across the HBEF landscape.

Drainage losses of dissolved organic carbon (DOC) are of particular interest because of the contribution of organic acids to the acid-base chemistry of drainage waters, the transport and speciation of trace metals and the effects of DOC on drinking water potability (Driscoll et al. 1994 a,b). Our previous studies of detrital organic matter in the reference (W6) watershed and in adjacent W5 at the HBEF have shown that pools of soil organic C are highest at the upper elevations (Fig. 6). We have hypothesized that this pattern is due to cooler temperatures, the predominance of coniferous vegetation and a relatively flat slope in the upper reaches of these south-facing watersheds but the relative importance of these factors remains uncertain. Soil carbon pools appear to coincide with leaching of DOC and associated elements (Fig. 7; Driscoll et al.

1988). Conifers comprise a larger fraction of the forest vegetation in the north-facing watersheds (Fig. 8) that generally have higher DOC concentrations in streamwater than the south-facing watersheds. However, differences in DOC are evident across the three north-facing watersheds, with significantly higher concentrations of DOC in W9 (7.1 mg C/L) than W7 (1.7 mgC/L) or W8 (2.9 mg C/L). We believe these patterns in DOC concentrations are due more to differences in watershed topography, than climate or vegetation. In contrast to W7 and W8, W9 is characterized by a relatively large flat area where restricted drainage may allow for the accumulation of soil organic C and contribute to the elevated DOC observed in W9.

Hypothesis 2.1. Watershed topography exerts primary control over soil organic C and stream DOC losses in upland catchments at HBEF, with forest vegetation composition (conifer vs. hardwood) playing a secondary role.

To test hypothesis 2.1, we propose to supplement our studies of organic C dynamics on the south-facing experimental watersheds with analogous work on north-facing W8 and W9. We will establish an elevation transect of four intensive monitoring sites in W8 and W9 and we will measure litterfall, microbial biomass and activity, and the chemistry of soil water and streams. Forest biomass will be estimated by measuring the dbh of all trees with dbh ≥ 10 cm on 120 randomly located plots in both W8 and W9 (i.e., 240 plots total). Forest floor samples will be collected at 100 randomly located sites in both W8 and W9 using the "pin-block" method (e.g., Federer et al., 1993). Mineral soil samples will be collected from 50 soil pits in each watershed, fifteen of which will be excavated using the quantitative approach of Huntington et al. (1988). Data collected in this effort will enable us to construct detailed C budgets for W8 and W9, as we have previously done for W6 and W5 (Johnson et al. 1995). We will compare patterns of C concentration and dynamics for W8 and W9, with our values for W6. The patterns of variation in vegetation, topography and soil and surface water carbon within and between these watersheds will enable us to elucidate the controls on the biogeochemistry of detrital organic C.

OBJECTIVE 2.2. To understand and quantify patterns of N cycling and loss.

Long-term monitoring of N in plant biomass, litterfall, soil solutions, stream water and microbial biomass has revealed interesting spatial and temporal patterns that will guide our research over the next six years. There are strong patterns of N cycling with elevation within watersheds of HBEF. Forest floor depth and microbial biomass and activity are highest at the highest elevations (Fig. 6), but concentrations of dissolved inorganic N (DIN) in the soil solutions and streamwater peak at intermediate elevations (Fig. 7). Soil depth and vegetation production decrease with increasing elevation. Patterns of N cycling with elevation are controlled by complex interactions between plant, soil, microbial, climatic and hydrologic factors.

The N saturation hypothesis suggests that leaching losses of NO_3^- will increase in forest watersheds under elevated inputs of DIN from atmospheric deposition and as the rate of accumulation of N in biomass decreases with increasing stand age (Stoddard 1994). The 80-yr stand on W6 at the HBEF is an ideal site to examine the linkage between atmospheric deposition of N, the accumulation of N in forest biomass and stream N loss. Biomass accumulation on W6 was

rapid through the early years of the study (1960s), then declined through 1982 and no net increase of living biomass has occurred since 1982 (Likens et al. 1994; Fig. 9). Early in the study period (1963-1976), we observed a pattern of increasing NO_3^- concentrations and loss in streamwater from W6 (Fig. 5,10). However, since the mid-1970's there has been a decline in stream NO_3^- . Streamwater loss of NO_3^- from W6 is currently the lowest value observed during the 33-yr study. This long-term pattern in stream NO_3^- loss is one of the most interesting and perplexing characteristics of the long-term biogeochemical record at the HBEF.

While the mechanism controlling interannual stream NO_3^- loss at the HBEF is not clear, climate may be an important determinant. Using the model PnET, Aber and Driscoll (1997) were able to explain 29% of the variance in annual NO_3^- loss in W6 (Fig. 10). Much of this variation as predicted in PnET was due to climatic variation.

To examine the longer-term response of the northern forest to atmospheric deposition of N, we calculated the annual retention coefficient of DIN ($\text{DIN}_{\text{bulk deposition}} - \text{DIN}_{\text{stream outflow}} / \text{DIN}_{\text{bulk deposition}}$) for a chronosequence of watersheds of different stand age in the HBV and mature forests at the nearby BNA and CPW (Fig. 11). This analysis suggests that young, strongly aggrading stands (recently cut W2, W4, W5) retain a large fraction of atmospheric inputs of N. With increasing stand age the extent of N retention decreases except for the CPW which was severely burned two centuries ago. While this pattern follows the general paradigm suggested for temperate forest ecosystems (Vitousek and Reiners 1975), there is considerable year-to-year and decade-to-decade variability in N loss and watershed retention. Hence, while the concept of N-saturation is a useful model of N loss over the time-scale of forest development (i.e., centuries), it is more problematic to assess the response of forest watersheds to atmospheric N deposition over the time scale of decades.

The effects of N or P additions on algal assemblages of stream ecosystems depend upon which nutrient limits primary production (Fairchild et al. 1985; Meyer et al. 1988). Within temperate forests, freshwater systems generally were considered to be P limited (Schindler 1974), but recent research in lakes has shown that N is limiting as often as P and that most aquatic systems are co-limited by N and P (Elser et al. 1990). We recently found in Bear Brook at the HBEF that stream DIN concentrations are now sufficiently low relative to P in the summer to cause N limitation of algal growth (E. M. Bernhardt, unpubl. data). These observations lead to the following hypotheses:

Hypotheses 2.2.1. Spatial patterns of N loss in streamwater are the result of complex interactions between climate, vegetation, soil, microbial activity and hydrologic conditions.

Hypothesis 2.2.2. The cessation of forest biomass aggradation at the HBEF will result in reduced net uptake of N, and streamwater concentrations of NO_3^- will increase particularly during the growing season.

Hypothesis 2.2.3. The degree of N limitation in stream ecosystems will be greater in more recently cut forests than more mature forests. The degree of N limitation of stream algal biomass will be greatest in summer when stream NO_3^- concentration is lowest.

We will use our ongoing biogeochemical measurements in the reference area west of W6 together with stable isotope data to test hypothesis 2.2.1. Litter quality, quantity and composition have been monitored in this area since 1984 (Hughes and Fahey 1994). Microbial biomass C and N content, microbial activity (potential net N mineralization and nitrification, denitrification, soil respiration) have been monitored since 1994 using methods in Groffman et al. (1996). Soil solution chemistry is monitored at three horizons at three elevations west of W6 using methods in Driscoll et al. (1988). Stream chemistry is measured at 5 stations along an elevational gradient in W6 (Likens et al. 1994). These data sets are critical for interpreting spatial, seasonal and annual variation in plant and microbial N cycling and will enable us to test hypothesis 2.2.1.

Stable isotopes are a useful tool for evaluating N cycling intensity and history of NO_3^- loss (Nadelhoffer and Fry 1994). Microbes discriminate against ^{15}N during microbial transformations of N, creating pools within the ecosystem with distinct isotopic signatures. At sites with high rates of N cycling and NO_3^- loss, remaining soil and plant material becomes enriched in ^{15}N . In a past study, we related nitrification rate to soil ^{15}N at three sites across a gradient of NO_3^- loss in the Hubbard Brook region (Fig. 12; Pardo et al., in prep.). In coming years we will continue to evaluate ^{15}N in soil and litter in relation to N cycling measurements at a variety of scales, from plots in HBEF to regional comparisons. In addition, we will begin to measure $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ in soil solutions to evaluate the intensity of N cycling by soil horizon and to determine the sources of plant available N. Monthly measurement of ^{15}N in soil solutions from Oa, B₁ and B₂ horizons at three elevations, in streamwater at five elevations and in precipitation will allow us to characterize the nature of N cycling. Finally, we will continue our long-term measurements of N in streamwater in the HBEF watersheds, CPW and the BNA to test hypothesis 2.2.2. We will continue to use PnET, and atmospheric deposition, vegetation and climatic data to probe factors regulating stream N loss.

To test hypothesis 2.2.3, we will examine nutrient limitation and transport in 2nd order streams of 8 watersheds in and around the HBEF, ranging from the BNA to a 1985 clear-cut (W5) and CPW (Fig. 11). We will assess nutrient limitation and nutrient transport at three seasons using nutrient diffusing substrates placed throughout each study reach following the method described by Winterbourn (1990), and Corkum (1996). Substrates will be enriched with N (NH_4NO_3) and P (PO_4^{3-}) in a factorial design. After 2 weeks, we will collect substrates and determine chlorophyll a biomass and algal assemblage structure. We expect chlorophyll a to be highest on substrates that provide the limiting nutrient. Epilithon N:P will be measured, and should reflect stream N:P ratios (P. J. Mulholland pers. comm.). We will add NO_3^- , NH_4^+ and PO_4^{3-} along with a conservative Cl^- tracer into streams to examine transport distance and uptake rates of these nutrients (Stream Solute Workshop 1990). We expect that streams that are N limited will have short N transport distances relative to P, as has been found in other streams (Munn and Meyer 1990, Marti and Sabater 1996).

OBJECTIVE 2.3. To evaluate controls on SO_4^{2-} loss from forest watersheds in the northeastern U.S.

We have observed a marked decline in annual volume-weighted concentrations of SO_4^{2-} in precipitation and streamwater at the HBEF, that closely corresponds to declines in emissions of SO_2 (Fig. 13). Assessing future recovery associated with continued reductions in SO_2 emissions is limited by uncertainty in sources of S inputs to watersheds. Several studies have documented a

discrepancy in the S budget for watersheds in the Northeast (Norton et al. 1988; Likens et al. 1990; Mitchell et al. 1996) and simulations using CHESS (Driscoll et al. 1998) suggest that either of two alternative mechanisms explain the missing S source: 1) significant underestimation of dry S deposition, and/or 2) internal watershed S sources, such as mineralization of soil organic S pools or weathering of S minerals. Close agreement between measured and model results precluded identification of which of the two mechanisms controlled long-term trends in stream SO_4^{2-} (Fig. 14). Model simulations indicated that soil adsorption reactions significantly delayed the response of stream water to declines in SO_4^{2-} inputs since 1970, but could not explain the discrepancy in watershed S budgets.

