Long-Term Ecological Research

Research Proposal Submitted to
The Division of Environmental Biology
National Science Foundation

by

University of Georgia Research Foundation, Inc.
Athens, Georgia 30602

Long-Term Ecological Research in Forested Watersheds at Coweeta

January 25, 1980

Principal Investigator:

D. A. Crossley, Jr.
Institute of Ecology
University of Georgia

Co-principal Investigators:

W. H. Caskey
Institute of Ecology
University of Georgia

Clayton S. Gist
Oak Ridge Associated Universities
Oak Ridge, Tennessee

Bruce Haines
Institute of Ecology
University of Georgia

Judy Meyer
Institute of Ecology
University of Georgia

George R. Parker
Department of Forestry
and Natural Resources
Purdue University

J. Dan Pitillo
Department of Biology
Western Carolina University

Harvey L. Ragsdale
Biology Department
Emory University

Wayne T. Swank
USDA Forest Service
Coweeta Hydrologic Laboratory

Robert L. Todd
Institute of Ecology
University of Georgia

Jack B. Waide
Environmental Science Division
Oak Ridge National Laboratory

J. Bruce Wallace
Institute of Ecology
University of Georgia

Jackson R. Webster
Biology Department
Virginia Polytechnic Institute
and State University

Other Co-investigators:

Coweeta Hydrologic Laboratory:
Bryant Cunningham
George Kuhlman
Dan Neary
L. W. Swift, Jr.

Emory University:
Willard H. Grant
William H. Murdy
Donald L. Phillips
James N. Skeen
Conrad E. Wickstrom

Table of Contents

VII. Publications, Theses and Dissertations

VIII. Annotated Bibliography of Publications on Watershed Management by the Southeastern Forest Experiment Station, 1928-1970.

X. Subcontract documents

XI. Budgets

List of Tables

17. Elemental determination for samples of sporocarps collected at Coweeta Hydrologic Laboratory.
18. Characteristics of streams at Coweeta Hydrologic Laboratory.
19. Past and future sampling schedule for stream studies.

List of Figures

I. Introduction

The one area in which our understanding of ecosystem dynamics may be the weakest concerns processes and behaviors occurring over long time periods. Over the past two decades research on ecosystem dynamics, in this country and elsewhere, has focused upon processes in undisturbed systems only over relatively short time periods, or on the very earliest phases of ecosystem response to specific experimental manipulations. Data on long-term dynamics of unmanipulated ecosystems, or on the entire successional sequence of ecosystem recovery from disturbance (natural or man induced), are essentially non-existant. Yet it is becoming clear that we must understand ecological processes which occur at frequencies lower than those commoly investigated in current ecological research. Such a conclusion applies whether we are interested in documenting anthropogenic influences on ecosystems, in managing biological and physical resources prudently, or in developing any general theory of ecosystem dynamics. In many cases short term studies, or studies which _a priori_ assume ecosystems to be in functional or compositional steady states, may lead to erroneous conclusions and may obscure fundamental principles of ecosystem organization.

In this proposal we outline a program of long-term ecological research on forest ecosystem dynamics to be conducted at the Coweeta Hydrologic Laboratory, North Carolina. This research program is designed to build upon more than a decade of ecosystem research at Coweeta, as well as on over forty years of baseline monitoring and research on forest soils, geology, climatology, and hydrology. We describe our broad objectives in the long-term research program and relate them to previous research on site. Advantages of Coweeta as a site for long-term ecological research are elaborated. Specific research projects are discussed by process area. We indicate how integration among research projects will be maintained and elaborate upon managerial details of the research program.

The Coweeta Hydrologic Laboratory, a U. S. Forest Service research facility located in the Nantahala Mountains about 17 km south of Franklin, North Carolina is eminently suited as a site for long-term ecological research. Since the site is owned by the U. S. Forest Service, and is a Biosphere Reserve, its availability for research on ecosystem dynamics over the long term is guaranteed. Over forty years of relevant baseline information on soil, geology, climate, hydrology and vegetation exists for Coweeta. Thus, we will not be constrained with the task of initially establishing such baseline information as part of this program. Rather, we will be able to build constructively upon existing information in our future research efforts.

Another major advantage of Coweeta is the physical layout of the site itself. The laboratory area is composed of two main drainage basins (Coweeta and Dryman Fort) which together comprise 2185 ha. A variety of experimental areas of varying topography, elevation, aspect, and size thus exist at Coweeta. Four major vegetation associations (oak-hickory, cove hardwoods, pine-hardwoods, and northern hardwoods) occur within the basin. All of these factors combine to produce a wide diversity of areas for ecological research. Some of these areas have been manipulated in past research, providing the opportunity to conduct studies in a variety of successional stages. Moreover, the opportunity exists for additional manipulation in future research. Also, Coweeta is representative of physical conditions and biotic communities of the southern Appalachians, and is currently remote from major sites of industrial activity. The latter fact has allowed us to develop data bases on undisturbed forest ecosystems, while at the same time providing the opportunity to document any future man-induced changes in ecosystem processes which may develop as the southeastern U. S. continues to industrialize.

Finally, a major advantage of Coweeta as a site for long-term studies is our ability to build upon more than a decade of NSF-funded research on forest ecosystems. Such past research, the objectives of which are described below, has provided us with extensive data sets on southern Appalachian forest ecosystems, and has allowed us to develop specific objectives in the work proposed here. We currently have a firm basis for defining key processes which need to be studied over a longer time period to improve our understanding of forest ecosystem dynamics in the southern Appalachians. Moreover, in the past work we have gained experience in managing large-scale ecosystem research projects. We have also demonstrated a continuity in research effort and leadership, as well as a strong long-term commitment to research on ecosystem-level phenomena.

Our objectives in this request for long-term research support at Coweeta fall into three broad areas. First, through our research efforts we hope to develop specific data bases which will allow us to detect accumulations of potentially toxic substances (e.g., heavy metals) within forest ecosystems. We plan to measure concentrations of select nutrients within soil arthropods, microbial fruiting bodies, and plant tissues at selected time intervals. The measurements of chemical concentrations in litter and soil horizons, as well as of solution chemistry collected at various points within forests, will also provide data for this objective. Our efforts in this area will be furthered by our practice, initiated in 1974 and to be continued in the future, of archiving select samples of soils, litter, sediments, plant tissue, and animals. Should a future need develop to measure some previously unmeasured substance in samples from prior years for comparative purposes, these collections will provide a valuable resource.

A second objective in our long-term research at Coweeta is to develop data bases which will allow us to evaluate long-term anthropogenic influences on forest ecosystems. Through our specific research initiatives on ecosystem components and on rate processes, we should be able to detect slowly developing, long-term changes in natural processes resulting from human impacts. Questions such as the following fall within this second objective: Are rates of organic matter production and decomposition changing as a result of increasing industrialization in the southeast? Are industrial activities or forest management practices causing changes in demographic processes in plant populations, and therefore altering the composition of plant communities? Are industrial activities or forest management practices leading to significant declines in soil fertility? While we certainly do not intend to address directly all possible questions of this sort, we do hope to develop the data bases which will allow us to examine specific questions should the interest or the need develop in the future. Again, the present remoteness of Coweeta, and the very real possibility that it may be more strongly influenced by significant future increases in industrialization within the southeast, together with increased demand for forest products within the country, make this second objective a viable one in our work.

Finally, the third objective in our proposed program of long-term research at Coweeta, and the one one which we will concentrate most directly and most intensively, relates specifically to the nature of long-term dynamics within forest ecosystems. We simply do not have an adequate understanding of long-term processes occurring in natural ecosystems and cannot completely evaluate anthropogenic influences on them until we do. For example, some of our recent work at Coweeta has focused on effects of defoliation --specifically by the fall cankerworm, Alsophila pometaria (Geometridae) -- on forest biogeochemistry. But the basic question still remains, over what time periods (10 years? 40 years? 100 years?) do cycles of defoliation occur in southern Appalachian forests and what factors are responsibile for initiating and for terminating such cycles? Or, how do forest ecosystems at Coweeta respond to climatic cycles on the order of decades? A third major question of this type concerns successional dynamics of forests. We have studied forested watersheds at Coweeta immediately following management disturbances, as well as over discrete time periods after disturbance, (e.g. 6-14 years). But we have only limited data and information on the longer-term successional responses of forest ecosystems in the southern Appalachians. How do rates of organic matter production and decomposition change over time, and what processes regulate such changes? How does the processing of allocthonous organic inputs to streams change following forest disturbances, as related to compositional shifts in stream fauna? How do the processes of nitrogen fixation, denitrification, and nitrification change during forest succession to regulate levels of available N in forest ecosystems? a fourth and final example (of a question of this type) relates to the types of natural "disturbance" (e.g. fires, major wind storms) which influence forest ecosystems in the southern Appalachians, and the time frame over which they operate. The need to understand such processes is especially accute for terrestrial ecosystems, such as forests at Coweeta, which are dominated by extremely long-lived species. Again this need represents perhaps the one area in which our understanding of ecosystems-level phenomena is currently weakest. Until we improve our understanding here, we will remain frustrated in our attempts to meet unambiguously the second objective stated above, that of documenting anthropogenic influences on forest ecosystems. Nor can we expect to generate substantive general theory of ecosystem dynamics in space and time until we more completely understand processes occurring over long time periods.

In regard to this third objective, ecosystems can conveniently be viewed as hierarchial systems (Simon 1962, 1973; Monk et al. 1977; Webster 1979; Schindler et al. 1980; Waide et al. 1980). For such systems, it is possible to order or array the observable system behaviors or responses into classes based upon the frequencies at which they occur. By setting sampling frequencies we are placing observational windows on complex ecosystems which thus allow us to recognize their dominant behavioral frequencies as well as the organization or structure of the system reflected in these temporarily ordered events. The point is that explicit recognition of hierarchical organization within ecosystems, manifested as frequency bands of recognizable system behaviors, organizes or structures our knowledge of the specific system under study. Once an observer sets the frequency window through which he views any system of interest, then the results of the study are constrained to fall within certain frequency bands. In previous work at Coweeta, we have viewed forests through a "frequency window" bounded by day-to-week cycles at the fast end and year-to-decade cycles at the slow end. With this proposal we seek to expand our focus at the slow or low-frequency end. Understanding the nature of low-frequency dynamics of ecosystems, the organization or structure of the ecosystem manifested in such low frequency behaviors, and the spatial areas over which such behaviors operate remain major challenges in contemporary ecosystem biology.

The above discussions represent our broad objectives in proposing a program of long-term research at Coweeta. In later sections of the proposal we discuss, by major process area, sets of more specific objectives we hope to accomplish. Within each major process area, we discuss what previous research conducted at Coweeta, what data sets exist, what our long-term goals are for research in that area, and what we specifically hope to accomplish during the next decade. In some instances long-term research opportunities are identified. We conclude that section of the proposal by discussing mechanisms by which internal process areas will be integrated and correlated.

Should this proposed work on long-term research at Coweeta be funded, we will make every effort to coordinate our work with other successful LTER sites. Throughout our past work at Coweeta, we have been cognizant of the need to assure comparability of ecosystem-level research results. For example, we have made concerted efforts to coordinate and to compare our previous work with similar studies in progress at Oak Ridge National Laboratory and at the H. J. Andrews Experimental forest (e.g., see Swank and Henderson 1976, Henderson et al. 1978, and Swank and Waide 1980). We will continue to do so in the future, and have included sufficient travel funds in our budget request to allow individual investigators to visit other LTER sites where appropriate, or to attend general meetings of LTER participants. We have also included sufficient funds so that an external review committee (see Section V) can visit Coweeta and review our research progress. We feel that such activities are essential to the success of the types of research proposed here.

The proposed research is multi-institutional in nature, as much of our previous work at Coweeta has been. The University of Georgia and the U. S. Forest Service have cooperated in this research effort since 1968. We have benefited from cooperation and joint project development with other research units such as the H. J. Andrews Experimental Forest in Oregon and the Environmental Sciences Division, Oak Ridge National Laboratory, Tennessee. Cooperators from other regional universities (Clemson University, Virginia Polytechnic Institute and State University) have participated in previous research. The present proposal includes investigators from Oak Ridge Associated Universities, Oak Ridge National Laboratory, Emory University, Virginia Polytechnic Institute and State University, Purdue University, and Western Carolina University, in addition to U. S. Forest Service and University of Georgia personnel. We anticipate even broader multi-institutional cooperation as long-term ecological research at Coweeta continues to develop.

II. History of ecosystem research at Coweeta.

In this section we provide a historical review of major research efforts conducted at Coweeta. The first sub-section discusses Forest Service research since the inception of the Coweeta Hydrologic Laboratory in 1934. The next two sub-sections provide details of NSF-funded research through the University of Georgia, both within IBP and more recently. A final subsection outlines details of other research conducted at Coweeta.

A. Forest Service Research

The forests of the southern Appalachians Mountains had been devastated by logging in the early 1900's. Extensive grazing, annual burning of woodlands, and mountain farming were commonplace in the 1920's. Logging was being conducted by persons who had little regard for the damage done to the forest and erosion of the woodlands. Even professional foresters were poorly informed on the interaction of forests, soils and climate, and were poorly equipped to cope with water resource problems related to the forest. Research on forest-water relations was unknown prior to 1926 when Dr. Charles Hursh was appointed to the staff of the Appalachian Forest Experiment Station. He initiated research to define the hydrology of Forested lands of the Appalachians. His early work was on the Bent Creek Experimental Forest near Asheville, but he sought an area suitable for comprehensive studies of watershed management. In 1933 the Coweeta Basin was selected and set aside for forestry research. Largely because of urging by Dr. Hursh, the Station Director issued instructions forbidding manipulations of the forest cover until watersheds were standardized or calibrated. Thereafter, full responsibility for administration of the

Basin was assumed by the Division of Forest Influences. Because of this early decision, other forest research interests pulled out of the Basin and Coweeta was used for the next 40 years almost exclusively for studying the effects of forest land use on water resources.