Hypothesis 2.3. Net mineralization of soil organic S pools supplies SO_4^{2-} to drainage water, thereby delaying the response of stream water to decreases in atmospheric S deposition.

To test hypothesis 2.3, we will continue to measure S in atmospheric deposition and streamwater. We will initiate new measurements of S in forest vegetation and litter to provide more detail on the S cycle at the HBEF. These measurements will be supplemented by measurements of stable S isotope ratios in archived precipitation and stream samples to attempt to assess the source(s) of SO_4^{2-} in streamwater (Mitchell et al., in press). Finally, we will expand PnET/CHESS to consider microbial immobilization of SO_4^{2-} and mineralization of soil organic S pools using the formulations and rate data provided in Fuller et al. (1986).

OBJECTIVE 2.4. To quantify the depletion of labile Ca^{2+} from soil pools in the HBEF and the northeastern U.S. and to assess the ecosystem response to this perturbation.

Long term biogeochemical studies at the HBEF have revealed a marked depletion of reactive Ca^{2+} from soil (Likens et al. 1996; 1998; Fig. 15). This depletion of soil Ca^{2+} is largely a consequence of elevated inputs of strong acids from atmospheric deposition and has been reported for several other acid-sensitive sites in eastern North America and Europe (Kirchner 1992; Bailey et al. 1996). Calcium is the major nutrient cation of the soil exchange complex and the major cation in drainage waters at HBEF. The supply of Ca^{2+} is a critical controller of the acid-base status of soil and drainage waters, and as a result is important in regulating the structure and function of the northern hardwood forest and associated stream ecosystems.

Hypothesis 2.4.1. The rate of soil Ca^{2+} depletion will decrease and the acid neutralizing capacity of surface waters will increase in response to decreases in atmospheric deposition of SO_4^{2-}

Hypothesis 2.4.2. The % Ca saturation of the soil exchange complex is an important master variable regulating the structure and function of the northern hardwood forest.

We will use two approaches to assess depletion of soil Ca^{2+} . First we will use the mass balance approach described in Likens et al. (1996). Second we will use PnET/CHESS as a research tool to evaluate soil Ca^{2+} depletion. Model simulations initially will be compared to measured mass balance calculations (Likens et al. 1996) to evaluate the effectiveness of model predictions. Then the model will be used to probe the recovery of soil and surface waters at the

HBEF in response to decreases in SO₂ emissions that are planned as a result of the 1990 Clean Air Act Amendments. In 1995 as part of the HBR-LTER a synoptic survey was conducted of the water chemistry of ponds in the WMEZ. This survey will be repeated in 2000 as part of this proposed study. We will use information from these surveys to assess the response of the WMEZ to changes in atmospheric deposition.

We have proposed, under separate funding, to manipulate the supply of Ca²⁺ to a small watershed (W1) at HBEF to investigate responses of soil chemistry, soil microbes and invertebrates, vegetation and animal communities and stream biota. This experiment was designed as a 50-year study. If funded, at the end of the five-year project period, measurements of the longer-term response of the ecosystem to the experimental treatment will be included as part of the HBR-LTER, including measurements of precipitation, chemistry, vegetation, litter, microbial biomass and activity, soil, soil water chemistry and stream chemistry for W1.

OBJECTIVE 2.5. To evaluate the impact of human settlement on water quality.

Our long-term data show marked changes in the water quality of the lower HBV. Housing development, with associated septic-field drainage, in the Mirror Lake watershed near the mouth of the Valley has increased in the last 5 yr. Comparison of data from Hubbard Brook at the outlet of the HBEF (unimpacted by human settlement) with the lower reaches of Hubbard Brook (population density = 30 per km² in a watershed area 8% of the HBEF) demonstrate that even relatively sparsely populated areas can have marked effects on water quality (Fig. 16). In particular, NO₃⁻ concentrations in streamwater below the reach of human housing are elevated during the low-flow summer period, in contrast to very low values draining the HBEF. Likewise our ongoing investigation of spatial controls on the water chemistry of the PMR basin show marked increases in solute concentrations and fluxes from the WMEZ wilderness areas to downstream areas of human settlement (highly urbanized areas of southern NH and northeastern MA; Fig. 17). Historical data that are available suggest marked changes in water chemistry have occurred in the Pemigewassett-Merrimack River since the early 1970's (Ceaser et al. 1976).

Hypothesis 2.5. Increasing concentrations of nutrients (e.g. NH₄⁺, NO₃⁻, dissolved organic N, total P, Ct) in surface waters reflect the extent of human settlement.

To test hypothesis 2.5 we will use our long-term data and continue measurements of water chemistry in the tributaries and outlet of Mirror Lake and from nests of piezometers and groundwater wells distributed around the Lake and from stream sampling sites along Hubbard Brook. We will conduct mass balances of solute loss at these stream sites to examine the role of human settlement on water quality anticipating continuing increases in local population density. This work will be integrated with the larger scale studies of the PMR basin to improve understanding of the roles of atmospheric deposition and residential development on regional surface water element fluxes.

3. VEGETATION DYNAMICS AND PRIMARY PRODUCTIVITY

By providing the energy base and the structure that regulate habitat quality and drive biogeochemical cycles, trees play a dominant role in forest ecosystem biology, and hence understanding controls on tree distribution, abundance and growth is central to any program of study of forest ecosystems. Our current conceptual model for the northern hardwood forest emphasizes the mutual interactions among disturbance, environment and tree life history characteristics, but at present takes only limited account of landscape-level patterns. The shifting-mosaic steady state that typified pre-Columbian forest dynamics in northern New England consisted of a patchwork whose structure, pattern and composition was set by a combination of frequent small-scale disturbance (individual tree falls) and rarer large-scale disturbances (hurricanes, ice storms) non-uniformly distributed across the matrix of climatic (elevation and aspect) and topoedaphic gradients (Bormann and Likens 1979). To provide an improved context for quantifying forest ecosystem structure and function and predicting responses to human-accelerated environmental change, we seek a better understanding of the mechanisms that have given rise to the current forest patterns in the HBV, especially those operating at the landscape level.

The HBV, as well as our old-growth reference watershed (BNA), are ecotonal landscapes at the interface between the broadleaf deciduous (northern hardwood) and needleleaf evergreen (spruce-fir) forest biomes. The coniferous forest dominates the highest elevations and interdigitates into the broadleaf forest at various landscape positions throughout these valleys (Fig. 8). We propose to advance understanding of forest dynamics at this ecotone by combining field sampling of forest disturbance, composition, productivity and nutrient status using our network of permanent plots; mapping of vegetation associations and foliar N content; terrain analysis using DEM and field sampling of glacial till and soils; and statistical and simulation modeling of vegetation distribution and primary productivity.

Permanent Plots. A network of permanent vegetation plots has been established in and around HBEF at different scales, intensities and extents to examine long-term changes in forest structure, composition and productivity (Table 4). The routine measurement of these plots is supported in part through LTER funding. Initially these plots were concentrated on the experimental watersheds where they have provided critical information for calculating watershed mass balances. More recently, we have established several other sets of permanent vegetation plots to provide a wider context for these studies, including 1) an intensive sample of contiguous plots in the hardwood forest zone ("bird-line plots", Fig. 3) for calculating spatial patterns of growth and mortality; 2) a Hubbard Brook Valley-wide set of 370 plots (.05 ha each) established on a grid (Fig. 3); 3) an analogous set of 200 plots in the BNA; and 4) a chronosequence of forests on abandoned fields near HBEF and with similar edaphic and climatic characteristics. Together these permanent plots provide essential basic information on vegetation distribution and abundance and changes through time at a variety of scales and under different disturbance histories. During this LTER funding cycle, remeasurements are proposed for W6 (Fig. 9); a 30-yr sample of regrowth on W2 to expand and update the analysis published by Reiners (1992); a 20-yr sample of regrowth on W5 to expand and update the analysis of Mou et al. (1993); biennial sampling of 10,000 tagged trees on the "bird-line plots" to continue the record of spatial patterns in growth and mortality

(Siccama et al., in prep.); and 25-year resampling of old-field chronosequence plots (Thorne and Hamburg 1985).

OBJECTIVE 3.1: Reconstruction of the recent disturbance history of the HBV and the BNA.

Hypothesis 3.1. Current spatial patterns of tree distribution and abundance are weakly correlated with disturbance history since the mid-1800s.

In previous work, we have quantified forest responses to major disturbances (C. Cogbill, in prep.; Merrens and Peart 1992) in some parts of the HBV. However, a comprehensive set of information covering the entire valley is needed to interpret the influence of disturbance on vegetation pattern. Towards this purpose, tree cores have been collected from old spruce and beech trees at each of the 370 valley-wide plots. We propose to analyze these cores for release dates using standard dendrochronology techniques. Disturbance history coverages will be digitized into the Hubbard Brook GIS and we will analyze elevational, topoedaphic and spatial influences on disturbance history using standard ordination methods (Jongman et al. 1995).

OBJECTIVE 3.2. To quantify spatial patterns of forest vegetation and environment in the HBV and the BNA.

Like most glacial landscapes, the HBV and the BNA exhibit a complex array of soil parent materials and soil taxonomic units. Variation in these topoedaphic factors locally alters environmental conditions and soil resource availability and influences the forest vegetation composition (Leak 1980) and together with elevation and disturbance history exerts primary environmental control over forest distribution patterns. Much of the apparent patchiness in distributions of the dominant species (Fig. 18) and vegetation associations in the HBV probably is associated with this topoedaphic variation.

It has been suggested (Delcourt and Delcourt 1992; Neilson 1993) that relatively homogeneous patches of vegetation are smaller in ecotonal areas because plant species are more environmentally constrained near the limits of their geographic distributions than at biome core areas. Similarly, the concept of centrifugal niche organization (Keddy 1990) proposes that the most productive habitat in a landscape can be considered the core area where the most competitive species in the landscape dominate, and less competitive species are constrained to a series of marginal, less productive habitats where special adaptations allow them to thrive.

Hypothesis 3.2.1. Overstory composition reflects the distribution of habitat types (sensu Leak, 1980) in the HBV and BNA.

Hypothesis 3.2.2. The patch structure of the forest vegetation is more strongly correlated with topoedaphic patterns as the ecotone between hardwood and conifer forest biomes is approached.

We will utilize existing high resolution (1:6000) color infra-red images (Enslin and Sullivan 1974) to subdivide hardwood-dominated sites into compositional units in the region

(Hershey and Befort 1995) thereby increasing the detail of our existing map (Fig. 8). Second, we will derive topographically-related factors from the DEM and construct logistic regression models for the distribution of principal vegetation associations using the topographic factors, disturbance history and vegetation maps (Brown 1994). The fit and accuracy of the models will be tested with R^2 and the κ statistic, respectively, by comparison with actual distributions measured in the Valley-wide plots. We expect that some of the unexplained variation in abundance patterns will be explained by soil properties associated with different parent materials. These will be sampled on a sub-set of the permanent plots by excavating soil pits to the C horizon and classifying till and soil types (Leak 1980).

The recognition of space as an ecological variable and spatial heterogeneity as an important feature of vegetation and ecosystem dynamics (Turner and Gardner 1991; Li and Reynolds 1994) represents an important conceptual advance that promises to improve our understanding of the mechanisms underlying ecological phenomena. We recently completed data collection on species abundances across a grid of permanent plots in HBEF, and initial geostatistical analyses indicate that different species exhibit spatial autocorrelation at different scales and intensities (Fig. 19). We propose to analyze residual spatial variability in species abundances and environment by combining geostatistical methods with Mantel tests (Leduc et al. 1992; Rossi 1996; Cesaroni et al. 1997) to test the following hypothesis:

Hypothesis 3.2.3. *After accounting for spatial variation in abundance resulting from environmental and disturbance factors, the remaining patchiness in distribution will reflect differences in tree life history characteristics, especially dispersal distance and method of reproduction (e.g., vegetative sprouting, buried seed, etc.).*

OBJECTIVE 3.3. To explain local and regional patterns of distribution of sugar maple regeneration in and around HBEF.

Recent observations strongly suggest that the core northern hardwood species, sugar maple, is undergoing a regional decline, particularly on shallow soils and at higher elevations (Wilmot et al. 1995; Likens et al. 1998), but the causes and consequences of the decline remain obscure (Bauce and Allen 1991; Long et al. 1997). Understanding the sensitivity of sugar maple recruitment to local variations in environment will be critical to predict future changes in its abundance. Two historical factors that may be affecting patterns of sugar maple recruitment are: 1) the regional expansion of sugar maple abundance that accompanied human disturbance in the 19th and early 20th century (Fujikawa 1997); and 2) the increase in root suckering of American beech in response to the invasion of beech bark disease and consequent intense competition in the understory. We propose to use existing and new information on sugar maple recruitment from each of our permanent plot networks in combination with experimental manipulations of beech sprouts to evaluate the following hypothesis.

Hypothesis 3.3. *Although regeneration of sugar maple is constrained by the same topoedaphic factors that regulate overstory abundance, its range is being further reduced by competition from beech sprouts and by a lack of large-scale disturbance.*

OBJECTIVE 3.4. To quantify interrelated spatial patterns of forest net primary productivity and foliar N concentration and their connection to patterns of N cycling and species composition.

Regional patterns of forest productivity depend primarily upon the climatic gradient (corresponding to elevation and slope aspect), as well as soil resource controls that locally modify NPP probably through effects on both tree nutrition and species composition (Fahey et al. 1998). At the hardwood-conifer ecotone, if patchiness in forest composition were to correspond largely to habitat quality, then a mutual connection with patterns of NPP would be expected. Moreover, feedbacks between tree nutrition and nutrient recycling (Stump and Binkley 1993) might either reinforce or counteract the local patch structure depending upon their direction (positive or negative) and intensity. We argue that an improved understanding of these interactions among NPP, forest composition and tree nutrition is essential for predicting their mutual responses to coincident changes in atmospheric CO₂, climate, N availability and other natural and anthropogenic forces in coming decades.

Hypothesis 3.4.1. Variation in NPP across the HBV is closely related to variations in canopy N content and overstory species composition; these patterns can be accurately predicted using remotely-sensed data combined with an ecosystem simulation model.

Recent surveys have illustrated the utility of high spectral resolution remote sensing data for predicting N content of forest canopies (Wessman et al. 1989; Martin and Aber 1997). We propose to use available images for the HBV from NASA's AVIRIS instrument to predict canopy N content. These predictions will be validated against direct measurements on a selected subset of the Valley-wide plots. Using PnET, we will predict NPP patterns across the Valley; our plot-level NPP measurements from the Valley-wide plots will be used to validate model predictions. We also propose to explore the intriguing relationships among macroclimatic and topoedaphic controls and the patch structure of forest composition and NPP patterns by contrasting the north and south facing slopes of the HBV. We expect that both the peak NPP, and the forest composition expressed at peak NPP, differ in response to the macroclimatic influence of slope aspect at the hardwood-conifer ecotone in the HBV.

Hypothesis 3.4.2. Nitrogen cycling is regulated strongly by tree species composition through the chemistry of litter, and this regulation is observable in relationships between species composition and nitrogen cycling at the watershed and landscape scales.

Litter quality can affect decomposition rate, which in turn controls N cycling in temperate forests. Thus, patchiness in vegetation translates to patchiness in nutrient cycling, and we suggest that a watershed is a mosaic of patches of soils that can be characterized by their N-mineralization and nitrification rates. We propose to measure N mineralization and nitrification rates in a subset of the 370 Valley-wide vegetation plots (Fig. 3) to determine empirically the relationship between species composition and these N cycling rates. This work will be coordinated with ¹⁵N sampling in several plots near the experimental watersheds (objective 2.2). Nitrogen mineralization and nitrification will be measured with both a laboratory incubation at constant temperature and

moisture and a field incubation using PVC mineralization tubes. We will then use the AVIRIS imagery to model soil N cycling spatially as a function of species composition.

4. ECOLOGY OF HETEROTROPH POPULATIONS

The food web in the HBEF provides a framework for understanding the cause-effect relationships underlying heterotroph population dynamics (Fig. 2). Rather than spreading our efforts across all groups, we have concentrated on the diverse assemblage of passerine birds. We propose to expand our heterotroph research to include detailed studies of the role of moose in regulating vegetation composition, energy flow and nutrient cycling at the hardwood-conifer ecotone.

Temporal patterns in population abundance of birds (Fig. 20) depends on natural variation in both seed production (masting) of dominant trees and the populations of defoliating insects. Bird reproductive success appears to vary inversely with mast production because rodent population increases following mast years result in high nest predation of breeding birds the following summer (Ostfeld 1986). The reduced reproductive success leads to lower recruitment and hence lower abundances (Sherry and Holmes 1992; Holmes et al. 1992). Irruptions of *Lepidoptera* larvae have a direct, food supply effect on populations of insectivorous birds (Holmes et al. 1986, 1991).

OBJECTIVE 4.1. To quantify long-term patterns in the abundances and demography of breeding bird populations at the HBEF and their relationships to defoliating insect abundances and masting cycles of trees.

There is widespread concern that many species of migratory birds, especially those that migrate to the tropics (Neotropical migrants), are declining in abundance (Fig. 20; Holmes and Sherry 1988). The causes of these declines, however, are not understood, and indeed are the subject of much controversy (Sherry and Holmes 1995, 1996). Current evidence from the long-term studies at the HBEF indicate that diverse factors influence bird abundance patterns, including 1) fluctuations in food availability, especially defoliating caterpillars, 2) year-to-year differences in abundances of nest predators, 3) changes in habitat structure that occur with forest maturation (e.g., through natural succession), and 4) mortality over the non-breeding period (Holmes et al. 1986; Holmes and Sherry 1988). Analyses of long-term demographic data on bird populations at the HBEF show that recruitment of yearling males into breeding populations is significantly and positively correlated with nesting success in the previous summers (Sherry and Holmes 1992; Holmes et al. 1992). Because recruitment essentially determines breeding population size, this finding strongly suggests that factors affecting reproductive output have a major impact on subsequent population dynamics and abundances of these species and importantly, may override the impact of events during migration or in winter.

The two most important ecological factors affecting breeding success of birds at the HBEF are food availability and nest predation (Reitsma et al. 1990; Holmes et al. 1991, 1992, 1996; Rodenhouse and Holmes 1992). Thus knowledge of annual changes in the abundance of *Lepidoptera* larvae (major food items for most breeding bird species), predator populations (mainly sciurid rodents), and avian reproductive success will provide a test of the importance of these

factors in determining population levels, and thus contribute to understanding the factors underlying changes in bird abundances.

Hypothesis 4.1.1. Fluctuations in abundances of birds breeding in northern hardwood forests are related most directly to changes in reproductive success, which are influenced most by food supply and nest predation operating during the breeding season. We predict that bird reproductive success and ultimately recruitment will be positively correlated with caterpillar numbers and negatively correlated with predator numbers, the latter varying with mast production.

Our approach will be 1) to monitor abundances of all bird species at the HBEF and nearby sites, using methodology employed since 1969 (see Holmes et al. 1986), 2) to monitor in depth the reproductive success of one species (black-throated blue warbler, *Dendroica caerulescens*), which nests in the shrub layer, thus making study of its demographic characteristics possible (methodology for demographic monitoring will follow that of Holmes et al. (1992, 1996), and 3) to relate bird demographic patterns to environmental factors (e.g., Lepidoptera larvae, nest predators), as described below.

In terms of potential impacts on forest ecosystem structure and function, phytophagous insects are probably the most important group of heterotrophs. Lepidopteran defoliators increase dramatically in abundance at periodic intervals and at these times can remove a large proportion (up to 100%) of photosynthetic leaf tissue (Barbosa and Schultz 1988). The periodicity of defoliator irruptions and their effects on forest ecosystem dynamics have not been well studied, especially in northern hardwood forests. We have sampled defoliators at the HBEF since 1969, and over this 29-yr period three irruptions have occurred (Fig. 21), peaking at 10-20 larvae/1000 leaves. In the periods between outbreaks, caterpillar densities have been low, averaging 5.2 larvae/1000 leaves (Holmes and Schultz 1988).

Hypothesis 4.1.2. Lepidoptera defoliators enter outbreak phase periodically, and while synchronous over large areas, are locally patchy in occurrence.

Our approach is to monitor phytophagous insects by visual censuses, malaise traps, and frass collectors (Holmes et al. 1986; Holmes and Schultz 1988; Holmes et al. 1991). A reference collection of adult and larval Lepidoptera is maintained at Dartmouth College. Monitoring will be conducted during the in-leaf period each year, with sampling at 2-week intervals, on permanent plots within the HBV and in the southern White Mountains.