A period of watershed calibration began in 1934. Up to 30 unit and multiple watersheds were gaged for varying lengths of time. A network of rain gages and numerous ground water wells were established to define rainfall amounts, patterns, and groundwater regimes. A permanent weather station was established in the valley and numerous temporary stations were used to define the climate of the basin.

By 1939, calibration of watersheds was adequate on some catchments to begin treatments, and watershed experimentation began. The experiments were of three types: 1) land use demonstrations designed to show the harmful effects of mountain farming, woodland grazing and unregulated logging; 2) forest cutting experiments designed to establish the effects of various levels of forest cutting on quality, quantity, and timing of stream flow; and 3) species conversion studies to quantify the effects of conversions from one type of cover to another on water resources.

By the mid 1950's, the land use demonstrations had served their purpose and were terminated. The forest cutting and conversion experiments had proved highly effective for precise measurement of changes in water resources which took place, but the paired watershed approach being used was not adequate for determining why the changes took place nor why these changes varied from watershed to watershed. Emphasis shifted from paired watershed experiments to studies of soil, plant, water, and stream processes and how these processes changed under management. The philosophy was that once the processes were understood, effects of forest management on water resources could be predicted with process models. Although highly informative, this phase of the program was never carried to conclusion by the U. S. Forest Service because of facilities and funding limitations and changing resource problems.

By the late 1960's, emphasis shifted toward water quality, a water resource parameter which had long been neglected. Cooperative research in mineral element cycling with the University of Georgia began in 1968, and a water chemistry laboratory was added at Coweeta in 1970. During the early 1970's, scientists were successful in developing a simple model for predicting effects of forest cutting on water yield; simultaneously, an evapo-transpiration model (PROSPER) was tested and found to work well. These developments materially reduced the need for new water yield studies, and the research program became oriented almost entirely toward nutrient cycling studies, plant productivity investigations stream research and to studies of nonpoint source pollution of streams draining forested lands. As 1980 begins, the Coweeta Basin and its unique watersheds and historical data base are being used primarily for nutrient cycling investigations in an ecosystem context. The research charter which outlines the current mission of Forest Service Research at Coweeta is included in Appendix I.

B. IBP research at Coweeta

NSF-funded ecosystem research was initiated at Coweeta in 1968 as a cooperative effort with the University of Georgia. Coweeta was selected as one of the intensive research sites of the Eastern Deciduous Forest Biome of IBP. Initially we set out to examine productivity and nutrient cycling processes on forested watersheds of diverse treatment histories. The research during this phase of our work focused upon four watersheds (Johnson and Swank 1973, Monk et al. 1977): a control hardwood forest watershed (WS 18), a 17-year old white pine plantation (WS 17), and 11-year old hardwood coppice forest (WS 13), and a 6-year old grass-to-forest successional watershed (WS 6). We measured a variety of basic ecosystem processes in the control forest and attempted through measurements on the three other watersheds to ascertain how processes had been altered by ecosystem manipulation. During this phase we also measured input-output budgets for all gaged watersheds within the basin (Swank and Douglass 1975, 1977). Such budget data for forested watersheds at Coweeta provide a measure of integrated ecosystem response in both natural and manipulated states, which are then explicable with reference of detailed measurements of nutrient cycling processes internal to experimental catchments (Monk et al. 1977).

This phase of research was extremely important to our overall program at Coweeta. We gained critical experience in investigating biogeochemical processes in southern Appalachian forest ecosystems. We established basic patterns of nutrient cycling in Coweeta forests, suggested biotic mechanisms which regulate nutrient losses via stream water, and developed specific hypotheses for further work on site (Monk et al. 1977). However, data on initial responses to forest manipulations immediately following treatment were lacking. This data gap lead to the next phase of our research program.

C. Current ecosystem research at Coweeta.

In 1973 we entered a second phase of research at Coweeta, again under NSF sponsorship via a cooperative agreement with the University of Georgia. Based on the initial phase of work outlined above, largely exploratory in nature, we established a set of specific hypotheses concerning the biogeochemistry of forest ecosystems at Coweeta and tested them by implementating a major ecosystem disruption: We clear-cut a 59 ha south-facing watershed (WS 7). Cable logging techniques were used to direct merchantable timber. We also took advantage of an outbreak of the fall cankerworm on high elevation watersheds at Coweeta (WS 27, 36, 37) to study the effects of defoliation on forest biogeochemistry.

Both of these studies were based upon three major organizational approaches to the investigation of complex ecosystem behaviors:

1) As stated above, input-output budgets of experimental watersheds provide an integrated measure of total ecosystem response. Detailed process-level studies on nutrient cycling within forested watersheds provide a mechanism for explaining integrated behaviors measured at ecosystem boundaries (Monk et al. 1977, Swank and Waide 1980).

2) Forest ecosystem may be conveniently viewed as hierarchical systems by explicitly recognizing the frequency bands over which ecosystem behaviors operate (Simon, 1963, 1973; Monk et al. 1977; Webster 1979; Shindler _et al_. 1980; Waide _et al_. 1980). In previous proposals we have outlined several hierarchical models of forest ecosystem dynamics which have been useful to us in synthesizing process-level research into an integrated picture of forest biogeochemistry.

3) Ecosystem responses to specific disturbances, natural or man induced, may be separated into two components (Webster et al. 1975, Waide and Swank 1976, Webster and Patten 1979, Swank and Waide 1980), resistance (the extent of displacement from a previous nominal level of function) and resilience (the rate of recovery to the previous level of function). These two components of an ecosystem's post-disturbance response may be quantified following a particular disturbance, or may be related theoretically to ecosystem persistence within temporially variable environments. We feel that different mechanisms regulate ecosystem resistance and resilience, and have in previous NSF proposals elaborated a set of process-level hypotheses which tie these two concepts to the specific research currently in progress at Coweeta.

Research on forest defoliation was undertaken during the period 1974-1976. We documented reduction in woody growth during the period of defoliation; measured litterfall and frass input to the forest floor; determined standing crops of organic matter and nutrients in soil and litter horizons; investigated a variety of microbial processes in soil and litter layers; and measured solution chemistry in precipitation, streamflow, throughfall, and litter and soil leachates via lysimeter collections. Research since 1976 has focused upon life history characteristics of the cankerworm at Coweeta and elsewhere in western North Carolina. We are currently preparing a monograph-length paper, as well as a number of shorter papers, based on this work.

Research was initiated on WS 7 in 1974. We obtained two years of background data on the catchment prior to its manipulation. Access roads were constructed during the spring and summer of 1976; logging and site preparation occurred during 1977. Research was reinitiated on the watershed as well as on adjacent control WS 2 in late 1977 and early in 1978. We will briefly outline the types of research which have been conducted on WS 2 and 7 in the process-level sections which follow later in this proposal. Current NSF support for this research continues through May, 1981. We feel that we have obtained extensive information on the immediate post-disturbance response of a southern Appalachian forest to acute disturbance. We have thus satisfied most of our initial objectives in this second phase of our work and will soon terminate some of our field research. Only select, key process measurements will continue for the remainder of this calendar year. We are now entering a period of data synthesis and writing to publish results of this research.

The long-term research we are proposing here essentially represent a third phase of research at Coweeta. It is designed to build logically upon past studies conducted on site. Were it not for the initial phase of our research program, we would not be in a position to propose a coordinated program of long-term research at Coweeta. But it is also clear that abrupt termination of our current program would result in critical information gaps in our studies of forest ecosystem dynamics in the southern Appalachians. We feel that we have a fairly complete understanding of short-term dynamics of unmanipulated forests, as well as of initial periods of recovery following ecosystem disturbance. But, we strongly feel the need to broaden our data bases, both on longer-term processes in natural forest ecosystems, and on the longer successional recovery periods of forests following perturbation. In this new phase of research, we propose to conduct the specific projects described below on various watersheds previously studied in detail to satisfy our long-term objectives. Only in this way can we obtain a fuller understanding of forest ecosystem dynamics at Coweeta.

D. Other cooperative research.

Because of the long research history, the variety of forest ecosystems, and the extant data base, Coweeta has an extensive record of cooperative research. During the past 30 years more than 40 cooperative projects have been conducted on site. At present there are 19 active, formal agreements which involve Forest Service scientists or data sets at Coweeta. These studies encompass 12 Universities, 6 different state or federal agencies, and private industry. The staff also frequently provides consultation to forest resource managers and administrators.

The laboratory has participated in a variety of International Programs including the FAO training programs, US/International Hydrological Decade, Eastern Deciduous Forest Biome of the US/International Biological Program and UNESCO Man and Biosphere Program. The laboratory has been designed as a Biosphere Reserve within the MAB Project 8 along with Great Smokey Mountains National Park and Oak Ridge National Laboratory to form the Southern Appalachian Cluster. Active research programs currently exist among these three sites and provides an excellent mechanism for the exchange of ideas and data. The site has been an active participant in the National Atmospheric Deposition Program since 1978. Coweeta is also included in the U. S. network of Experimental Ecological Reserves.

III. Site description

The Coweeta Hydrologic Laboratory is a 2185 ha experimental area located in the southwest corner of North Carolina in the southern Appalachian mountains. The site is administered by USDA, Forest Service, Southeastern Forest Experiment Station and has been dedicated to forest hydrology research since establishment in 1933. The area lies within the Blue Ridge geologic province and elevations range from 679 to 1592 meters. The diverse topography includes valley bottoms, coves, different slope positions and ridges; sites vary from very high to very low productivity. Approximately 50 km of streams drain the area and include first through fourth order drainages which flow to the Little Tennessee River.

The regional climate is classified as marine with cool summers, mild winters and adequate rainfall during all seasons. Precipitation is typically cyclonic in origin with air masses frequently coming from the Gulf of Mexico and sometimes from the Atlantic Coast or subarctic regions of North America. The steep mountains produce orographic precipitation and frequent thunderstorms during the summer months. Annual precipitation is high and variable over the area with an average of 178 cm at lower elevations to over 250 cm on the upper slopes. Snow typically contributes less than 2 percent to total precipitation. October is usually the driest month with an average precipitation of 9 cm and the wettest month is March with 20 cm. The streamflow regime follows a similar annual pattern and perennial flow occurs for watersheds as small as 6 ha. Quickflow (or direct runoff) comprises less than 10 percent of the total runoff, and there is essentially no overland flow on undisturbed catchments. Mean annual temperature is 13° C; the coldest month is January with a mean temperature of 3.5° C, and July is the warmest month with a mean of 21°C.

Prior to 1842 when the basin was settled by the white man, Cherokee Indians inhabited the area. Light semiannual burning of the woods and grazing were the principal land practices until about the turn of the century. Controlled selection logging was conducted in the period between 1909 to 1923. Cutting operations were concentrated in the valleys and accessible coves and lower slopes. The Forest Service acquired all rights to the area in 1924 and only experimental treatments have altered the landscape in ensuing years.

The site is located in a predominately agricultural county and tourism is also important to the local economy. However, in the past 5 years, there has been a strong and successful effort to attract small industries to the county. It is expected that industrialization trends will accelerate over the next 20 years which may signficantly alter atmospheric chemistry. Moreover, Coweeta is the first major mountain range encountered by the air mass moving over the industrialized Piedmont region to the south. Analyses of precipitation chemistry have shown the importance of both local and regional activities on nutrient inputs to forest ecosystems at Coweeta (Swank and Henderson 1976; Swank 1979) and changes in the form and amount of anthropogenic inputs are important to the interpretation of many ecosystem processes.

The laboratory is composed of two main basins, 1626 ha Coweeta and 559 ha Dryman Fork (Figure 1). The latter area is more isolated than the Coweeta basin; no experimental manipulations have occurred on the area, and the site has been held in reserve for future long-term studies. A number of potential gaging sites have been located in Dryman Fork and two adjacent catchments have been surveyed for area, permanent vegetation plots are established, inventoried, and data are summarized. Thus, Dryman Fork represents an excellent opportunity for expansion of ecological research and manipulation over the next several decades. The Coweeta Basin contains numerous small catchments with well-defined topographic boundaries (Figure 1). An existing road and trail system provides adequate access to research areas and the environmental impact of traffic is minimal. The administrative area occupied by Forest Service and University personnel is conveniently located at the valley entrance.