Many tree species in temperate forests produce large quantities of seed intermittently; such mast fruiting at the HBEF has been monitored periodically: 1968-1971 (Gosz et al. 1972) and 1976-1979 (Nothnagle 1980); it has been part of our LTER monitoring program since 1991. All the dominant trees at the HBEF exhibit masting, but it is most pronounced in the large-seeded beech. Together with census data on small mammal populations these measurements allow us to test the following hypothesis.

Hypothesis 4.1.3. Patterns of seed production vary significantly among major tree species and among years and tree species x year interaction will often be significant. Changes in rodent populations are correlated with seed abundance, especially that of the large-seeded beech.

We will continue to monitor seed production in litter traps in the main Bird Area (Fig. 3). The major nest predators at HBEF are red squirrels and eastern chipmunks (Sloan et al. 1998), and we will concentrate monitoring on their populations. Because these species are active diurnally, we will use the point count census method with points located systematically at 100 m intervals through the study area.

OBJECTIVE 4.2. To examine landscape level patterns in the distribution and abundance of breeding bird populations across the wider HBV.

Most studies of animal communities have been conducted at very small temporal and spatial scales, making assessments of the effects of natural or human-induced perturbations difficult (Kareiva and Andersen 1988). Furthermore, it is not clear the degree to which conclusions from studies at such small scales can be extrapolated to larger scales (Böhning-Gaese et al. 1994). For considerations of avian population abundances and community dynamics, studies have usually been conducted either on sites <50 ha in area or at very large, continental-wide scales (e.g., the Breeding Bird Survey - Peterjohn et al. 1995). Comparisons of results from these two disparate scales suggest that conclusions from one are not readily extrapolated to the other (Böhning-Gaese, et al. 1994). Data are therefore needed on the distribution and abundance of species at intermediate or landscape levels. Such information is lacking for northern hardwoods ecosystems, as well as most other regions (but see Bolger et al. 1997 for California shrub communities).

Demographic studies of bird reproductive success and survival at the HBEF and elsewhere indicate the importance of variation in habitat quality in regulating population abundances (Holmes et al. 1992, 1996; Hunt 1996, 1998). Across the HBEF spatial variation in environment and vegetation composition results in sharp contrasts in bird habitat quality, but the exact nature of bird responses to habitat variation at this landscape scale are not known. We propose to examine the abundance of all bird species across the 30 km² HBV by sampling on the Valley-wide vegetation grid (Fig. 3) and applying multivariate and spatial statistical models to the coincident variations in environment, vegetation and bird populations.

Hypothesis 4.2. Distribution and abundance of bird species vary in relation to habitat characteristics (e.g., vegetation, elevation, aspect and other environmental features) at different spatial and temporal scales.

Our approach will be to conduct point counts (Ralph et al. 1995) of birds of all species seen or heard in the Valley-wide plots. We propose to conduct a complete census in year 1 (summer 1999), and then to use these to choose a sub-set of plots that represents the range of variation in bird abundance and habitat quality for resurvey in subsequent years to assess annual variations in bird abundance and distribution in relation to proximal factors (insects, masting and nest predators).

OBJECTIVE 4.3. To quantify spatial patterns of moose distribution and herbivory in the HB Valley.

Although the key role played by large herbivores in regulating the dynamics of many terrestrial ecosystems has long been appreciated their role in forests often has been discounted because energy and nutrient flow through the consumer food chain in forests is usually low. The most important mechanism of large herbivore influence in forest ecosystem dynamics results from the effects of selective browsing in shifting vegetation species composition (e.g., Anderson and Loucks 1979) and consequent feedbacks on productivity and nutrient cycling (Pastor et al. 1988). For example, heavy selective browsing by moose has shifted vegetation composition on Isle Royale, MI, towards white spruce and away from more preferred species including paper birch, mountain maple and balsam fir (McInnes et al. 1992).

We have measured vegetation response to selective moose browsing on hardwood trees in the higher elevations of W5 after clear-cutting: the release of spruce from competition with hardwoods has been striking (Fahey, unpublished data). We hypothesize that by favoring conifers over hardwoods, moose browsing will alter energy flow and nutrient cycling patterns in the hardwood-conifer forest ecotone of the HBEF, and we are planning a small watershed-level exclosure experiment to test this hypothesis. In preparation for submission of a separate proposal for this purpose, we propose with LTER funds to quantify spatial patterns of moose activity within the HBEF by quantifying browsing along transects on the north-facing watersheds. These surveys will assure that the exclosure experiment will be conducted in an area where moose are active.

5. CROSS-SITE STUDIES

Cross-site studies, particularly those involving other LTER sites, are an important component of the HBES. The HBR-LTER is participating in a number of LTER cross-site studies, including the long-term intersite decomposition study (LIDET), the lotic intersite nitrogen experiment (LINX), the stream hydrology synthesis, and the cross-site comparisons using the ZELIG model (Urban et al. 1991). During the current LTER we initiated a cross-site study of trifluoroacetate retention in soil (Richey et al. 1997a,b). Also during the current LTER we initiated a workshop with PI's from the Harvard Forest LTER to discuss common research interests and plan future research initiatives. The principal new cross-site study proposed in this funding cycle is a comparison of simulated nutrient uptake at the root scale based on a root uptake model (Yanai 1994) and ecosystem budgets at selected LTER sites. Nutrient uptake at the ecosystem scale integrates information about vegetation dynamics, hydrology, microbial activity, and chemical cycling. Predicting uptake of a variety of elements for diverse ecosystem types therefore provides a rigorous test of current understanding of a wide range of processes. Ecosystem budgets for a variety of elements are available at a range of LTER sites and most of the parameters required to apply the root uptake model are also available at these sites. The important missing parameters will be measured; others can be estimated from other sources. The two methods of estimating uptake are quite independent: ecosystem budgets depend on estimates of annual nutrient fluxes in litterfall, root turnover, and biomass accumulation. Simulated uptake depends on root length and

radius, soil chemistry, and uptake kinetics (Yanai 1994). Initial comparisons between budgeted and simulated uptake will be made with attention to the probable accuracy of the estimates.

6. SYNTHESIS

By providing a tangible framework for integration, the unit of the experimental watershed has provided an effective vehicle for synthesis of the HBES (Bormann and Likens 1979; Likens and Bormann 1995). Our understanding of forest biogeochemistry at this scale has stimulated explorations of ecological patterns, processes and interactions at smaller and larger scales and at increasing levels of complexity of interspecific and biogeochemical interactions. Synthesis and integration of the research in the HBES is approached both in the design of our current and proposed research program and in the recent and future expected products of the program, including monographs, books and simulation models. By analyzing biogeochemical and species abundance patterns at plot and landscape scales and placing these patterns in both a mechanistic perspective and a regional context, we expect to improve general understanding of the ecology of the northeastern forest. Similarly, in our proposed long-term manipulation of soil Ca^{2+} availability we will explore the complex interactions between biogeochemical processes and species abundance patterns.

The HBR-LTER is a large complex study involving many investigators whose responsibilities we summarize in Table 5. We hold quarterly workshops to help integrate the LTER studies. We are in the process of integrating much of the long-term, biogeochemical information through a series of monographs. Monographs on K (Likens et al. 1994) and Ca (Likens et al. 1998) have been completed; monographs on N, C, Mg, Cl, Na, Si and S are under way; and our goal is to synthesize these into a book, where the interrelations among element cycles will be explored. Beyond achieving a synthesis of the long-term biogeochemical information from the experimental watersheds at the HBEF, these monographs are designed as a comprehensive overview of the current understanding of element cycles in temperate forest ecosystems. Parallel efforts have been completed on the controls of passerine bird assemblages at the HBEF (Rodenhouse et al. 1997; Holmes and Sherry 1997). Although we are not yet in a position to attempt a grand synthesis of the relationships among population, community, landscape and regional ecological phenomena, our coordinated efforts in the HBES are directed toward that long-term goal. Continuation of the HBR-LTER project is an essential means toward our pursuit of that goal.

3.0 - LITERATURE CITED

- Aber, J.D. and C.T. Driscoll. 1997. Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests. *Global Biogeochem. Cycles* 11:639-648.
- Aber, J.D. and C.A. Federer. 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia*. 92: 463-474.
- Aber, J.D., S.V. Ollinger, C.A. Federer, P.B. Reich, M.L. Goulden, D.W. Kicklighter, J.M. Melillo and R.G. Lathrop, Jr. 1995. Forest biogeochemistry and primary production altered by nitrogen saturation. *Water Air Soil Pollut.* 85:1665-1670.
- Aber, J.D., S.V. Ollinger and C.T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecol. Modelling* 101:61-78.
- Anderson, R.C. and O.L. Loucks. 1979. White-tailed deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forest. *J. Appl. Ecol.* 16:855-861.
- April, R.A. and R.M. Newton. 1985. Influence of geology on lake acidification in the ILWAS watersheds. *Water Air Soil Pollut.* 26:373-386.
- Bailey, S.W., C.T. Driscoll and J.W. Hornbeck. 1995. Acid-base chemistry and aluminum transport in an acidic watershed and pond in New Hampshire. *Biogeochemistry* 28:69-91.
- Bailey, S.W., J.W. Hornbeck, C.T. Driscoll and H.E. Gaudette. 1996. Calcium imports and transport in a base-poor forest ecosystem as interpreted by Sr isotopes. *Water Resour. Res.* 32:707-719.
- Barbosa, P. and J.C. Schultz. 1988. *Insect Outbreaks*. Academic Press, NY.
- Bauce, E. and D. C. Allen. 1991. Etiology of a sugar maple decline. *Can. J. For. Res.* 21: 686-693.
- Böhning-Gaese, K., M. L. Taper, and J. H. Brown. 1994. Avian community dynamics are discordant in space and time. *Oikos* 70: 121-126.
- Bolger, D.T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird densities in an urbanizing landscape in coastal Southern California. *Conservation Biology* 11: 406-421.
- Bormann, F. H. and G. E. Likens. 1967. Nutrient cycling. *Science* 155:424-429.

- Bormann, F. H. and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag New York Inc. 253 pp.
- Bowden, R.D., J.M. Melillo, P.A. Steudler, and J.D. Aber. 1991. Effects of nitrogen additions on annual nitrous oxide fluxes from temperate forest soils in the northeastern United States. *J. Geophys. Res.* 96:9321-9328.
- Brown, D.G., 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *J. Veg. Sci.* 5:641-656.
- Brunke, M. and T. Gonser. 1997. The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* 37:1-33.
- Bukaveckas, P.A., G.E. Likens, T.C. Winter and D.C. Buso. 1998a. A comparison of methods for deriving southe flux rates using long-term data from streams in the Mirror Lake watershed. *Water Air Soil Pollut.* (in press).
- Bukaveckas, P.A., G.E. Likens, D.F. Charles, B.F. Cumming, S. Dixit, P.R. Leavitt, R.E. Moeller, M. Paterson, C.L. Schelske, and J.P. Smol. 1998b. A comparison of recent and historical human impacts on Mirror Lake based on water quality monitoring and sediment stratigraphy. (in review).
- Ceaser, J., R. Collier, J. Edmond, F. Frey, G. Matisoff, A. Ng and R. Stallard. 1976. Chemical dynamics of a polluted watershed, the Merrimack River in Northern New England. *Environ. Sci. Technol.* 10:697-704.
- Cesaroni, D., P. Matarazzo, G. Allegrucci and V. Sbordoni. 1997. Comparing patterns of geographic variation in cave crickets by combining geostatistic methods and Mantel tests. *J. Biogeogr.* 24:419-431.
- Christ, M., Y. Zhang, G.E. Likens and C.T. Driscoll. 1995. Nitrogen retention capacity of a northern hardwood forest soil under ammonium sulfate additions. *Ecol. Appl.* 5:802-812.
- Corkum, L.D. 1996. Responses of chlorophyll-a, organic matter, and macroinvertebrates to nutrient additions in rivers flowing through agricultural and forested land. *Archiv. fur Hydrobiologie* 136:391-411.
- Cronan, C.S. and C.L. Schofield. 1979. Aluminum leaching response to acid precipitation: effects on high-elevation watershed in the Northeast. *Science* 204:304-306.
- Cronan, C.S. and C.L. Schofield. 1990. Relationships between aqueous aluminum and acidic deposition in forested watersheds of North America and northern Europe. *Environ. Sci. Technol.* 24:1100-1105.

- Dahlgren, R.A. and C.T. Driscoll. 1994. The effects of whole-tree clear-cutting on soil processes at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Plant Soil* 158:239-262.
- Delcourt, P.A. and H.R. Delcourt. 1992. Ecotone dynamics in space and time. In: F. diCasti and A.J. Hansen (eds.). *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer-Verlag, New York. pp. 19-54.
- Driscoll, C.T. 1991. Northeast overview. In: D.F. Charles (ed.) *Acidic Deposition and Aquatic Ecosystems: Regional Case Studies*. Springer-Verlag, New York. pp. 129-132.
- Driscoll, C.T. and R.M. Newton. 1985. Chemical characteristics of acid-sensitive lakes in the Adirondack Region of New York. *Environ. Sci. Technol.* 19:1018-1024.
- Driscoll, C.T., R.D. Fuller and D.M. Simone. 1988. Longitudinal variations in trace metal concentrations in a northern forested ecosystems. *J. Environ. Qual.* 17:101-107.
- Driscoll, C.T. G.E. Likens, and M.R. Church. 1998. Recovery of soil and surface waters in the northeastern U.S. from decreases in atmospheric deposition of sulfur. *Water Air Soil Pollut.* (in press).
- Driscoll, C.T., C.E. Johnson and G.E. Likens. 1992. Patterns in biogeochemistry at the Hubbard Brook Experimental Forest, New Hampshire, USA. In: A. Teller, P. Mathy and J.N.R. Jeffers (eds.) *Responses of Forest Ecosystems to Environmental Changes*. Elsevier Science, Essex, England. pp. 244-255.
- Driscoll, C.T., J.K. Otton and A. Iverfeldt. 1994a. Trace metals speciation and cycling. In: B. Moldan and J. Cerny (eds.) *Biogeochemistry of Small Catchments: A Tool for Environmental Research*. J. Wiley & Sons, Chichester, England. pp. 299-322.
- Driscoll, C.T., M.D. Lehtinen and T.J. Sullivan. 1994b. Modeling the acid-base chemistry of organic solutes in Adirondack, NY lakes. *Water Resour. Res.* 30:297-306.
- Enslin, W.R. and M.C. Sullivan 1974. The use of color infrared photography for wetlands assessment. In: R. Shahrokhi (ed.). *Remote Sensing of Earth Resources*, vol. 3. University of Tennessee, Tullahoma, TN. pp. 697-719.
- Eilers, J. M. and A. R. Selle. 1991. Geographic overview of the regional case study areas. In: D.F. Charles (ed.). *Acidic Deposition and Aquatic Ecosystems: Regional Case Studies*. Springer-Verlag New York Inc. pp. 107-125.
- Elser, J.J. E.R. Marzoff and C.R. Goldman. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. *Can. J. Fish. Aquatic Sci.* 47:1468-1477.

- Fahey, T.J., J.J. Battles, and G.F. Wilson. 1998. Response of early successional northern hardwood forests to changes in nutrient availability. *Ecol. Monogr.*, in press.
- Fairchild, G.W., R.L. Lowe and W.B. Richardson. 1985. Algal periphyton growth on nutrient-diffusing substrates: an in situ bioassay. *Ecology*. 66:465-472.
- Federer, C.A. and D. Lash. 1978. Simulated streamflow response to possible differences in transpiration among species of hardwood trees. *Water Resour. Res.* 14:1089-1097.
- Federer, C. A., L. D. Flynn, C. W. Martin, J. W. Hornbeck and R. S. Pierce. 1990. Thirty years of hydrometeorologic data at the Hubbard Brook Experimental Forest, New Hampshire. USDA Forest Service, General Technical Report NE-141. 44 pp.
- Federer, C.A., C.E. Turcotte and C.T. Smith. 1993. The organic fraction-bulk density relationship and the expression of nutrient content in forest soils. *Can. J. For. Res.* 23:1026-1032.
- Fisher, D.C. and M. Oppenheimer. 1991. Atmospheric nitrogen deposition and the Cheapeake Bay Estuary. *Ambio* 20: 102-108.
- Fujikawa, W. 1997. A reconstruction of the presettlement forest in the White Mountains of New Hampshire. *Honors Thesis, Center for Environmental Science, Brown University.*
- Fuller, R.D., C.T. Driscoll, S.C. Schindler and M.J. Mitchell. 1986. A simulation model of sulfur transformations in forested Spodosols. *Biogeochemistry* 2:313-328.
- Gosz, J.R., G.E. Likens and F.H. Bormann. 1972. Nutrient content of litter fall on the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* 53(5):769-784.
- Groffman, P.M., G.C. Hanson, E. Kiviat and G. Stevens. 1996. Variation in microbial parameters in four different wetland types. *Soil Sc. Soc. Am. J.* 60:622-629.
- Hershey, R.R. and W.A. Befort. 1995. Aerial photo guide to New England forest cover types. USDA For. Serv., Gen. Tech. Rep. NE-195.
- Hicks, A.C. 1986. The history and current status of the moose in New York. *Alces* 25:245-252.
- Holmes, R.T. 1988. Community structure, population fluctuations, and resource dynamics of birds in temperate deciduous forests. *Proc. XIX Internat. Ornith. Congr. (Ottawa)* 10:1318-1327.
- Holmes, R.T., J.C. Schultz and P.J. Nothnagle. 1979. Bird predation on forest insects: an enclosure experiment. *Science* 206:462-463.
- Holmes, R.T., T.W. Sherry and F.W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. *Ecol. Mongr.* 56(3):201-220.

- Holmes, R.T. and J.C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Can. J. Zool.* 66:720-728.
- Holmes, R.T. and T.W. Sherry. 1988. Assessing population trends of New Hampshire forest birds: Local versus regional patterns. *The Auk* 105:756-768.
- Holmes, R.T., T.W. Sherry and F.W. Sturges. 1991. Numerical and demographic responses of temperate forest birds to annual fluctuations in their food resources. *Proc. XX Internat. Ornithol. Congr.*, pp. 1559-1567.
- Holmes, R.T., T.W. Sherry, P.P. Marra and K.E. Petit. 1992. Multiple-brooding and productivity of a Neotropical migrant, the Black-throated blue warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *The Auk* 109(2):321-333.
- Holmes, R.T., P.P. Marra, and T.W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *J. Animal Ecology* 65:183-195.
- Holmes, R. T., and T. W. Sherry. 1997. Ecological factors influencing biodiversity in a northern hardwoods ecosystem: Contributions of long-term studies of bird populations at Hubbard Brook. LTER Biodiversity Series: http://atlantic.evsc.virginia.edu/Lter_biod/.
- Holmes, R. T., and T. W. Sherry. Bird population trends in a maturing northern hardwoods forest: 30-year record at Hubbard Brook. In prep.
- Hornbeck, J.W., S.W. Bailey, D.C. Buso and J.B. Shanley. 1997. Streamwater chemistry and nutrient budgets for forested watersheds in New England: Variability and management implications. *Forest Ecol. Manage.* 93:73-89.
- Hughes, J.W. and T.J. Fahey. 1994. Litterfall dynamics and ecosystem recovery during forest development. *For. Ecol. Manage.* 63:181-198.
- Hunt, P.D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwoods forest: evaluation of habitat quality. *The Auk* 113:875-888.
- Hunt, P. D. 1998. The importance of early successional habitat to the American Redstart: evidence from a population model. *Conservation Biology* in press.
- Huntington, T.G. D.F. Ryan and S.P. Hamburg. 1988. Estimating soil nitrogen and carbon pools in a northern hardwood forest ecosystem. *Soil Sci. Soc. Am. J.* 52:1162-1167.

- Johnson, C. E., C. T. Driscoll, T. J. Fahey, T. G. Siccama and J. W. Hughes. 1995. Carbon dynamics following clear-cutting of a northern hardwood forest ecosystem. pp. 463-488. *In: J. M. Kelly and W. W. McFee (eds.). Carbon: Forms and Functions in Forest Soils. American Society of Agronomy, Madison, WI.* pp. 463-488.
- Johnson, C.E., T.G. Siccama, C.T. Driscoll, G.E. Likens and R.E. Moeller. 1995. Changes in forest lead cycling in response to decreasing atmospheric inputs. *Ecol. Appl.* 5:813-822.
- Johnson, C.E., R.B. Romanowicz and T.G. Siccama. 1997. Conservation of exchangeable cations after clear-cutting of a northern hardwood forest. *Can. J. For. Res.* 27:859-868.
- Jongman, R.H.G., C.J.F. ter Braak, O.F.R. van Tongeren. 1995. *Data Analysis in Community and Landscape Ecology.* Cambridge Univ. Press, Cambridge.
- Kareiva, P., and M. Andersen. 1988. Spatial aspects of species interactions: the wedding of models and experiments. *In: A. Hastings (ed.) Community Ecology* Springer, New York. pp. 38-54.
- Keddy, P.A. 1990. Competitive hierarchies and centrifugal organizational in plant communities. *In: J.B. Grace and D. Tilman (eds.). Perspectives on Plant Competition.* Academic Press, Inc., San Diego. pp. 265-290.
- Kirchner, D.W. 1992. Heterogeneous geochemistry of carchment acidification. *Geochim. Cosmochim. Acta* 56:2311-2327.
- Leak, W.B. 1973. Species and structure of a virgin northern hardwood stand in New Hampshire. USDA Forest Service. NEFES. Research Note NE-181. 4 p.
- Leak, W.B. and Graber, R.E. 1974. Forest vegetation related to elevation in the White Mountains of New Hampshire. USDA Forest Service, NEFES, Research Paper NE-299. 7 p.
- Leak, W.B. 1980. The influence of habitat on silvicultural prescriptions in New England. *J. Forestry* 78:529-533.
- Leduc, A., P. Drapeau, Y. Bergenon and P. Ledgendre. 1992. Study of spatial components of forest cover using partial Mantel tests and path analysis. *J. Veg. Sci.* 3:69-78.
- Li, H. and J.F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* 75:2446-2455.
- Likens, G.E. (ed.). 1985. *An Ecosystem Approach to Aquatic Ecology: Mirror Lake and its Environment.* Springer-Verlag, New York. 516 pp.