Experimental areas are distributed over the wide range of environmental gradients found on the area and include both control and manipulated ecosystems. A summary of past disturbances and current status of ecosystems by watershed number are given in Table 1 and keyed to Figure 1. Research has been conducted on 8 mixed hardwood control areas and 13 catchments where forest management prescriptions have been applied. Past treatments include varying intensities of cutting ranging from light selection through clearcutting; conversion of hardwoods to white pine; conversion of hardwoods to grass and subsequent succession back toward hardwoods; multiple use management; mountain farming; and the application of herbicides and fertilizer. Research

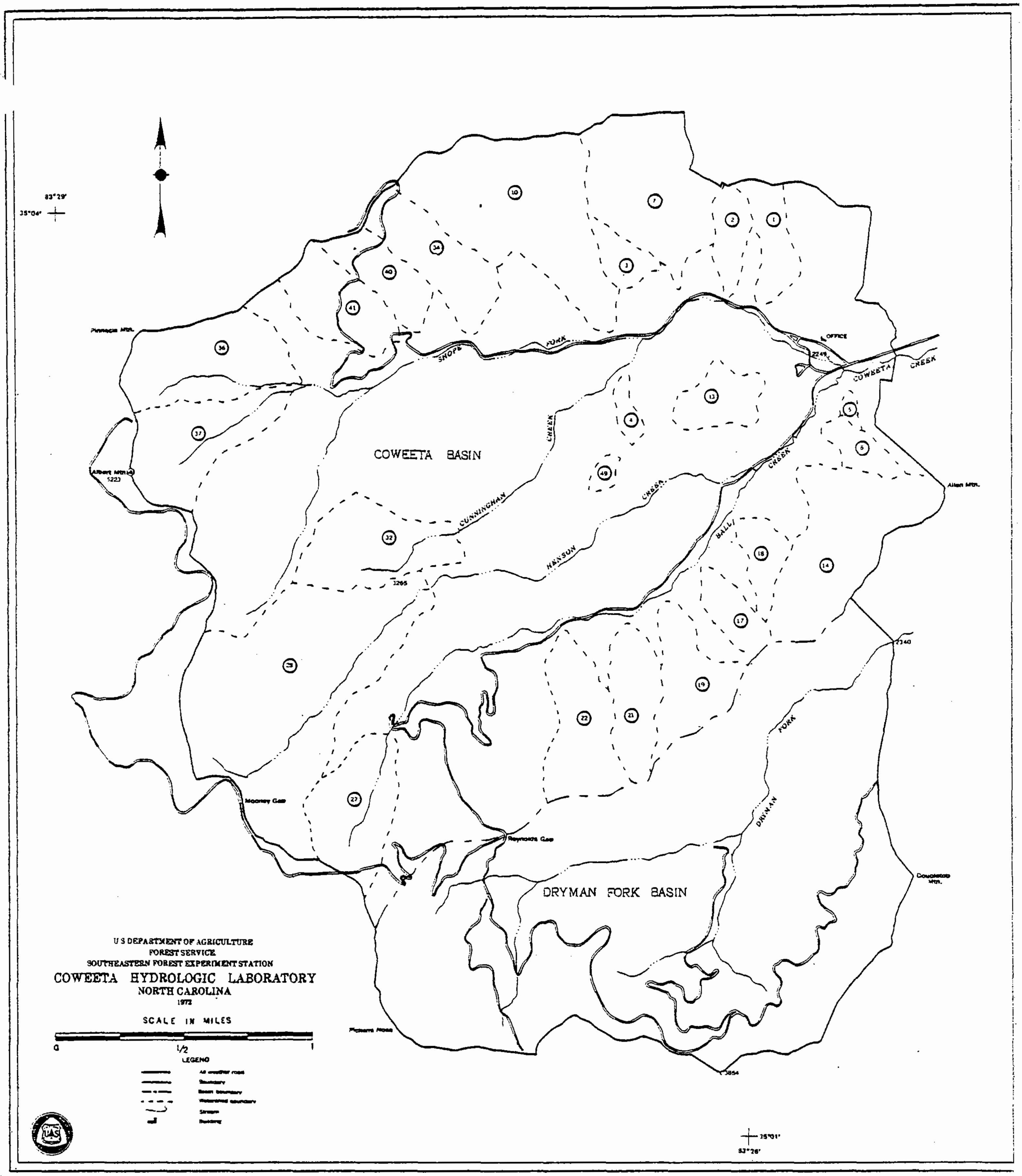


Figure 1 . The 2185 ha Coweeta experimental area is comprised of numerous catchments located in two main basins.

Table 1. Summary of watershed treatments at Coweeta and current status of ecosystems.

Watershed number	Treatment	Area in hectares	Vegetation
1	All trees and shrubs cut in 1956-57, no products removed; white pine planted in 1957	16.2	White pine, 23 years
2, 14, 18, 21, 32, & 34	All control	12.1, 61.1, 12.5, 24.3, 41.3, & 32.0 respectively	All mixed mature hardwoods
3	Unregulated agriculture 1940-52 followed by planting yellow poplar and white pine	9.3	3 ha in 24-year-old poplar; 2 ha in 24-year-old white pine; 4 ha in 30-year-old coppice
6	Cut in 1958 and products removed; limed, fertilized, and grassed in 1959; refertilized in 1965; herbicided in 1966 and 1967	8.9	Grass-to-forest in 13th year of succession
7	Woodland grazing from 1941 to 1952; clearcut and cable logged in 1977	58.7	Coppice, 3 years
8, 9, & 16	Combination watersheds; contain control and treated watersheds	759.6, 723.6, & 301.6 respectively	Mixture of mature hardwoods and regrowth
10	Commercial timber cut with 30 percent basal area removed in 1942-56	85.8	Mostly mature hardwoods with some regrowth
13	All trees and shrubs cut in 1939, recut in 1962; no products removed	16.2	Coppice, 19 years
17	All trees and shrubs cut in 1942, recut annually through 1955, no products removed; white pine planted in 1956	13.4	White pine, 24 years
19	Laurel and rhododendron understory cut in 1948-49; about 22 percent basal area	28.3	Mixed mature hardwoods
22	All trees and shrubs in alternate 33-foot strips deadened by chemicals in 1955; no products removed	24.3	50 percent mature hardwoods; 50 percent 26-year-old regrowth
27	Control, but partially defoliated by fall cankerworm infestation	38.8	Partially defoliated mature hardwoods
28	All trees and shrubs cut on 77 ha, cove forest of 39 ha thinned, no cutting on 28 ha; products removed	144.1	77 ha of 10-year-old coppice; 39 ha of regrowth and poplar; 27 ha mature hardwoods
36	Control, but partially defoliated by fall cankerworm infestation	48.6	Partially defoliated mature hardwoods
37	All trees and shrubs cut in 1963; no products removed	43.7	Coppice, 17 years
40	Commercial timber cut with 22 percent basal area removed in 1955	20.2	Mostly mature hardwoods
41	Commercial timber cut with 35 percent basal area removed in 1955	20.7	Mostly mature hardwoods

histories of each area are documented in publications and reports located in Coweeta files. Ecosystems which have been the subject of intensive study the past decade include Watersheds 2, 6, 7, 13, 14, 17, 18 and 27. Many of the long-term ecological investigations contained in this proposal will address hypotheses related to these ecosystems.

IV. Plan of research

A. Baseline Research Information

1. Climatology and Hydrology

The hydrologic research mission at Coweeta has entailed a thorough, broad collection of basic climatological data over a 47-year period. Records are too extensive for detailed explanation in this proposal and we will only summarize the types of records available, the current status of physical measurements, and additional research needed to provide environmental characterization for future ecological investigations. Standard climatic data have been collected at a permanent station located in the Basin valley (Figure 2). Table 2 provides a summary of measured parameters, instrumentation and frequency of observations. Established procedures are used to edit records and to compile the data onto cards, with subsequent summarization using various computer programs. Resources have been inadequate to maintain all compilations but examples of several summaries are given in Appendix (I) to illustrate the type of information currently or potentially available. Data from the base climatic station are published monthly by the Environmental Data and Information Service, NOAA in "Climatological Data - North Carolina." Additional climatic data have been collected at a number of locations within the Basin in relation to specific studies. The types of data and length of record for each station are indicated in Table 3 and their locations are shown in Figure 2.

Since 1934, more than 2,000 gage years of precipitation data have been collected at 130 different sites in the basin. Gaging densities ranged from one gage per 25 hectares to one per 4 hectares for experi-

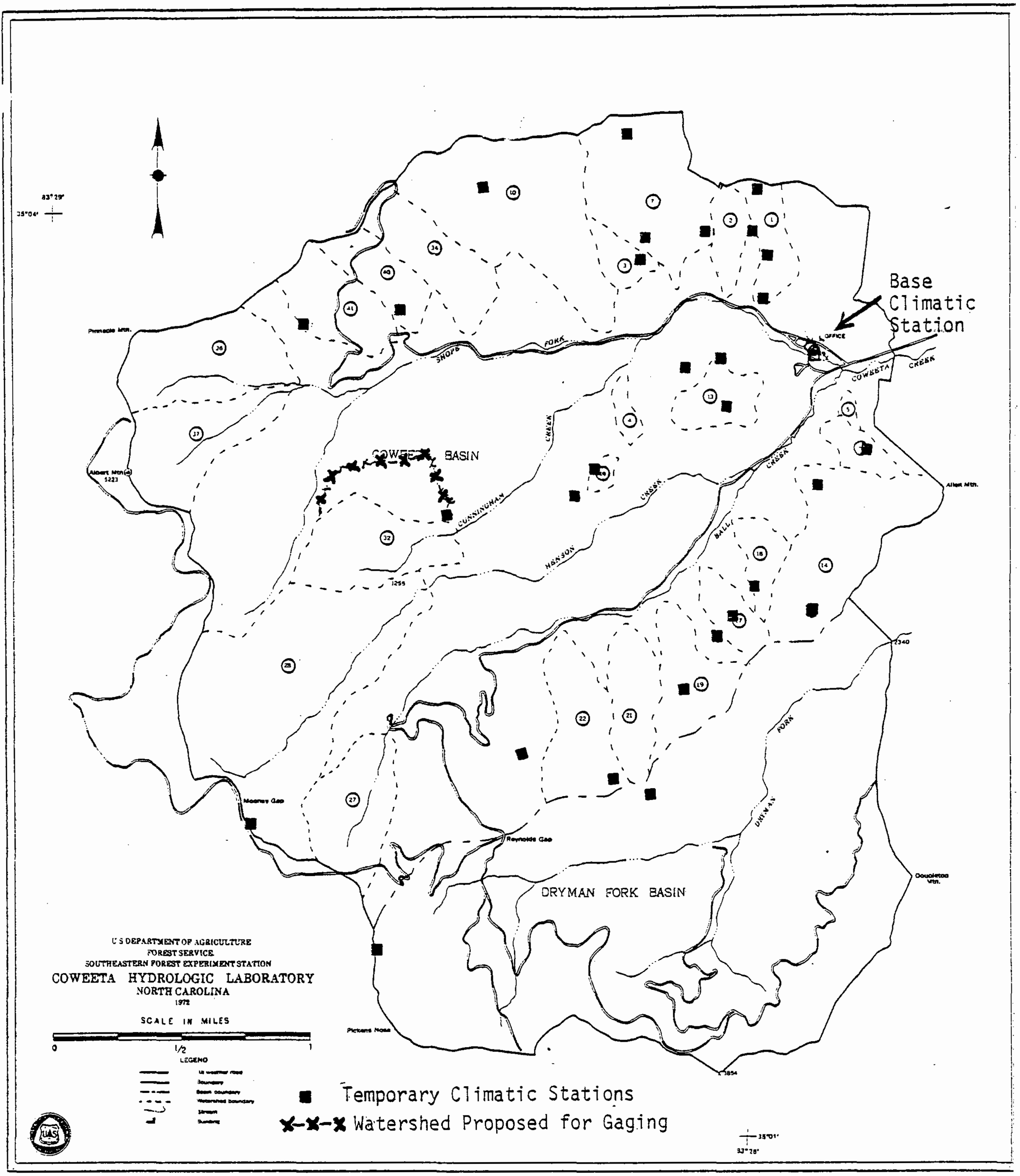


Figure 2. Location of climatic stations and proposed stream gaging station.

Table 2. Description of base climatic station at Coweeta Hydrologic Laboratory.

Measurement	Instrument	Frequency of Collections or Observations
Precipitation	Standard Rain Gage	Daily
	Friez Weighing Precipitation Recorder	Weekly
Temperature	Maximum and Minimum Thermometers	Daily
	Friez Hydrothermograph	Weekly
	Thermistor	Hourly
Humidity	Hydrothermograph	Weekly
	Foxboro Dewcell	Hourly
Wind Speed	Belfort 5-349 3 Cup Totalizing Anemometer	Daily
Wind Director	Electric Speed Model F420C Anemometer	Hourly sun
	8 Point Vane	Hourly
Solar Radiation	Eppley Temperature Compensated Radiometer	Continuous record Daily integrated total
Evaporation	36" dia. Sunken Pan	Daily (manual)
	18" deep	Hourly (recorded)

Table 3. Climatic Data Sites--Coweeta Hydrologic Laboratory

		ADP	Parameters Measured					
Site	Record Length	Record Length	Air Temp	Soil Temp	Relative Humidity	Solar Radiation	Wind	Evaporation
CS1	10/34 - Present	1/60-10/79	x	x	x	x	x	x
CS2	10/36 - 6/39	none	x	x	x			x
CS3	10/36 - 11/39	none	x	x	x		x	x
CS4	12/36 - 6/39	none	x	x	x			x
CS4	2/43 - 11/58	none	x		x			
CS5	10/36 - 6/39	none	x	x	x		x	x
6	10/36 - 6/39	none	x	x	x			x
6A	7/55 - 11/62	none	x	x	x			
7	10/36 - 6/39	none	x	x	x			x
7	6/61 - 11/62	none	x		x			
8	5/40 - 12/44	none	x	x	x			x
8	4/48 - 5/54	none	x		x			
9	5/40 - 12/44	none	x	x	x		x	x
10	3/40 - 8/44	none	x		x			
11	4/40 - 8/44	none	x		x			
12	6/41 - 6/55	none	x		x			
13	6/41 - 6/55	none	x		x			
14	2/43 - 10/62	none	x		x		x	
14A	7/55 - 11/58	none	x		x			
15	7/61 - 5/62	none	x		x	(Tree canopy and ground)		
16	6/66 - 12/68	6/66-12/68	x		x		x	
17	10/69 - Present	10/69-11/79	x	x	x		x	
18	8/73 - 6/74	8/73-6/74		x			x	
19	1/49 - 3/54	none	x		x			
20	8/73 - Present	8/73-11/79	x	x	x		x	
21	7/74 - Present	7/74-11/79	x		x		x	
22	6/74 - 5/76	7/74-4/76	x		x			
23	7/74 - Present	7/74-10/79	x	x				
40	4/50 - 10/55	none	x		x			
W1	9/60 - 9/61	none						x
W2	4/61 - 8/61	none						x
W3	4/61 - 9/61	none						x
W6	11/61 - 4/63	none						x
W11	8/70 - 5/71	none						x

ments on individual watersheds and one per 0.25 hectare for detailed studies of rainfall distribution. Based upon this extensive record, an isohyetal weighting system was developed to estimate total precipitation on steep mountain slopes and it was possible to reduce the system to 12 recording gage sites which currently provide satisfactory areal estimates for individual watersheds. Precipitation records are routinely processed using several programs and examples are given in Appendix II. Data from two Coweeta gages are published monthly by the Tennessee Valley Authority in "Precipitation in the Tennessee River Basin."