- Likens, G.E. and F.H. Bormann. 1995. *Biogeochemistry of a Forested Ecosystem*. Second Edition, Springer-Verlag New York Inc. 159 pp.
- Likens, G.E., F.H. Bormann, R.S. Pierce, J.S. Eaton, and N.M. Johnson. 1977. *Biogeochemistry of a Forested Ecosystem*. Springer-Verlag, New York, NY. 146 pp.
- Likens, G.E., F.H. Bormann, R.S. Pierce, J.S. Eaton and R.E. Munn. 1984. Long-term trends in precipitation chemistry at Hubbard Brook, New Hampshire. *Atmos. Environ.* 18:2641-2647.
- Likens, G.E., F.H. Bormann, R.S. Pierce and J.S. Eaton. 1985. The Hubbard Brook Valley. In: G.E. Likens (ed.) *An Ecosystem Approach to Aquatic Ecology: Mirror Lake and its Environment*. Springer-Verlag, New York. pp. 9-39.
- Likens, G.E., F.H. Bormann, L.O. Hedin, C.T. Driscoll and J.S. Eaton. 1990. Dry deposition of sulfur: a 23-yr record for the Hubbard Brook Forest Ecosystem. *Tellus* 42B:319-329.
- Likens, G.E., C.T. Driscoll, D.C. Buso, T.G. Siccama, C.E. Johnson, D.F. Ryan, G.M. Lovett, T.J. Fahey and W.A. Reiners. 1994. The biogeochemistry of potassium at Hubbard Brook. *Biogeochemistry* 25:1-65.
- Likens, G.E., C.T. Driscoll and D.C. Buso. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* 272:244-246.
- Likens, G. E., S. L. Tartowski, T. W. Berer, D. G. Richey, C. T. Driscoll, H. G. Frank and A. Klein. 1997. Transport and fate of trifluoroacetate in upland forest and wetland ecosystems. *Proc. Nat. Acad. Sci. USA* 94:4499-4503.
- Likens, G.E., C.T. Driscoll, D.C. Buso, T.G. Siccama, C.E. Johnson, G.M. Lovett, T.J. Fahey, W.A. Reiners, D.F. Ryan, C.W. Martin and S.W. Bailey. 1998. The biogeochemistry of calcium at Hubbard Brook. *Biogeochemistry* (in press).
- Long, R.P., S. B. Horsley and P. R. Lija. 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. *Can. J. For. Res.* 27:1560-1573.
- Lovett, G.M., G.E. Likens and S.S. Nolan. 1992. Dry deposition of sulfur to the Hubbard Brook Experimental Forest: A preliminary comparison of methods. In: S.E. Schwartz and W.G.N. Slinn (coord.) *Fifth Internat. Conf. on Precipitation Scavenging and Atmosphere-Surface Exchange. The Summers Volume (3): Applications and Appraisals*. Hemisphere Publishing, pp. 1391-1402.
- Marti, E. and F. Sabater. 1996. High variability in temporal and spatial nutrient retention in Mediterranean streams. *Ecology* 77:854-869.

- Martin, C.W. 1979. Precipitation and streamwater chemistry in an undisturbed forested watershed in New Hampshire. *Ecology* 60:36-42.
- Martin, M.E. and J.D. Aber. 1997. High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes. *Ecol. Appl.* 7:431-443.
- McInnes, P.F., R.J. Naiman, J. Pastor and Y. Cohen. 1992. The effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* 73:2059-2073.
- Merrens, E.J. and D.R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. *J. Ecology* 80(4):787-795.
- Meyer, J.L., W.H. McDowell, T.L. Bott, J.W. Elwood, C. Ishizaki, J.M. Melack, B.L. Peckarsky, B.J. Peterson, and P.A. Rublee. 1988. Elemental dynamics in streams. *J. No. Am. Benthol. Soc.* 7:410-432.
- Mitchell, M.J., C.T. Driscoll, J.S. Kahl, G.E. Likens, P.S. Murdoch and L.H. Pardo. 1996. Climatic control of nitrate loss from forested watersheds in the northeastern United States. *Environ. Sci. Technol.* 30:2609-2612.
- Mitchell, M.J., C.T. Driscoll and D.J. Raynal. 1996. Biogeochemistry of a forested watershed in the Central Adirondack Mountains: temporal changes and mass balances. *Water Air Soil Pollut.* 88:355-369.
- Mitchell, M.J., C.R. Krouse, B. Mayer, A.C. Stam and Y. Zhang. 1997. Use of stable isotopes in evaluating sulfur biogeochemistry of forest ecosystems. In: C. Kendall and J. McDonnell (eds.). *Isotope Tracers in Catchment Hydrology*. Elsevier, The Netherlands (in press).
- Munn, N.L. and Meyer, J.L. 1990. Habitat-specific solute retention in two small streams: an intersite comparison. *Ecology*. 71: 2069-2082.
- Mou, Pu, T.J. Fahey and J.W. Hughes. 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem on W5, Hubbard Brook Experimental Forest. *Journal of Applied Ecology* 30:661-675.
- Nadelhoffer, K.J. and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. In: K. Lajtha and R.H. Michener (eds.). *Stable Isotopes in Ecology and Environmental Science*. Blackwell Scientific Publishers, Cambridge.
- Neilson, R.P. 1993. Transient ecotone responses to climatic change: some conceptual and modelling approaches. *Ecol. Appl.* 3:385-395.

- Norton, S.A., J.S. Kahl, D.F. Brakke, G.F. Brewer, T.A. Haines, and S.C. Nodvin. 1988. Regional patterns and local variability of dry and occult deposition strongly influence sulfate concentrations in Maine lakes. *Sci. Total Environ.* 72:183-196.
- Nothnagle, P.J. 1980. Mast fruiting and seed predation in a northern hardwood forest. *Bull. Ecol. Soc. Am.* 61:112.
- Ollinger, S.V., J.D. Aver, G.M. Lovett, S.E. Millham, R.G. Lathrop and J.M. Ellis. 1993 A spatial model of atmospheric deposition for the northeastern U.S. *Ecol. Appl.* 3:459-472.
- Pardo, L.H., C.T. Driscoll and G.E. Likens. 1995. Patterns of nitrate loss from a chronosequence of clear-cut watersheds. *Water Air Soil Pollut.* 85:1659-1664.
- Pardo, L.H., J. Pett-Ridge and H.F. Hemond. Natural abundance of ^{15}N in soil and litter across a nitrate-output gradient in New Hampshire. (in prep.)
- Pastor, J., R.J. Naiman, B. Dewey and P. McInnes. 1988. Moose, microbes, and the boreal forest. *Bioscience* 38:770-777.
- Peterjohn, B. G., J. R. Sauer, and C. S. Robbins. 1995. Population trends from the North American breeding bird survey. In: T. E. Martin and D. M. Finch (eds.). *Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues.* Oxford University Press, New York, pp. 3-39.
- Postek, K.M., C.T. Driscoll, J.D. Aber and R.C. Santore. 1995. Application of PnET-CN/CHES to a spruce stand in Solling, Germany. *Ecol. Modeling* 83:163-172.
- Reiners, W.A. 1992. Twenty years of ecosystem reorganization following experimental deforestation and regrowth suppression. *Ecol. Mongr.* 62:503-523.
- Reitsma, L.R., R.T. Holmes and T.W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on next predation in a northern hardwood forest: an experiment with artificial nests. *Oikos* 57(3):375-380.
- Reuss, J.O. and D.W. Johnson. 1986. *Acid Deposition and the Acidification of Soils and Waters.* Springer-Verlag, New York.
- Richey, D.G., C.T. Driscoll and G.E. Likens. 1997a. Soil retention of trifluoroacetate. *Environ. Sci. Technol.* 31: 1723-1727.
- Richey, D.G., C.T. Driscoll and G.E. Likens. 1997b. Soil retention of TFA in LTER soil. *Network News, U.S. LTER Newsletter* 20:10-11.

- Rodenhouse, N.L. and R.T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73(1):357-372.
- Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site dependent regulation of population size: a new synthesis. *Ecology* 78: 2025-2042.
- Romanowicz, R.B., C.T. Driscoll, T.J. Fahey, C.E. Johnson, G.E. Likens and T.G. Siccama. 1996. Changes in the biogeochemistry of potassium following a whole-tree harvest. *Soil Sci. Soc. Am. J.* 60:1664-1674.
- Rosenberry, D. O., P. A. Bukaveckas, D. C. Buso, G. E. Likens, A. M. Shapiro and T. C. Winter. 1998. Movement of road salt to a small New Hampshire lake. *Water Air, Soil Pollut.* (in press).
- Rossi, J.P. 1996. Statistical tool for soil biology. XI. Autocorrelogram and Mantel test. *Env. J. Soil Biol.* 32:195-203.
- Santore, R.C. and C.T. Driscoll. 1995. The CHESS model for calculating chemical equilibria in soils and solutions. In: R. Loeppert, A.P. Schwab and S. Goldberg (eds.) *Chemical Equilibrium and Reaction Models*. Soil Sci. Soc. America, Madison, WI, pp. 357-375.
- Schaefer, D.A., C.T. Driscoll, R. van Dreaseon and C.P. Yatsko. 1990. The episodic acidification of Adirondack lakes during snowmelt. *Water Resour. Res.* 26:1639-1647.
- Schindler, D.W. 1974. Eutrophication and recovery in experimental lakes: implication for lake management. *Science* 184:897-899.
- Sherry, T.W. and R.T. Holmes. 1992. Population fluctuations in a long distance neotropical migrant: demographic evidence for the importance of breeding season events in the American redstart. In: J.M. Hagan and D.W. Johnston (eds.). *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press. pp. 431-442.
- Sherry, T. W. and R. T. Holmes. 1995. Summer versus winter limitation of populations: conceptual issues and evidence. In: T. E. Martin and D. M. Finch (eds.). *Ecology and Management of Neotropical Migratory Birds: a Synthesis and Review of Critical Issues*. Oxford University Press, New York. pp. 85-120.
- Sherry, T.W. and R.T. Holmes. 1996. Winter habitat limitation in Neotropical-Nearctic migrant birds: Implications for population dynamics and conservation. *Ecology* 77:36-48.
- Sherry, T. W., and R. T. Holmes 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.
- Siccama, T.G., C. Johnson, T. Sherry, E.G. Girdler, G.E. Likens, T.J. Fahey and P. Schwarz. Population and biomass dynamics of a mature northern hardwood forest, NH, in prep.

- Sloan, S. S., T. W. Sherry, and R. T. Holmes. 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwood forest. *J. Wildl. Manage.*, in press.
- Steudler, P.S., R.D. Bowden, J.M. Melillo and J.D. Aber. 1989. Influence of nitrogen fertilization on methane uptake in temperate forest soils. *Nature* 341:314-316.
- Stoddard, J.L. 1994. Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences. In: L.A. Baker (ed.) *Environmental Chemistry of Lakes and Reservoirs*, Amer. Chem. Soc., Washington, DC. pp. 223-284.
- Stream Solute Workshop. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. *J. No. Am. Benthol. Soc.* 9:95- 119.
- Strong, A.M., T.W. Sherry, and R.T. Holmes. Do insectivorous birds indirectly affect growth of sugar maple through predation on leaf-chewing insects? An exclosure experiment. (in prep.)
- Stump, L. M., and D. Binkley. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. *Can. J. For. Res.* 23:492-502.
- Thorne, J.F. and S.P. Hamburg. 1985. Nitrification potentials of an old-field chronosequence in Campton, New Hampshire. *Ecology* 66(4):1333-1338.
- Turner, M.G. and R.H. Gardner (eds.). 1991. *Quantitative Methods in Landscape Ecology*. Springer Verlag, New York.
- Urban, D.L., G.B. Bonan, T.M. Smith and H.H. Shugart. 1991. Spatial applications of gap models. *For. Ecol. Manage.* 42:95-110.
- Valiela, I., G. Collins, J. Kremer, K. Lajtha, M. Geist, B. Seely, J. Browley and C.H. Shaw. 1997. Nitrogen loading from coastal watersheds to receiving estuaries: New method and application. *Ecol. Appl.* 7:358-380.
- Veen, D., D.C. Buso, C.A. Federer and T.G. Siccama. 1994. Structure and function of the Hubbard Brook Data Management System. *Bull. Ecol. Soc. Amer.* 75:45-48.
- Vitousek, P.M., and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: an hypothesis. *Bioscience* 25: 376-381.
- Wessman, C.A., J.D. Aber, and D.L. Peterson. 1989. An evaluation of imaging spectrometry for estimating forest canopy chemistry. *Int. J. Remote Sensing* 10:1293-1316.
- Wilmot, T. R., D. S. Ellsworth, and M. T. Tyree. 1995. Relationships among crown condition, growth and stand nutrition in seven northern Vermont sugarbushes. *Can. J. For. Res.* 25: 386-397.

Winter, T.C., J.S. Eaton and G.E. Likens. 1989. Evaluation of inflow to Mirror Lake, New Hampshire. *Water Resour. Bull.* 25:991-1008.

Winterbourn, M.J. 1990. Interactions among nutrients, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biol.* 23:463-474.

Yanai, R.D. 1994. A steady-state model of nutrient uptake improved to account for newly-grown roots. *Soil. Sci. Soc. Am. J.* 58:1562-1571.

4.0 - SITE MANAGEMENT

Primary and ultimate responsibility and authority for administering the HBEF on this federal property is, by law, the Chief of the U.S. Forest Service (FS) who in turn delegates authority to the Director of the Northeastern Forest Experiment Station (NFES). The FS has agreed to share the management of long-term ecological research at the HBEF with research institutions, recognizing the need for all parties to commit funds, personnel, and equipment to attain common long-term objectives in research and education. Principal investigators representing the U.S. Forest Service, Institute of Ecosystem Studies, Yale University, Cornell University, Dartmouth College, Syracuse University and the USGS currently constitute the HBES Scientific Advisory Committee (SAC). They are responsible for the planning, direction and management of the research programs at the HBEF. Because of the remote location of the Forest, general supervision of the Forest, is under the Forest Service principal investigator, the Project Leader, as delegated by the Director of the NFES. Actual day-to-day operations on the Forest are supervised by the resident Research Forester-Manager of the NFES (C.W. Martin).

A. OPERATION OF THE HBES

Long-term research at the HBEF is conducted jointly by the USFS NFES and cooperating institutions. Each of these parties cooperates to plan, develop, and utilize the HBEF as a center for research and demonstration. The development and management of the HBEF is guided by the following objectives:

1. To provide landscape space for conducting basic and applied research in natural and manipulated environments. This includes setting policy that permits making space administratively available and providing reasonable means of access to sites.
2. To establish a system for making available information on biogeochemistry, climate, soils, vegetation, streamflow, animal behavior, and other important environmental parameters; and to facilitate long-term collection of ecological and biogeochemical data. Included in this activity are the collection and preservation of samples (e.g., soil, vegetation, etc.) for future examination and comparison with current samples. This information is supportive and essential for many studies and is vital in determining long-term trends.
3. To make available support facilities and space for on-site accommodation of scientists, technicians and student researchers, as funds, space, and personnel permit.
4. To strive to maintain a congenial spirit of cooperation among all users of the Forest. Past experience and productivity at Hubbard Brook show that research accomplishments of the research team in large measure stem from individual research freedom coupled with a willingness to share data and to consider the needs of fellow workers.
5. To promote the integration of the findings of individuals into a better understanding of the ecosystem as a whole.

B. STRUCTURE AND ROLE OF THE HUBBARD BROOK SCIENTIFIC ADVISORY COMMITTEE

The Hubbard Brook SAC has the responsibility to develop goals and to provide leadership and oversight in the selection, integration and monitoring of research projects and educational activities of the HBES. The SAC advises the USFS in its operation and maintenance of the HBEF. The SAC has the authority to form subcommittees to meet the changing demands of the HBES. Three standing committees (Information Oversight, Facilities and Data Management) report to the SAC.

The SAC is composed of at least five members, including a non-voting chair (who must be a USFS employee) and a non-voting Executive Director. The voting members are senior researchers with a demonstrated long-term interest and participation in the research at the HBEF. The chair is charged with calling meetings, calling votes and may cast a vote in the event of a tie (if the SAC consists of an even number of members). A quorum is a simple majority; votes by telephone or other means may be obtained, and on important issues, a strong attempt is made to assemble the entire group. Members have a term of 6 years. Members are appointed by the Hubbard Brook Research Foundation.

The SAC meets at least three times per year. The meetings occur once in early summer near the time of the Annual Cooperator's Meeting, in late fall, and in early spring. The agenda of the SAC consists of: 1) reviewing proposals for research within the HBEF and giving advice on these proposals to the USFS chair, who has the authority to decline or accept proposals; 2) integration of results and projects of the HBES, and promoting integration of these results toward larger synthesis of forest ecosystem processes and suggestions for practical management; and 3) education of students and the public.

Reports and recommendations from the standing committees are passed to the Executive Director, who informs the SAC of the content and pursues some action with the SAC. The USFS has the final say on what research will and will not occur within the HBEF. All research proposals must be approved by the USFS chair of the SAC before the proposed research can be initiated and all proposals should be submitted to the USFS with sufficient lead time to allow a rational decision to be reached. Some proposals, generally for small, non-manipulative projects, can be acted upon directly by the USFS chairperson of the SAC. More commonly, the USFS solicits the opinion of the Executive Director who informs the SAC of the content and solicits recommendations from the SAC. Considering this advice, the USFS chair acts on the proposal. Proposals impinging on any of the standing committees are forwarded to the chairperson of those committees for comment before the proposal goes to the SAC for voting.

Management of facilities within the HBEF is the responsibility of the USFS Project Leader. Facilities at Camp Osceola (Mirror Lake property) cabins and other improvements, e.g. roads, water, and sewage systems, also are the responsibility of the USFS Project Leader. However, input for managing Camp Osceola is sought from the SAC, while day-to-day management is handled by IES. Pleasant View Farm Complex is managed by IES with input from the SAC.

5.0 - DATA AND INFORMATION MANAGEMENT

5.1 Structure

The HBES homepage (<http://www.hbrook.sr.unh.edu>) currently resides on a UNIX-based server located at the University of New Hampshire. The Hubbard Brook data manager, John Campbell, is a USDA Forest Service employee. The Data Manager coordinates the efforts of all HBES cooperators by uploading and maintaining their data sets, either on this "umbrella" site, or at the major nodes that are linked to this site. Data bases currently "on line" are listed in Table 2.

A Scientific Advisory Committee (SAC) provides scientific leadership and oversight for the HBES. An Information Oversight Committee (IOC) oversees documentation, the development of metadata, and internet publication of the long-term data sets and other information from the HBES. The Data Management Subcommittee, as a working group under the IOC's supervision, reports annually to the IOC and SAC on issues of data acquisition, physical sample storage and subsampling protocols, and anticipated computer hardware needs.

5.2 Data input

More than many LTER sites, HBR has a multi-institutional research program, with a long history. These characteristics have made the development of procedures for uniform data management of the type described by Ingersoll et al. (1996) problematic. Data sets, metadata and documentation are contributed by HBES researchers to the HBES Data Manager following strict protocols, but regular updating is the responsibility of each principal investigator. Data procedures for the major institutions contributing to the HBES data system are described below:

USDA Forest Service. USFS researchers are responsible for the collection and management of precipitation, streamflow, phenology, soil temperature and moisture and hydrometeorological data. Data collected during the current year are backed up on 3.5 inch floppy disks when the data files are altered or appended. The entire database for the current year is backed up monthly on a 100MB zip drive. Backup disks are stored at the Robert S. Pierce Ecosystem Laboratory at Hubbard Brook and also at an off-premise location. Data formatting and QA/QC checks are made at Hubbard Brook with a series of manual inspections and computer programs. Corrected files are transferred annually to the Northeastern Forest Experiment Station in Durham, New Hampshire where they are stored in a DBMS. Backups of the entire long-term database are made in Durham and are stored at both Hubbard Brook and Durham. The corrected data are posted on the WWW in ASCII format immediately after they are received in Durham.