Streamflow has been gaged at 31 locations within the laboratory and nearly 1,000 gage years of records have been compiled (Table 4). These data constitute the longest continuous record of streamflow of high quality from forested catchments in the United States. Data processing routines and hydrograph analyses developed at Coweeta have become a standard in forest hydrology research. In fact, the laboratory contracts translation and compilation services to other forest hydrology projects in the country. Data are routinely reduced and summarized into four different forms: 1) time-CSM coordinates, 2) mean daily CSM, 3) flow frequency, and 4) hydrograph flow separation. Illustrations for each compilation are presented in Appendix III.

Climatic and hydrologic data are also processed to provide a convenient ranking of measurements so that a particular event, season, or year can be placed in perspective with regard to the total length of record. For example, from the ranking of annual precipitation given in Table 5, it is evident that precipitation during the four year period of 1973-76 greatly exceeded average values and was followed in 1978 by

Table 4.--Summary of drainage area installations and characteristics at Coweeta Hydrologic Laboratory.

COWEETA HYDROLOGIC LABORATORY

Drainage Area Installations

Watershed number	Name of stream	Area in hectares	Date of first record	Length of record (yrs.)	Type of notch	Average land slope (%)	Channel length (m)	Maximum discharge (csm)
*1	Copper Branch	16.2	6/13/34	46	90° V-notch	48	400	209.46
*2	Shope Branch	12.1	6/22/34	46	90° V-notch	60	390	220.19
3	Little Hurricane	9.3	7/05/34	25	CIA deep notch	51	150	1,854.38
4	Jenny Branch	4.0	7/05/34	6	Water supply	--	--	--
5	Creasman Branch	1.6	6/30/34	6	90° V-notch	--	--	--
*6	Sawmill Branch	8.9	7/10/34	46	90° V-notch	54	240	344.45
*7	Big Hurricane	59.5	7/31/34	46	90° V-notch	57	1,760	199.29
*8	Shope Fork No. 1	759.6	10/06/34	46	12' Cipolletti	--	5,120	153.98
*9	Ball Creek No. 1	723.6	10/12/34	46	12' Cipolletti	--	4,400	225.11
10	Camprock Creek	85.8	3/07/36	19	120° V-notch	50	3,240	77.48
11	Cunningham Creek No. 1	178.1	3/05/36	10	5' Rectangle	--	--	97.42
12	Henson Creek No. 1	202.7	3/17/36	9	6' Cipolletti	--	--	187.20
*13	Carpenter Branch	16.2	3/12/36	44	120° V-notch	49	600	99.55
*14	Hugh White Branch	61.1	5/26/36	44	120° V-notch	49	2,200	101.14
15	Ball Creek No. 2	380.4	12/21/36	7	8' Cipolletti	--	--	129.20
16	Shope Fork No. 2	381.6	6/04/36	7	6' Rectangle	--	--	172.00
*17	Hertzler Branch	13.4	6/06/36	44	90° V-notch	57	350	96.83
*18	Grady Branch	12.5	7/03/36	44	120° V-notch	52	290	124.00
19	Snake Den Branch	28.3	5/16/41	30	120° V-notch	48	1,050	117.09
20	Ball Creek No. 3	206.8	7/30/37	6	6' Rectangle	--	--	115.50
21	Sheep Rock Branch	24.3	7/22/38	30	120° V-notch	42	1,760	164.00
*22	Lick Branch	34.4	2/18/37	31	120° V-notch	53	2,830	160.51
*27	Hard Luck Creek	38.8	11/02/46	35	120° V-notch	55	1,230	516.54
28	Henson Creek No. 2	144.1	5/31/37	39	6' Rectangle	52	3,920	185.68
32	Cunningham Creek No. 2	41.3	10/25/41	34	120° V-notch	46	1,750	123.64
*34	Bee Branch	32.8	10/13/38	43	120° V-notch	52	940	91.85
*36	Pinnacle Branch	48.6	4/29/43	38	120° V-notch	65	1,330	398.85
37	Albert Branch	43.7	4/15/42	34	120° V-notch	71	1,260	491.25
40	Wolf Rock Branch	20.2	12/04/38	36	90° V-notch	61	340	91.40
41	Bates Branch	28.7	8/23/40	31	120° V-notch	62	920	108.09
49(100)	Barker's Cove	2.8	3/14/38	25	90° V-notch	--	--	62.88

*Active on January 1, 1980

Table 5. Annual precipitation by increasing amounts (inches), Coweeta SRG 96.

Sequence	Year	Amount
1	1941	54.65
2	1963	63.83
3	1941	66.44
4	1978	66.84
5	1940	67.11
6	1938	69.39
7	1968	70.74
8	1953	71.13
9	1945	72.20
10	1965	73.10
11	1947	73.25
12	1956	73.41
13	1954	74.24
14	1966	74.53
15	1944	75.96
16	1952	76.86
17	1977	76.92
18	1942	77.10
19	1971	77.30
20	1958	77.55
21	1961	77.80
22	1937	78.84
23	1970	79.08
24	1948	79.15
25	1950	80.04
26	1939	81.63
27	1972	82.12
28	1960	82.30
29	1955	82.82
30	1959	82.84
31	1967	84.81
32	1957	85.01
33	1943	85.31
34	1946	85.90
35	1969	87.65
36	1962	89.00
37	1973	91.56
38	1976	91.87
39	1975	92.23
40	1936	94.56
41	1964	95.67
42	1974	99.59
43	1979	105.95
44	1949	114.83

one of the driest years on record and then in 1979 by one of the wettest. Such perspectives are invaluable in the interpretation of biological findings which may be derived at infrequent intervals.

The Forest Service will continue to provide the resources for collecting baseline climatic and hydrologic measurements at current levels of effort. However, it is important that some existing records be edited and key-punched so they are readily available to investigators. During this proposal period the hair hygrothermograph will require replacement and an aspirated psychrometer obtained to improve the quality of the humidity record. Another base climatic station will also probably be needed within the basin at high elevations. However, we feel such an installation would be more efficiently designed and located during the fourth or fifth year of the LTER effort. The most urgent need for development of baseline hydrologic data is the establishment of an additional gaging site (Figure 2) to provide a pair of catchments for future experimental manipulation. The last weir constructed at Coweeta was in 1946 and with the recent clearcut manipulation on WS 7, we do not have a paired-catchment experimental design available for future studies. The installation of a 120° V notch weir on Mill Branch (WS 31) would provide an excellent pair with adjacent WS 32. There is already good access to the construction site and bedrock is located near the surface which will insure a water tight cut-off installation. Moreover, the watershed boundaries have been surveyed, 106 permanent .08 ha vegetation plots have been established and inventoried, and data have been summarized. Thus, with a modest additional investment, we could begin paired calibration of hydrologic and chemical parameters for mature hardwood covered catchments.

Previously manipulated watersheds will continue to provide opportunities to test a variety of ecosystem hypotheses, but this additional weir would represent the only possibility to examine future questions related to experimental manipulation of relatively undisturbed mixed hardwoods.

2. Water and Sediment Chemistry

Precipitation and stream chemistry data at Coweeta are among the largest continuous records available for forest ecosystems in the United States. Limited analyses were started on a routine basis in 1969, were substantially expanded in 1972, and several important supplements were added in later years. Chemistry of bulk precipitation, wet and dry-fall, and stream water are measured at weekly intervals while Coshocton and sediment samples are usually collected on a weekly or bi-monthly basis. Throughfall, litter, and soil water samples have been collected at intervals defined by specific study objectives. Changes in water chemistry during storm events have also been documented.

A summary of parameters measured for each type of water sample is provided in Table 6. Data listing, editing, and compilation are standardized and records are routinely summarized at about four month intervals. Samples of data compilation for selected parameters are given in Appendix IV. A complete manual of analytical procedures is maintained in Coweeta files (Beale 1979) and methods are updated as modifications are implemented in the laboratory. A generalized summary of methods is provided in Table 7. Quality control is emphasized in laboratory procedures and an example of external reference is shown in Table 8, where EPA standards are used as a check over the normal ion concentration range found at Coweeta.

The precipitation chemistry network is coupled to rain gage stations and twelve sites over the basin are routinely analyzed. Stream water chemistry has been documented for 24 drainages and input-

Table 6. Summary of the analyses performed on each type of water sample and associated sediments and the general collection techniques used.

Type Sample	Collector	pH	Conductivity	Tot. Suspended Solids	Kjeldahl N	Diss.Org. N	NO_3-N	NH_4-N	PO_4	Tot. P	K	Na	Ca	Mg	Cl	SO_4	HCO_3	SIO_2	Heavy Metals	DOC
Bulk Precipitation	Polypropylene Funnel	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X
Dryfall	Wong Sampler Volchock Samp.	X			X		X	X	X	X	X	X	X	X	X	X	X	X		
Wetfall	Wong Sampler Volchock " EPA Sampler	X	X		X		X	X	X	X	X	X	X	X	X	X	X	X	X	
Throughfall	Troughs	X			X	X	X	X	X		X	X	X	X	X	X				X
Litter Leachate	Lysimeters	X			X	X	X	X	X		X	X	X	X	X	X				
Soil Leachate	Lysimeters	X			X	X	X	X	X		X	X	X	X	X	X				X
Stream, proportional	Fredriksen Sampler	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X
Stream, grab	Polypropylene Bottles	X					X	X	X	X	X	X	X	X	X	X	X	X		X
Road Drainage	Coshocton Whl.	X		X	X	X	X	X	X	X	X	X	X	X	X	X		X		
Sediment	Coschockton & Fredriksen				X					X	X	X	X	X						

Table 7. General methodologies for each parameter measured at Coweeta

PARAMETER	PRETREATMENT AND PREPARATION	METHOD OF ANALYSIS
Turbidity	Filtration through Whatman GF/C filters	Weight by analytical balance
Total Kjeldahl nitrogen	Digestion with H_2SO_4, K_2SO_4, and Se	Colormetric: cyanurate-salicylate method
Total phosphorus	Digestion with perchloric acid	Technicon Method #93-70W
Total sulfur	Digestion with HNO_3, $HClO_4$, HCl	McSwain
Sulfate	None	McSwain
Chloride	None	Technicon Method #99-70W*
Silicate	None	Technicon Method #7-68W
Ammonia-N	None	Technicon Method #108-71W
Nitrate-N	None	Technicon Method #100-70W
Bicarbonate	Titration to pH 4.5 with 0.2 N H_2SO_4	Standard Methods
Cations	None	Atomic absorption Perkin Elmer
Dissolved fraction	None, except dryfall is distilled-water leached	N/A
Solid fraction	Separation by filtration or centrifugation	Weight determined on analytical balance

*Modified appreciably

Table 8. Coweeta Quality Control Check

9/25/79

(mg/l)

	NO_3-N		NH_3-N		O-PO_4		SO_4^{-2}		Cl-		Na+		K+		Ca++		Mg++	
Sample	EPA	COW	EPA	COW	EPA	COW	EPA	COW	EPA	COW	EPA	COW	EPA	COW	EPA	COW	EPA	COW
1A	.110	.107	.230	.224	.051	.049	.936	.920	.880	.840	.466	.462	.098	.106	.406	.413	.084	.088
1B	.011	.010	.023	.022	.005	.006	1.404	1.395	1.320	1.300	.699	.680	.147	.152	.609	.614	.126	.130
1C	.005	.005	.012	.012	.003	.004	--	--	--	--	--	--	--	--	--	--	--	--
2A	.380	.360	1.59	1.52	.190	.188	.720	.715	1.84	1.74	.820	.805	.210	.197	.530	.532	.180	.184
2B	.038	.035	.160	.155	.019	.019	.072	.076	.185	.185	.082	.089	.021	.019	.053	.055	.018	.020
2C	.019	.018	.080	.075	.009	.009	--	--	--	--	--	--	--	--	--	--	--	--
2/3/79																		
1A	.105	.107	.227	.236	.019	.021	1.20	1.18	2.81	2.83	.518	.510	.257	.270	1.49	1.46	.297	.300
1B	.037	.038	.148	.149	.052	.049	.600	.589	.840	.855	.261	.250	.128	.135	.773	.730	.154	.150
2A	.010	.011	.015	.017	.005	.005	3.07	3.09	1.40	1.44	1.18	1.19	2.42	2.42	1.37	1.35	.430	.432
2B	--	--	--	--	--	--	1.02	1.01	.864	.850	.408	.397	.085	.084	.466	.460	.144	.147

output budgets have been constructed for catchments (Swank and Douglass 1977). Input-output information has formed the basis for developing and testing numerous hypotheses related to ecosystem processes (Swank and Waide in press, Johnson and Swank 1973, Todd et al. 1975, Johnson et al. in press, Henderson et al. 1978). The maintenance of precipitation and streamflow chemistry records is essential to the objectives of our research and therefore we propose to continue current levels of measurements. This involves routine sample collection and analysis at 12 precipitation sites and at 7 stream gaging sites (WS 2, 6, 7, 8, 17, 18, and 27). During the second year of research we plan to reexamine stream chemistry for 17 drainages previously studied and thereby ascertain if changes in levels or patterns of nutrient discharge have occurred. Such information could provide a basis for new hypotheses on processes.