Institute of Ecosystem Studies (IES). The HBES long-term stream and precipitation chemical data are compiled, checked for quality assurance, and flux values calculated on a pair of Pentium-processor based, peer-networked computers in the Robert S. Pierce Ecosystem Laboratory at the HBEF, under the supervision of the IES Field Research Manager. Each chemical data file is run through a series of subroutines that determine ion balance and identify potential keypunching errors and/or possible contamination by comparisons to long-term means and standard deviations. No data records are removed or otherwise edited unless physical evidence or re-analyses confirm that the sample is contaminated. Updating of data files on the HBES WWW site is done by replacement of the complete data set, and not by appending new data to the old values. This procedure ensures that any corrections

to the original files are incorporated into the public dataset. Backup files are made onto 100MB removable cartridges, which are sent to IES at regular intervals. Backup cartridges, containing all data, are updated at the end of each working day and are stored in offsite locations.

IES investigators are also responsible for long-term datasets on throughfall and microbial biomass and activity. These datasets are collected, analyzed, and submitted to the HBES data manager by the individual investigators. IES has just installed a new Windows NT server and TCP/IP running over ethernet. All IES HBES data will be stored on this server and backed up daily for security.

Syracuse University. Researchers at Syracuse University conduct long-term measurement on soil, soilwater and streamwater. Samples collected and processed in the field, are analyzed at Syracuse University and logged into spread sheets. The data base is checked and a backup file established each month. The quality of the data is ensured by a quality assurance/quality control (QA/QC) program which includes sample and analytical replicates, sample splits with other laboratories, charge balance checks, analysis of standard reference materials and blind audit samples. Data are submitted to the HBES Data Manager yearly for inclusion into the HBES data base.

Cornell University. Cornell University researchers are responsible for the collection, analysis and data management of monitoring efforts for foliage chemistry, litterfall mass and chemistry and fine root dynamics. Foliage samples from overstory trees are collected in late summer every year, ground and stored in the HBES sample archive. Litterfall is collected four times each year from a network of 80 traps. These samples are sorted by tissue type and species, including direct counts of all leaves. QA/QC is performed by the PI (Fahey) each year. Fresh leaf litter is collected during peak litterfall over a 3-day rainless interval, and samples are dried, ground and stored in the sample archive. Foliage and litterfall samples are analyzed chemically at Yale University. Fine root dynamics are measured by minirhizotron (since 1995). Original videos are stored in the sample archive. Digitized images are currently being analyzed and a final data management and storage protocol is under development for this extremely complex data set.

Yale University. Researchers at the Yale School of Forestry and Environmental Studies conduct long-term research on the forest biomass, nutrients and population dynamics as well as forest floor mass and nutrients. Forest plots on the reference watershed (WS-6) are inventoried at 5-year intervals. Standard summaries are prepared of the phytosociology (basal area, density and frequency by species) and biomass calculated using HBEF-specific allometric equations. Total nutrient amounts in the forest biomass are calculated. Raw field data on a plot by plot basis are entered into ASCII files and also entered onto the WWW. A tagged-tree inventory is maintained on 10 ha with all the individual trees over 10 cm monitored at 2-year intervals. Quantitative measures of the forest floor mass and chemistry are monitored on the reference watershed at 5-year intervals. Chemical analyses for base cations, P, N and Pb are done on the forest floor material. Data are also available in ASCII format and on the WWW when completed and approved for public access. Physical samples of forest floor material are archived in the HBEF sample archive building for long-term preservation.

Dartmouth College. The HBES long-term bird and insect data have been collected since 1969 by a number of scientists, along with post-docs, students, and numerous field assistants. Methods for data collection, analysis, and quality control are accessible in numerous publications (see HBES WWW Page under Richard T. Holmes). Data are updated and submitted to the HBES Data Manager annually. Insect specimens are in the process of being catalogued and archived for future chemical or

other analyses. Holmes uses a McIntosh personal computer system based at Dartmouth, with data entered and checked for quality daily as they are collected in the field.

5.3 Sample Archive

All HBES samples of precipitation, stream water, lake water, vegetation and soil are repositied in the physical sample facility at HBEF. Cataloging, barcoding, and storage of these analyzed and preserved water samples is expected to continue for the foreseeable future, although space limitations may require priority storage eventually. Electronic linkages between the HBEF GIS, the long-term chemical database, and the physical sample inventory are in development. Requests for reanalysis of these samples (e.g. for sulfur isotopes or heavy metals) average two or three times each year, so this archival system obviously has become attractive to researchers at HBEF and elsewhere. A manuscript exhaustively detailing the methods used to collect and analyze water samples at HBEF, since the inception of the HBES in 1963, has been prepared (Buso et al. 1998). A document archives located and maintained at IES includes field books, data books and records, correspondence, theses, proposals, and all publications of the HBES.

5.4 Data availability

Our HBR-LTER data have been available publicly since 1988 through a direct-dial, computer bulletin board, "The Source of the Brook" (SOTB), which was one of the first fully functional database retrieval systems established at an LTER site (Veen et al. 1994). The SOTB provided, for example, data on streamflow, precipitation, meteorology, vegetation, soils, and monthly chemical data for precipitation and stream water for the HBES. A blind search of web sites that reference the HBES data collections finds several hundred cross-references. In addition, dozens of "outside" researchers over the years have used or referred to the long-term data bases from the HBES.

The draft "data access policy for the LTER network" circulated in August 1997 has generated much discussion among the HBES researchers. Based on long-term policy, HBES biogeochemical data are made public 5 years after collection. Hydrological, meteorological and some biological (at the discretion of the investigator) data are made public within 1 or 2 years of collection. These policies are consistent with the draft data access policy for the LTER network, whereby we view the biogeochemical data as Type II, i.e. "exceptional data sets", based on the assumption that some data sets require more effort to get on-line and that no "blanket policy" is going to cover all data sets at all sites. However, we feel that the data access issue is much more complex than this proposed policy would suggest and requires much more discussion both within the LTER network and within the scientific community at large. HBES researchers are ready and willing to play a leading role in this discussion.

6.0 - SITE OUTREACH

We will continue to build on the strengths of the scientific program at Hubbard Brook, and the talents of the scientists and technical support staff, to share our knowledge and understanding of ecosystem science and environmental issues with a diverse audience of students, visiting scientists, resource managers, policy-makers, the media, and the public. During the past LTER funding cycle Hubbard Brook annually hosted an average of 20 college classes, 30 scientists from other countries, 2-3 site visits associated with professional conferences, 3-5 continuing education courses for resource management professionals, 1-3 major media contacts, and a seminar series for the local community. Each year we provide a broad range of activities at Hubbard Brook that fall under the category of site outreach. These activities can be grouped into education, extension, and communication. The recently formed Hubbard Brook Research Foundation will expand the scope of site outreach beyond these traditional areas and share the knowledge gained through research from the HBES with a wider audience.

Education: In addition to providing student education through the graduate programs of participating universities and work experience for many undergraduates, Hubbard Brook hosts over 20 college classes each year for field trips or portions of field courses. During the past academic year, class visits to Hubbard Brook were made from Yale, Brown, The University of New Hampshire, Dartmouth, Keene State College, Plymouth State College, The University of Wolverhampton, England, Paul Smith's College, The University of Connecticut, Sterling College, Bentley College, The University of Vermont, and MIT. The focus of most field trips is on the long-term biogeochemistry studies and the effects of watershed-scale manipulations on forest and associated aquatic ecosystems at Hubbard Brook, although some are more specialized (e.g., forest hydrology).

Extension: The depth and diversity of research at Hubbard Brook provides an excellent basis for extension and outreach activities that meet the informational needs of scientists, foresters, resource managers, soil scientists, land owners, non-governmental organizations, and policy-makers. Scientists from HBES conduct an average of 10 sessions per year which fulfill the continuing education requirements of resource professionals working in forestry or soil science, with 3-5 of these being hosted at the HBEF. Field trips as part of national scientific meetings visit Hubbard Brook on average of 1-2 times a year. Recent trips have been associated with the Ecological Society of America, Gordon Conferences and Geological Society of America meetings. During the past LTER funding cycle, HBES hosted 2 visits by congressional representatives and a group of selectmen, town managers and town conservation committee members from 5 nearby towns. The purpose of these visits was to gain an understanding of current resource management and environmental issues. We have also provided programs on the HBES and tours of HBEF to a number of non-governmental organizations including The Sierra Club, The Audubon Society, the Northern New Hampshire Foundation, the Switzer Environmental Leadership Program, the Northern Forest Alliance, and the Pew Scholars Program.

There are two significant international efforts associated with the HBES. First, Steve Hamburg is participating in the International LTER program. He has been working closely with scientists from Taiwan to develop the Taiwanese Ecological Research Network. As part of this effort, there have been several exchanges of scientists between the HBEF and Taiwan. Second, through the United Nations Man and the Biosphere Program, HBES scientists have a cooperative research program with the Russian Institute of Geography in Moscow and the Caucasus Biosphere Reserve.

Communications: During the past year a considerable amount of information about the HBES, including access to data, were consolidated in the Hubbard Brook World Wide Web Homepage (<http://hbrook.sr.unh.edu>). Topics include descriptions of the site and its history, summaries of major research findings, CV's of the PIs, a list of the more than 1300 publications that have been produced by the HBES over the past 30 years, news and activities, and current research programs. We have also recently updated three descriptive documents on the HBES each of which is directed to different audiences; a brochure, a 16 page booklet, and a longer description of the HBES. A major forum for communication within the HBES is the annual cooperators meeting. Currently held in early July, this two day meeting has over 150 participants and features between 50 and 60 presentations, including several on the policy implications of HBES research.

Hubbard Brook Research Foundation: The Hubbard Brook Research Foundation (HBRF), a private non-profit 501c3 organization, was established in 1993 with the objectives of 1) advancing scientific understanding of forests and associated aquatic ecosystems by promoting and supporting scientific research studies, 2) promoting the utilization of scientific findings of the HBES in improved management of terrestrial and aquatic ecosystems, 3) promoting the scientific education of students, and 4) promoting public awareness of the ecological importance of forests and associated aquatic ecosystems and the scientific findings of the HBES. To expand on the education, extension and communication efforts described above, the HBRF is developing a "Science Links" program in which it will partner with HBES scientists and the USDA Forest Service to systematically enhance the flow of information from HBES researchers to practitioners and policy-makers throughout the region. One component of this program will bring together HBES scientists and conservation, management and policy leaders through annual round-table discussion series to identify critical ecosystem questions facing the region, synthesize HBES research to help address these questions, and communicate these findings through forums, conferences and publications geared toward a non-scientific audience.