Coweeta was an initial participant in the National Atmospheric Deposition Program and sampling began in June, 1978. An EPA wetfall sampler is also installed on site and samples are regularly collected and transmitted to the EPA Research Triangle Laboratory, N.C. for analysis. We will retain both sampling systems at the Laboratory as long as these programs exist.

3. Throughfall and Lysimeter Chemistry

We have also investigated solution chemistry in forests at Coweeta via throughfall and lysimeter collections. In earlier phases of our work, throughfall and lysimeter (zero-tension only) samples were collected on WS 6, 13, 17 and 18 and analyzed for cation concentrations only (Best and Monk 1975). Throughfall and lysimeter collections have also been made on WS 2, 7, and 27 and analyzed as shown in Table 6. On WS 27 we used zero-tension lysimeters only. On WS 2 and 7 we have zero-tension, porous plate, and porous cup lysimeters, to compare different lysimeter types and to provide a complete characterization of litter-soil leachate chemistry. In January, 1980 we went entirely to porous cup lysimeters because of their relative ease of operation, reliability and frequency of collection as compared with other types. Long time periods of cross-comparison among the three types, however, will insure comparability of research results obtained with each collection method.

In this research, we have shown clearly that the three lysimeter types sample soil solution differently, thereby yielding samples which have differing chemical characteristics. This results from the interaction of the occurrence of discrete precipitation events, the processes of ionic solubilization off litter-soil exchange sites, and the design characteristics of the lysimeters themselves (specifically, their tension and hydraulic resistance) (Waide et al. in prep.). We have also shown distinct seasonal patterns in ionic concentration differences among vegetation zones on WS 7 (Haines et al. in prep). Following cutting (WS 7), concentrations of Ca^{+2}, NO_3^- -N, and H^+ increased in zero-tension lysimeters beneath litter layers, whereas concentrations of $N4_4^+$ -N, PO_4^{-3}, and K^+ declined. Similar comparisons of litter tension lysimeters suggest that concentrations of H^+, NO_3^- -N, NH_4^+ -N, PO_4^{-3} , and total N increased following logging, while concentrations of K^+ and Ca^{+2} appeared to decrease. For throughfall samples, post-cutting concentrations of H^+, PO_4^{-3}, K^+, and Ca^{+2} appeared to increase, especially PO_4^{-3} which increased roughly 6-fold over prelogging values.

We plan to continue our emphasis on throughfall and lysimeter chemistry in future long-term work at Coweeta. Such data provide a direct link with measurements of input-output chemistry, indicate nutrient concentrations available for uptake by plants or microbes, and provide direct information on nutrient transport through the forest canopy and soil-litter layers. However, manpower required to collect and analyze such samples dictate that we will conduct the work only on WS 2 and 7. We propose specifically to measure nutrient concentrations in throughfall and lysimeter (porous cup only) samples using existing methods at 5 (1982-83), 7 (1984-85), 10 (1987-88), and 13 (1990-91) years following clearcutting. Only the time period September, 1982 - August 1983 will be covered by the support requested here.

4. Geology and Sediments

A topographic map with 10 and 50 foot contour intervals, based on a third order survey, was completed in 1972 and is available at scales of 1:14,400 (Appendix VI) and 1:7200. A detailed study of bedrock geology (for both Coweeta and Dryman Fork Basins) has been completed by Dr. Robert Hatcher, Florida State University, and a full report is in the final stages of preparation. The Coweeta area is underlain by complexly-folded, thrust-faulted, and metamorphosed sediments of the Coweeta Group and Tallulah Falls formation. The affinities of these rocks are of late Precambrian to early Paleozoic age. Stratigraphy of the area is described in Table 9 and the distribution of formations is illustrated in Figure 3.

A preliminary geochemical study was conducted on the Basin in 1976 to examine the contributions of chemical weathering to dissolved

Table 9. Stratigraphy of the Coweeta Hydrologic Laboratory

Formation		Description
	Trondhjemite	
	Carrol Knob Formation	Fine-grained Mafic and Ultra-Mafic Complex, Undivided
COWEETA GROUP	Ridgepole Mountain Formation	Clean Quartzite, Muscovite-Chlorite Quartzite, Coarse Biotite Garnet Schist, and Pelitic Schist
	Coleman River Formation	Medium-grained Metasandstone and Quartz-Feldspar Gneiss Interlayered with Aluminous Schist
	Persimmon Creek Gneiss	Massive Oligoclase - Quartz - Biotite Gneiss
	Tallulah Falls Formation	Predominantly Interlayered Metagraywacke, Amphibolite and Muscovite-Biotite Schist with Variable Amounts of Aluminous Schist, Quartzite, and Hornblende Gneiss. At the top of the unit is a Metaquartzite consisting of Quartz-Muscovite-Biotite-Microcline-Plagioclase-Carbonate-Quartzite Interlayered with Muscovite-Biotite Schist.

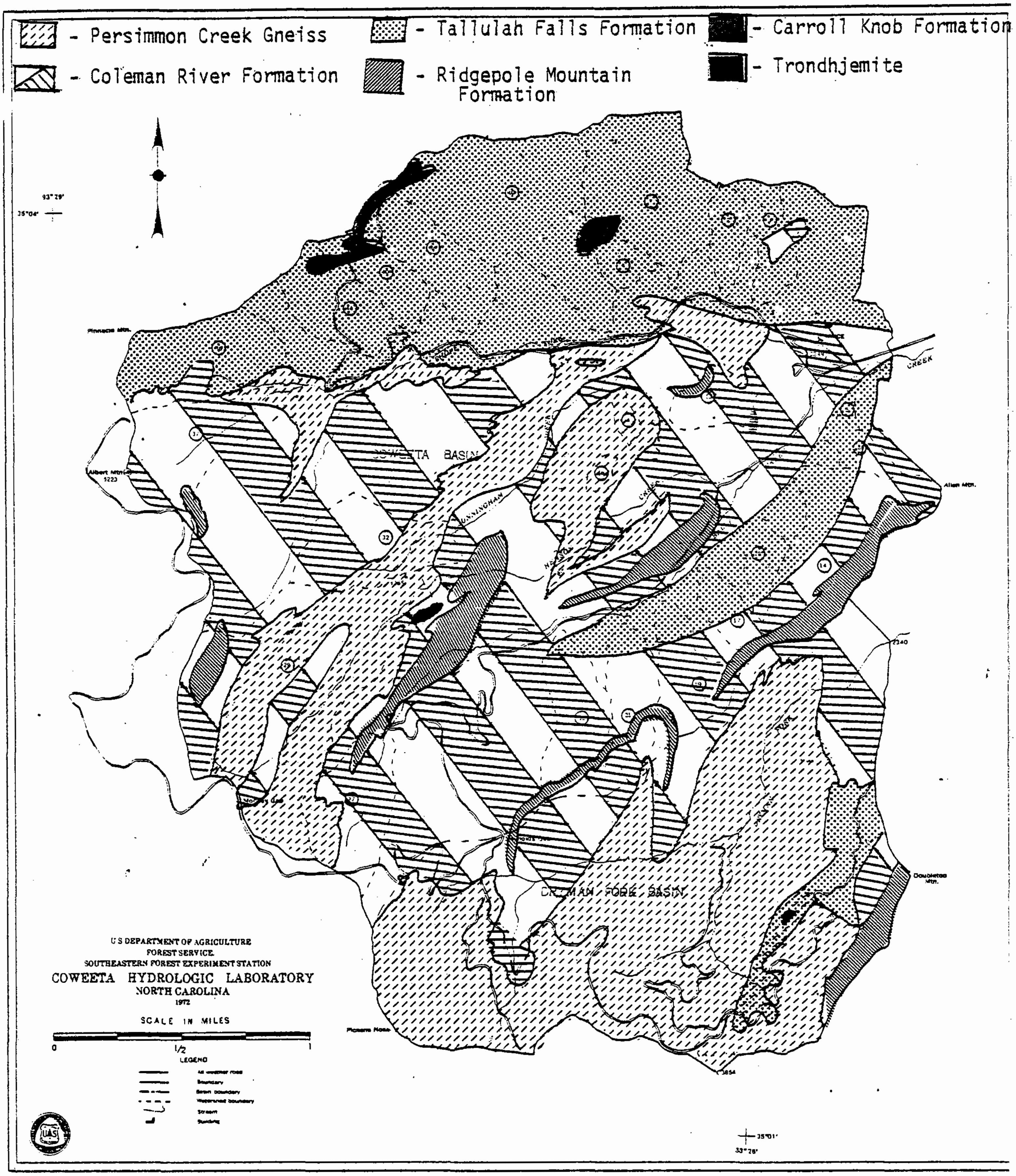


Figure 3. Distribution of Coweeta bedrock formations.

nutrient loads of streams (Berry 1976). Five boreholes were drilled through the regolith of residual soils and extended into bedrock. Mineralogic alterations were determined from samples collected throughout the profile and used to calculate weathering rates. Although cation losses calculated from these data for two watersheds compared favorably with nutrient budget data, critical limitations were inherent in the weathering rate data. It is important to all phases of nutrient cycling research that the mineralogical data base be strengthened and this proposal contains new research which will more firmly establish weathering rates.

Methods

Local geologic maps will be utilized or developed as needed for selected compositionally uniform subunits crossing all varieties of topography. Each selected subunit will be sampled by coring from the surface down to bed rock. Sample sites will be located in undisturbed hardwood forests along a catena ranging from flat ridge tops to the edges of alluvium at the base. Such a series will require taking several sets of 5 to 10 borings at each sample location. Microclimatic considerations require sampling on both north and south facing slopes. These samples will be analyzed for mineralogical variation over both soil depth and slope. Figure 4 shows a block diagram with possible geologic and pedologic relations with sample sites. The soil and saprolite samples will be subjected to quantitative analysis for clay minerals, hydrated oxides, weatherable minerals and residual minerals.

Weathering rates will be estimated by measuring the 001/002 x-ray

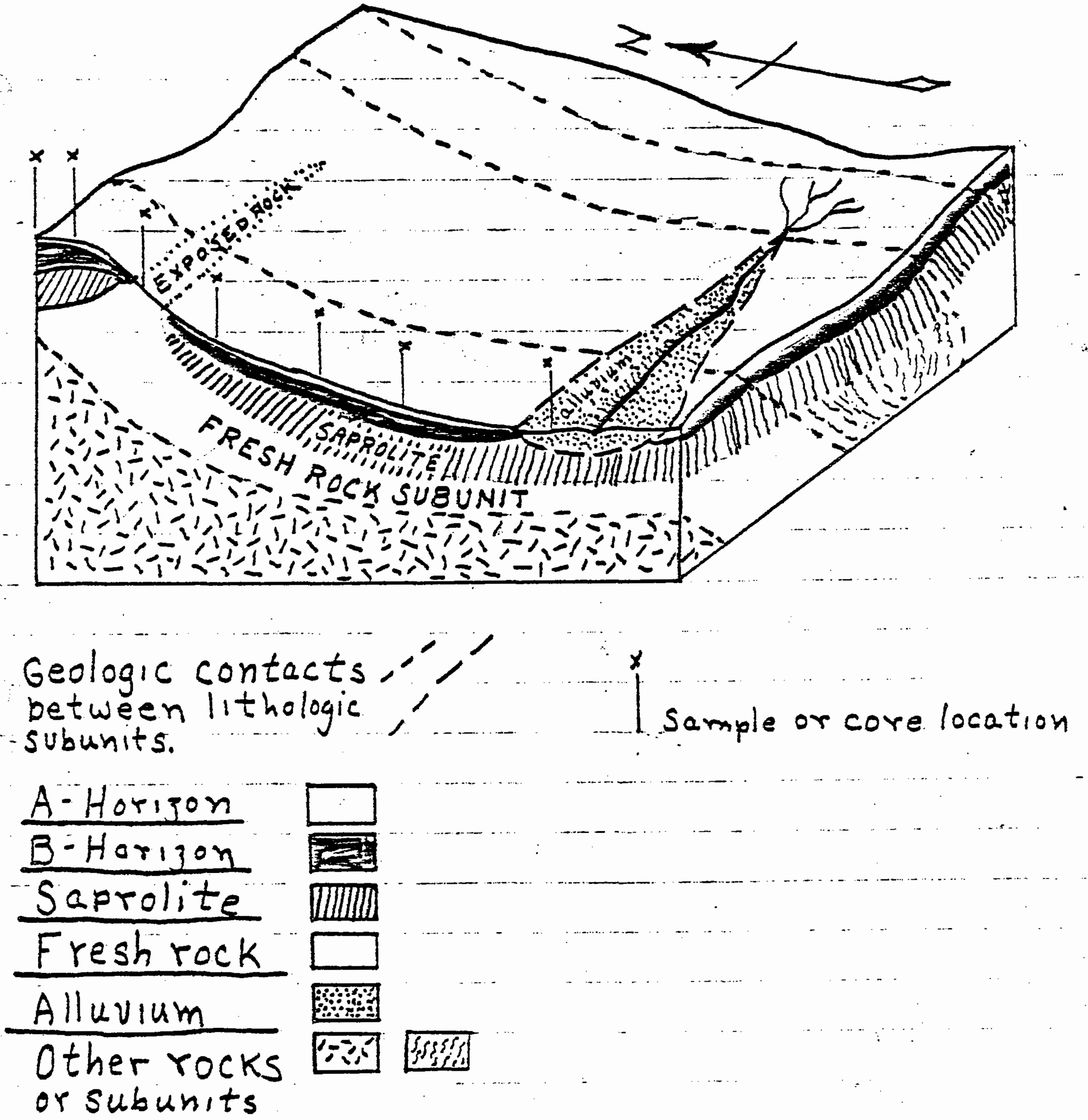


Figure 4. Possible geologic and pedologic relations within a sample site.

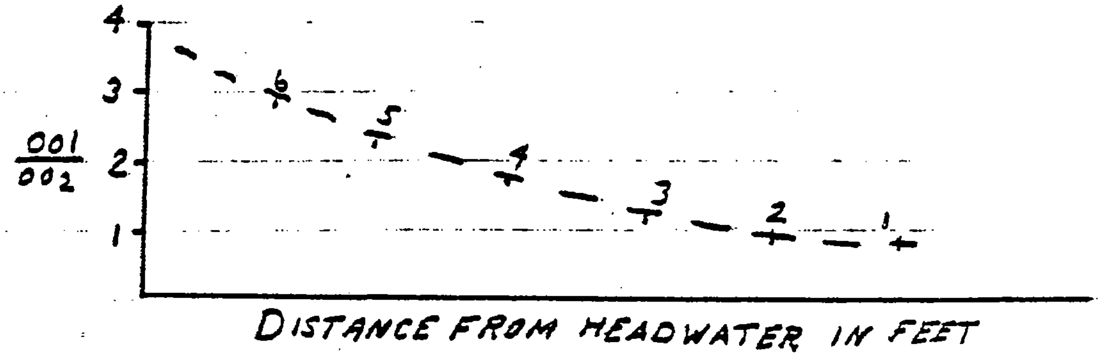


FIGURE 5. Expected results from sampling successive head water areas.

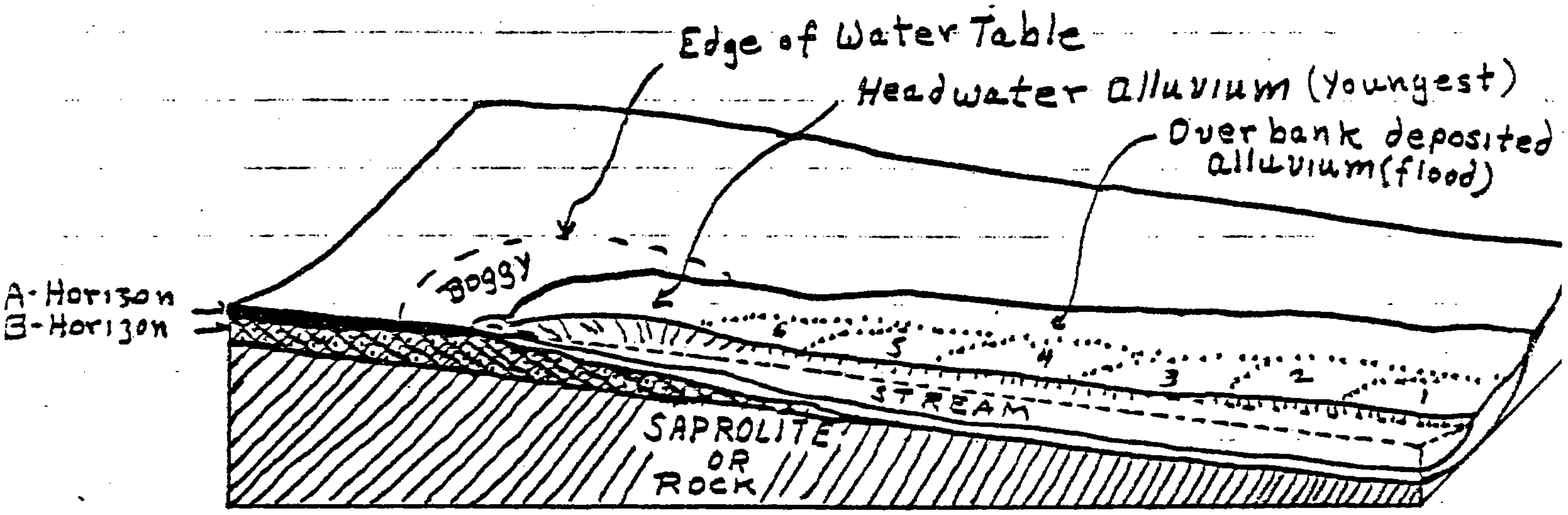


Figure 6. Successively younger, (1,2,3, etc.) alluvial deposits of the headwater type all buried under overbank deposits except the youngest.

diffraction peak ratios of weathering muscovite since it has been determined that the 001/002 ratios of weathering muscovite are related to time in a uniform way. The sampling scheme is based on collection of muscovite from alluvium. Stream headwaters migrate slowly upslope at rates of about a few feet per hundred years. As this headwater erosion proceeds, a layer of largely gray clay (headwater alluvium) is deposited. As headwater erosion continues, the central apart of this alluvium is removed by bed and bank erosion while the outer edges remain. Thus, the edges of the alluvium are exposed to mineral weathering, including the muscovite, which records the weathering process by changing its 001/002 ratio (Fig. 5). The sampling system and a longitudinal section of a hypothetical stream showing the mechanism involved is shown in Figure 6. It is entirely possible that during the sampling for micas that buried wood and other carbonaceous matter may be found. If so, the carbonaceous matter may be used for radiocarbon dates which would make it possible to express 001/002 ratios in years rather than relative time.

A second possible benefit of 001/002 ratios would be an application to the soil saprolite profiles. This could possibly give ages to the soils and saprolites along the catenas. It is expected that the oldest soil profiles are on the ridge tops and at the base where slopes are minimal. Steeper slopes are expected to show younger weathering profiles.

Alluvium will be subjected to a quantitative determination of weatherable minerals, clay minerals, and hydrated oxides. This will provide data on the completeness of weathering prior to erosion. Large proportions of weatherable minerals will indicate rapid erosion.

A study of cation exchange capacity will be conducted using saprolite and soil samples collected from the fresh rock to the surface as explained in the weathering study. Particle sizes smaller than 63 um will be fractionated and analyzed for cation exchange capacity to determine the relationship between change in cation exchange capacity as a function of weathering. It seems likely that the early formed clay minerals will show higher cation exchange capacity. As weathering continues and clay mineral growth occurs, the particle size of the clay minerals should increase along with a decreasing surface area, hence the cation exchange capacity will decline. It is also expected that there is some dissolution of clay minerals in the A-horizon. This should result in an increase in C.E.C. in this layer.

Soils were mapped in 1973 over the experimental area using 7th Approximation criteria and ten soil types were delineated (Table 10). A map showing soil boundaries and standard descriptions established by the National Cooperative Soil Survey for each soil series are available in Coweeta files.

Sediment yield has been examined for a variety of manipulated ecosystems and control areas (Monk, 1975). The longest continuous length of record for total erosional loss (suspended plus bedload) is available for a control (WS2) and adjacent clearcut (WS7) watershed with the initiation of measurements in June, 1974. The Fredrikson proportional samplers currently in use have been operating for 6 years and are experiencing frequent maintainence problems. There is a critical need to update the suspended sediment sampling technology. To meet this need, two Manning S-4050 portable, discrete, suspended solids samplers will be

Table 10. Soil types and family classifications of the Coweeta Hydrologic Laboratory.

Soil Type	Classification
Chandler loam 30 to 60% slopes	Typic Dystrochrept, coarse-loamy, micaceous mesic
Codorus fine sandy loam 0 to 3% slopes	Fluvaquentic Dystrochrept, fine-loamy mixed, mesic family
Edneyville fine sandy loam 30 to 60% slopes	Typic Hapludult, fine-loamy, mixed, mesic family
Jeffrey stony loam and rock outcrop, 40 to 80% slopes	Umbric Dystrochrept, coarse-loamy mixed, mesic family
Porters stony loam 30 to 60% slopes	Humic Hapludult, fine-loamy, mixed, mesic family
Tate loam 8 to 15% slopes	Typic Hapludult, fine-loamy, mixed, mesic family
Tusquitee stony loam 15 to 40% slopes	Humic Hapludult, fine-loamy, mixed, mesic family
Saluda stony loam 30 to 60% slopes	Typic Hapludult, loamy, mixed, mesic, shallow family
Watauga loam 15 to 50% slopes	Typic Hapludult, fine-loamy, micaceous, mesic family
Watauga loam 30 to 50% slopes	Typic Hapludult, fine-loamy, micaceous, mesic family

purchased. These automatic samplers incorporate several unique features such as an adjustable velocity pressure-vacuum intake system, vortex induction sample handling system, and an intake line purge/rinsing mode. These features have resulted in the Environmental Protection Agency rating the S-4050 as producing the most reliable suspended solids data. Suspended sediment is sampled with a proportional sampler and ponding basin collections are measured at four-to-six month intervals. We propose to continue these measurements in WS2 and 7 during the three year study period to define more clearly baseline sediment losses for hardwood forests and also to document the trends of sediment discharge which accompany ecosystem recovery. During the past five years, erosional losses from the undisturbed catchment have ranged from 65 to 410 kg/ha/yr and the variability is partially attributable to unusual hydrologic events. Moreover, although three years have elapsed since disturbance, sediment yield is still quite high from WS7 and it may be necessary to continue these studies in subsequent years. Current Forest Service studies on the amount and sources of sediment within WS7 will also be continued. Further, during the second year of the study, we propose to remeasure sediment yields from four ecosystems with contrasting vegetation (WS 6, 13, 17, 18). Erosional losses were first documented from September, 1969 to September, 1971 for catchments in grass-to-forest succession (WS 6), white pine (WS 17), coppice (WS 13), and mature hardwoods (WS 18). Sediment remeasurements will provide valuable temporal data on erosion processes and interpretive data for proposed aquatic studies.

IV. Plan of research

B. Vegetation studies

Overview

This long-term research is directed toward establishment of a baseline for future long-term studies and the development or continuation of existing long-term ecological experiments at the Coweeta site. Baseline studies are proposed to develop a flora and knowledge of the habitats, plant associations, and metallic element distribution in tree rings and soils. Long-term experiments focused on species dynamics are planned. White pine migration from planted monocultures into the southern hardwood forest will be evaluated in both disturbed and control areas and on north and south facing slopes. The establishment of permanent plots will allow determination of long-term trends of white pine invasion and subsequent success in the southern hardwood forest. Species-level studies with hypovirulent strains of the chestnut blight fungus will be conducted to determine the effects, long-term growth, and interaction of hypovirulent strains with virulent strains of the chestnut blight fungus. Plant community dynamics will be examined through continuation of existing analysis of the recovery of a clearcut watershed, the analysis of white pine stand dynamics as it relates to evapotranspiration and stream flow, and analysis of 400 permanent plots assayed in 1934 and in 1970 to evaluate long-term succession following the loss of American chestnut from the hardwood forest. Ecosystem processes to be studied include analyses of tree ring growth and nutrient concentration before, during, and after tree defoliation by the fall cankerworm. Above-ground vegetation processes, including net primary productivity, leaf area index, and elemental concentrations, will be evaluated for a 13-year period following clearcutting. Below-ground, root biomass will be determined for correlation to above-ground studies.

1. Reference vascular plant collection

In dealing with ecosystem dynamics, quantification of energy and mineral pathways must eventually be related to specific structural components of the system. It is thus appropriate to have a reference set of plant samples available for study by the investigators at an experimental site such as Coweeta.

The reference collection of vascular plants should consist of tree, shrub, herb (including grass, sedge, fern, and fern ally) samples. Specific and descriptive habitat information as well as locations of the collections in the basin should also be described on the reference collection labels. For ecological studies, any of the life forms from seedlings to mature plants as well as plants of the flowering or fruiting stages, must be known. Thus this form of reference collection differs somewhat from the usual herbarium material consisting of flowering or fruiting specimens needed for taxonomic identification.

Both the indigeneous and introduced flora of the entire Coweeta Basin will be sampled. All tree, shrub, and herb species will be sampled in several growth forms, including seedlings, shade leaves, dormant twigs, and stump sprouts, as will available flowering and fruiting species. After consultation with Coweeta staff and interested researchers, a general reconaissance will be made of the entire basin, noticing locations. of major habitat types with associated plant communities.

A transect or transect series will be determined for systematic sampling throughout the growing season. This technique should assure at least a 95% representative collection of the vascular plants present in the Coweeta Basin.

Collections of the plant material will be processed at Western Carolina University. Collections will be journalled, pressed, labelled, mounted on herbarium cards, and organized by genera and families in alphabetical order. Common name and scientific name indexes will be prepared to assist researchers in locating voucher materials. Western Carolina University's herbarium now contains 18,000 specimens of vascular plants, perhaps 80% of which have been collected form the southern Appalachian Highlands region. This, plus the close proximity (33 miles) to Coweeta, makes the University well suited for this project. Duplicate collections will be deposited at Western Carolina University herbarium (WCUH).

The project will begin in March, 1981. Collections will be taken biweekly starting in early March, 1981. Emphasis during the first year will be on the native species, with most field effort directed toward sampling the undisturbed control watersheds along established transects. Some effort will be expended in sampling special habitats (rock outcrops, seepage areas, diverse cove hardwoods, etc.) and general sampling of disturbed areas. Cataloging and preparation of most of this material will be carried out in the winter of 1981-82. In the following growing seasons, emphasis will be placed upon collection of disturbed sites where weedy species are being established. Areas that were clearcut in recent years will be systematically sampled. Sampling of the indigeneous species which may have been overlooked during the previous year, not in reproduction or not collected in a particular life stage, will be completed. As specimens are processed, they can be replaced in the reference collection at Coweeta and all material, including a final report, indexes, and specimens will be completed by April of 1983.

2. Habitats and plant associations

In order to carry on a wide range of long-term ecological research at a site such as Coweeta it is essential that an inventory be made of available habitats and an analysis conducted to determine major and minor plant associations. Before critical assessments can be made of natural or man-made changes to forest communities at the site and elsewhere, it is necessary to have comprehensive data on what the communities are like today and (where possible) what they were like in the recent past. Moreover it is important that habitat and plant association designations be supported by quantitative data obtained from carefully designed field sampling, which can be repeated at future times.

The work will be coordinated with both the floristic survey and the geological research on weathering and will draw upon the findings of others who have conducted research on forests of the southern Appalachians (Cooper and Hardin, 1970; Whittaker, 1956). Cooper and Hardin (1970) summarized the results of research on vegetation patterns in the nearby gorges of the Blue Ridge Escarpment. They described a number of major and minor vegetation types, which they associated with different habitats and elevation.

Based upon site proximity, the plant associations or community-types that might be anticipated on the Coweeta site should closely parallel those described by Shanks (1954) and Whittaker (1956) for the nearby Great Smoky Mountains (Figure 7). These should include Cove Hardwood Forests in the lower mesic coves, Hemlock Forests along the stream-courses at the lower and middle elevations (up to approximately 4000 ft.), Closed Oak Forests on intermediate to dry slopes at low and middle altitudes, Open Oak and Pine Forests on dry rocky exposed slopes and ridges of the low and middle altitudes, and possibly, Northern Hardwood Forests at the higher elevations. Species components of arborescent, shrub, and herbaceous strata, relative topographic position and probable altitudes of occurrence are attached (Table 11).

These forest types with their diverse plant assemblages coupled with the varieties of slope, exposure, and altitude present on the Coweeta site offer an outstanding opportunity both to describe the extant plant associations and to define the habitat-types and micro-climatic regimes which they occupy. The proposed research will couple floristic surveys, detailed habitat analyses, underlying geology and surface soils, and dynamic community analyses in an integrated fashion.

Analysis of the data on habitats and plant association should reveal several other valuable insights, including relationships between species richness and habitat, age class distributions, which reflect the state of change of a community, and the effects of a variety of past forest management practices on the present structure of plant communities.

The proposed studies will provide a data base which will enable investigators to: 1) assess future perturbations within the Coweeta

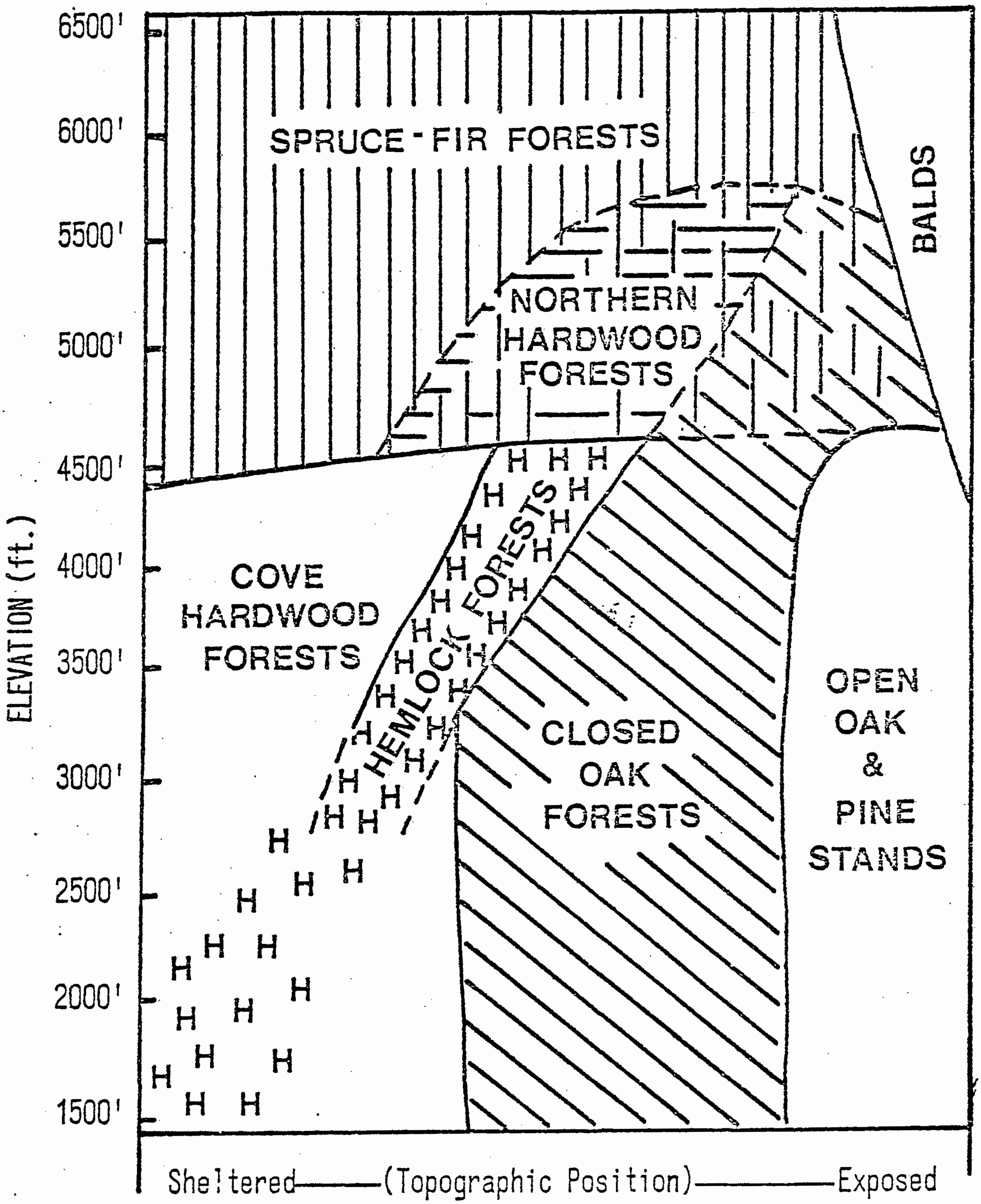


Figure 7. Vegetation pattern of the Great Smoky Mountains based on pattern diagrams by Shanks (1954) and Whittaker (1956).

Table 11. Important Plants of Different Eastern Forest Types (with emphasis on the southeastern mountains)

COVE HARDWOOD FOREST
elevational limits: generally below 4500'
dominant trees: no clear dominant species, truly a mixed forest with 25-40 important species; indicator species are yellow buckeye and basswood
other important tree species: yellow (tulip) poplar, mountain silverbell, eastern hemlock, white ash, sugar maple, yellow birch, American beech, black cherry, northern red oak, cucumber magnolia, mountain (Fraser's) magnolia
important shrub species: sweetshrub, spicebush, strawberry bush, rosebay rhododendron
important herbaceous plants: a veritable spring wildflower garden with 25-60 extremely showy species

HEMLOCK FOREST
elevational limits: along streams to 3500-4000'; occasionally along exposed ridges to around 5000'
dominant tree: eastern hemlock
associated tree species: red maple, sugar maple, American beech, yellow birch, sweet birch, black cherry, pin cherry, American holly, yellow poplar, mountain silverbell
important shrub species: rosebay rhododendron, catawba rhododendron, smooth hydrangea, thornless blackberry, mountain laurel, dog-hobble
important herbaceous plants: far less variety and diversity than in the cove hardwood forests

NORTHERN HARDWOOD FOREST
elevational limits: above 4500', below 6000'
dominant trees: yellow birch, American beech; spruce-fir forests are generally found nearly surrounding or at least at the upper limits of the northern hardwoods type
associated tree species: up to 5000'--sugar maple, black cherry, eastern hemlock; up to 6000'--red maple, striped maple, yellow buckeye, Allegheny serviceberry
important herbaceous plants: less variety than in the hemlock forests

SPRUCE-FIR FOREST
elevational limits: above 4500-6000'
dominant trees: red spruce, Fraser fir
associated tree species: yellow birch, pin cherry, American mountain-ash, mountain maple
important shrub species: catawba rhododendron, Carolina rhododendron, scarlet elder, thornless blackberry, roundleaf gooseberry, dog-hobble
important herbaceous plants: toothed woodfern, common polypody fern, hayscented fern; creeping bluet, Virginia springbeauty, American wood-sorrel, painted trillium, erect trillium--all spring bloomers; pink turtlehead, Indian pipe--summer/early fall bloomers

CLOSED OAK FOREST

elevational limit: intermediate to dry slopes at low and middle altitudes

dominant trees: white oak, chestnut oak, northern red oak, black oak, pignut hickory, red hickory, mockernut hickory

associated trees: red maple, sweet birch, sourwood, yellow poplar, blackgum, black locust, mountain silverbell

understory trees and shrubs: flowering dogwood, witch-hazel, mountain laurel, rosebay rhododendron, flame azalea, smooth hydrangea

herbaceous plants: trailing arbutus, galax, lousewort

OPEN OAK AND PINE FOREST

elevational limit: dry, rocky exposed slopes and ridges, low and middle altitudes

dominant trees: scarlet oak, white oak, chestnut oak, black oak table-mountain pine, pitch pine, Virginia pine

associated trees: white pine, shortleaf pine, red maple, sourwood, blackgum, sassafras, Allegheny serviceberry, black locust, American chestnut (basal sprouts)

shrubs: similar to those found in the closed oak forests with the addition of blueberries and huckleberries

herbaceous plants: generally similar to the closed oak forests

'BALDS'

Heath Balds

important plants: catawba rhododendron, mountain laurel, sand myrtle, blueberry (possibly also rosebay and Carolina rhododendron)

Grassy Balds

important plants: various grasses and sedges, flame azalea

Basin; 2) assess the impact of anthropogenic stresses on similar systems elsewhere; and 3) initiate studies to determine how species and plant association distributions are related to physical and/or biotic features of the environment.

Habitats will be designated by consulting available data on watersheds and their past treatment and topographic, soil and geologic maps. A preliminary classification will be made based on physical factors such as moisture, slope, aspect, soil, drainage and elevation. This work will be accompanied by on-site reconnaissance in a feed-back relationship between what can be inferred from available data and what is actually there.

Habitat and plant association relationships will be determined. Habitats will be characterized critically by obtaining additional data on soils, moisture, etc. which are not now available. Plant communities will be sampled and analyzed in order to develop the data base for correlation to habitat. Plant communities or vegetational associations have been analyzed and evaluated by a variety of means over the past fifty years. No single means of analysis or evaluation has proved entirely adequate or satisfactory for diverse community-types with numerous species distributed over great areal or vertical units of space. Among the methods of analysis that have often been employed are association designations based on life forms, spatial or areal species mapping, subjective evaluations of abundance such as frequency and cover, and quantitative measures of abundance such as density, measured cover, yield, or 'performance' parameters such as size, leaf area index, etc. (Kershaw 1973). Other systems of analysis have been based upon physiognomic designations, floristic surveys, studies of community dynamics (e.g., studies of succession in place from a variety of different-aged sites over a region or studies of succession over time from periodic re-surveys from permanently-established plots) and detailed community analyses. Such analyses include designation of associations based on 'dominants' defined in some fashion (e.g., density, yield, size, etc.) or perhaps on presence/absence data. Associated means of analysis include employing coefficients of species association or 'togetherness', community designations based upon relative importance values, or evaluation of continuua (Phillips 1959). Still other means of community analysis have been based on environmental units (e.g., Koppen climatic classifications, Great Soil Groups, Holderidge's altitudinal/latitudinal 'life zones'), vegetation dynamics or pattern change over time, and, more recently, numerical analysis (Whittaker 1978).

A multiplicity of approaches will be employed in analyzing the vegetation of the Coweeta site and the associated habitat-types. For example, community analysis will derive from a combination of floristic surveys, geological and soils analyses, and studies of community dynamics. The existence of permanent plot data from 400 plots over the Coweeta Basin originally surveyed in 1934 and re-inventoried in the 1970's offers a baseline seldom encountered for evaluating changes over time. The development over the past few years of new techniques of numerical analysis applicable to vegetational systems as well as improved techniques of ordination coupled with large-capacity, high-speed computers makes possible the handling of large amounts of data and the consequent analysis and evaluation of complex communities and vegetational units which would have been impossible only a few years ago.

3. Metallic element distribution in tree rings and soils

The analysis of aged tree rings for metallic elemental concentrations is a method used to develop historical patterns of long-term changes in elemental concentrations for a forested ecosystem. However, investigation using this approach to study both short-term (episodic) and long-term changes in metallic element burdens have met with both positive (Rolf 1974, Ward et al. 1974, Sheppard and Funk 1975) and negative (Szopa et al. 1973) results. In a recent study (Baes and Ragsdale 1980) it was shown that historical patterns of lead concentration were both species and site specific. Utilizing forest sites with elevated and background lead soil concentrations, it was found that some genera (*Pinus* and *Liriodendron*) did not show a pattern of lead accumulation while other genera (*Carya* and *Quercus*) had patterns of lead concentration reflecting long-term (100 year) increases of lead in the environment. However, *Carya* was the only species which showed an historical pattern of lead concentration increase at sites having low to background lead soil concentrations.

Lead and other metallic elements associated with the standing wood biomass of forests represent a reservoir of elements which are accumulated at low concentration in the wood and subject to long-term release to decomposer food chains with potential bioaccumulation of these elements through the fungi. Metallic elements, unlike some other arthropogenic pollutants, are not subject to decomposition and can remain in an ecosystem for long time periods subject to removal only by erosion or harvesting. The widespread toxicity of metallic elements among biota provides the potential for directed change in ecosystem function. Hence, there is a need for knowledge of the historical change in metallic element concentration, the present distribution and concentration of metallic elements, and the potential for release to food chains.

Historical patterns of metallic element concentration in tree rings will be determined using aged tree cores taken from 100-year-old Carya trees selected from undisturbed control watersheds of the Coweeta site. Standard techniques for sample collection, handling and analysis have been developed (Baes and Ragsdale 1980), to minimize contamination and provide reproducibility. In addition to analyses of hickory wood rings, other species will be sampled on a limited basis to determine if historical patterns can be observed in species other than hickory. Metallic elements to be measured will be determined by reviewing the historical data on metallic element concentration in dry fall and rainfall collection at Coweeta. Presently, lead, copper, and zinc will be included in the analyses since these are known to be metallic element inputs to the Coweeta site.

Patterns of metallic element distribution in the soil column will be determined for replicate soil cores collected in association with each tree sampled. Preliminary studies will be performed to determine appropriate soil sampling depths and core sectioning. Generally, 30 cm cores have been sufficient to reach constant soil lead concentration and core sections of 1 to 5 cm have been used to develop the patterns of metallic element distribution with increasing soil depth.

Metallic element concentrations will also be determined for soil samples collected in the proposed mineralogical weathering study.

These samples will reveal concentration changes associated with elevational gradients and weathering.

Tree cores will be obtained within one undisturbed watershed and analyzed for metallic element content in order to calculate the burden of metallic elements in the standing woody biomass pool and to determine the variability in elements and concentrations among species. This study will be coordinated with other proposed research on metallic element concentration and elemental transfer in the Coweeta hardwood forests. The standard sampling methods will be used. The tree rings will be analyzed in larger blocks of years (10-15 year periods) which will allow for more accurate calculation of whole tree burden if there are concentration differences among tree rings.

Atomic absorption spectroscopy (AAS) and energy dispersive x-ray (EDX) analysis will be used to determine metallic element concentrations in wood and soil samples. Both techniques are employed with locally standardized methods. The AAS analyser will be conducted using an automated graphite furnace and relating recorder peak heights to concentration. Graphite furnace parameters have been standardized for a variety of elements through experimentation in order to provide both replicability and accuracy in the determinations. The energy dispersive x-ray analysis is conducted using standard radiometric counting statistics and relating counts to concentration through standards with known concentrations.

4. White pine migration within the Coweeta site

Coweeta has a long history emphasizing watershed hydrology, water balance effects of stand conversion to native softwoods (principally white pine) and forage grasses, and associated watershed influences.

One of the chief unanswered long-term questions being currently posed for the forests of the southern mountains is the overall ecological effect resulting from the management practice of large-scale conversions from naturally-regenerating low-grade hardwoods to intensively-managed stands of softwoods. The specific research proposed here addresses the question of white pine invasion of the southern hardwood forest. Although little is known regarding the potential for sexually reproducing white pine monocultures to migrate in to surrounding hardwood forest, existing field analyses at the Coweeta Site suggest that white pine has migrated from established monocultures into surrounding habitats.

Coweeta represents an outstanding long-term experimental site at which to study white pine migration from monocultures into adjacent hardwood forests. Three sets of paired watersheds, each having an undisturbed hardwood watershed control adjacent to a watershed planted in white pine, are available for study. These watersheds are located on north, south, and southeast facing slopes and have elevational gradients of about 1000 feet. The white pine stands range from 20 to 33 years old. Additionally, a 33-year-old white pine stand is located in the low elevation valley (2300 ft) of the Coweeta Site. Thus, the opportunity exists to compare white pine migration between the valley and north and south facing slopes, and along elevational gradients within slopes.

Field reconnaissance coupled with analysis of aerial photography will be used to determine both the habitats and extent of white pine migration from existing white pine monocultures. The low elevation valley has been disturbed with road and building construction and a pine bark beetle invasion resulted in complete harvest of a loblolly stand adjacent to a white pine planting. Additionally, a variety of ecotones such as field-forested edges and habitats such as stream margins exist in the valley. On the slopes, the margins between the white pine monocultures and adjacent hardwood control watersheds, naturally occurring gaps in control watersheds, and the watershed streams' banks represent habitats which could be invaded by white pine.

The rate of white pine migration from existing monocultures will be measured for all areas invaded by white pine. Presently, white pine has invaded an adjacent clear-cut loblolly stand in the Coweeta valley. Transects will be extended from the existing white pine stand through the adjacent clear-cut loblolly stand. Uniformly spaced plots will be used to estimate the species present and basal diameters for calculation of patterns (density, relative importance, and species mix) resulting from white pine migration.

In addition to the rate and pattern studies in the Coweeta Valley, the watersheds of the Coweeta slopes will be analyzed for white pine invasion and resulting patterns. Watersheds 1 and 17 are 20-year-old white pine monocultures and WS40 was selectively cut about 25 years ago with white pine planted under the remaining canopy. Downslope transects and permanent plots will be established in the control watersheds (WS 2, 18, and 41) paired with each white pine planted watershed. These permanent plots will be used to estimate white pine's rate of invasion into the southern hardwood forest and the patterns resulting from white pine invasion.

The long-term migration of white pine into the southern hardwood forest and the long-term success of the invading white pine will be evaluated through continued analyses of the permanent plots.

5. The effect of hypovirulent strains of _Endothia parasitica_ on canker development on American Chestnut

The objectives of these studies are to determine: (1) the effects of treatments with hypovirulent isolates of _Endothia parasitica_ on canker development; (2) the capacity for long-term survival, growth, and sporulation of hypovirulent strains in western North Carolina; and, (3) the interaction of different hypovirulent strains with the large number of virulent isolates in local areas of western North Carolina.

Hope for a cure for chestnut blight in eastern North America has created considerable interest. The American chestnut had been a dominant tree in the eastern hardwood forests. After the blight was introduced into this country, this tree has been reduced to a minor, short-lived, understory species.

In Italy hypovirulent strains of _Endothia parasitica_, the fungus causing chestnut blight disease, are reported to have spread naturally and limited killing of European chestnuts by virulent strains (Grente 1965, Grente and Berthelay-Sauret 1979). Although scattered reports of the occurrence of this phenomenon have been made since 1959 from Italy and France, no documented experiments proving this phenomenon is responsible have been published. In 1975 scientists at the Connecticut Agricultural Experiment Station published results that showed the hypovirulent factor was cytoplasmically transmitted between some isolates of the fungus (Van Alfern et al. 1975). Later work from Connecticut suggested canker development was slowed by treatment with hypovirulent isolates in short-term experiments (Elliston and Jaynes 1977, Jaynes and Elliston 1979).

In France, where considerable effort is being made in field control, inoculations of cankers with hypovirulent strains are made successively for four years to wounds in order to establish the hypovirulent form (Grente and Berthelay-Sauret 1979). The hypovirulent strains then spread only at the rate of 1-2 meters per year from the inoculations. In contrast the virulent strains spread at the rate of 10 miles per year following their introduction into the United States in 1904. Thus, the virulent forms spread at a rate over 16,000 times faster than the hypovirulent forms. Even at this fast rate it took the virulent forms nearly 50 years to spread over the range of the American chestnut.

Grente (1965) suggested that sporulation by hypovirulent forms must continue on cankers for 10-20 years to insure success. However, in Italy hypovirulent strains have low pycnidial production that soon stops (Mittempherghber 1979). Long-term survival of the hypovirulent strains is imperative because the virulent forms have already demonstrated this capacity in isolated centers in British Columbia, Oregon, and California.

The factor responsible for hypovirulence is carried in the cytoplasm of affected strains. Transfer of the hypovirulent factor to virulent strains occurs only if cytoplasmic exchange is made. This exchange happens if the hyphae of the two strains are vegetatively compatible. Anagnostakis (1979) found 46 compatibility groups in the Northeastern United States, whereas in France only 30 hypovirulent strains are used in the field control program. Apparently there are fewer virulent strains in France (Anagnostakis 1979). A large variation in compatibility will necessitate maintaining an equally large number of compatible hypovirulent strains in local areas in the United States.

Four aspects of hypovirulence need to be investigated to determine its potential for controlling chestnut blight disease. These are (1) can trees be kept alive by treating cankers with hypovirulent isolates, (2) can hypovirulent isolates survive and spread in western North Carolina, and (3) can a sufficient variety of hypovirulent isolates survive in North Carolina to provide control against the many virulent isolates that are present.

Justification for Funding: Research on this problem was initiated at Coweeta in 1976 with money from the Northeastern Forest Experiment Station. This funding is no longer available because no appropriations were made for this research in the 1980 budget. The Station Director of the Southeastern Forest Experiment Station has indicated research on this disease should be continued because of the importance of this tree to the Southern Appalachians.

Research Proposed for Next Three Years: Objective 1. Control of cankers.--Control of cankers by inoculating with compatible hypovirulent isolates is being compared with check treatments. In one experiment, the hypovirulent isolates are being introduced either to wounds around the canker margin or as a spore suspension to the canker surface. Appropriate check treatments are applied. In a second experiment, cankers are wounded with an axe and the check or hypovirulent treatments painted over the canker surface. These treatments will be applied for several summer seasons to ensure they are similar to European studies and to provide data on survival of the trees for at least four years. Measurements on canker development, sporulation, and callusing will be made.

Objective 2. The capacity for survival, growth, and sporulation by hypovirulent strains.--The apparent lack of virulence demonstrated in the past by hypovirulent isolates of Endothia parasitica in North Carolina is evidenced by a failure to form cankers or produce spores. A comparison of pathogenicity and sporulation by virulent and hypovirulent isolates has been established in studies at Coweeta, N.C., and Natural Bridge, Virginia. In each study, four virulent and four hypovirulent isolates were used to inoculate chestnut sproutes of 1/2-1" diamter at three different times during the summer (June, July, September). Branch segments were also inoculated at the same time and laid on the ground to determine if the saprophytic capacity of these isolates is different from the pathogenic capacity. Canker size and sporulation by the fungus will be recorded for up to three years after inoculation. Retention of the hypovirulence factors will be determined for hypovirulent isolates.

Objective 3. The interaction of virulent and hypovirulent isolates.--An effort will be initiated to reconcile the large number of compatibility groups among virulent isolates in the eastern U.S. forests with the need to maintain hypovirulent groups of the same compatibility types. Laboratory studies will be used to determine the relationships among the 100 virulent and 150 hypovirulent isolates in our collection. The Anagnostakis' technique will be used to determine compatibility groups among the virulent isolates. The hypovirulent strains will be paired with the virulent strain used to produce the hypovirulent strain and with related virulent strains.

The range of effectiveness of the hypovirulent strains in transforming virulent strains will be determined by means of these pairings.

Two studies will provide field data on the interactions of virulent and hypovirulent strains over an extended time period. One study at Coweeta is designed to determine how readily compatible hypovirulent isolates can control virulent cankers. Cankers developing from inoculations with virulent isolates were inoculated with compatible hypovirulent strains. Comparisons of canker development, sporulation and callus formation of hypovirulent treated vs. water-treated cankers will be made yearly. The second study involves 3 virulent and 3 hypovirulent isolates selfed and paired in all virulent plus hypovirulent combinations. Canker development will be measured each year.

6. Long term succession studies

One of the most basic needs for long-term ecological studies is a description of the vegetation. This is true for a number of reasons: plants form the basis for the trophic web of the ecosystem, they may act as indicators of edaphic differences between areas, they have a large effect on the microclimate of an area, to name but a few. Along with the description of vegetation at a single point in time, it is imperative to have an understanding of its dynamics. Changes in size and age structure of populations, species composition changes, and tendencies toward co-occurrence or mutual exclusion of species are all important parameters of vegetation dynamics. Periodic man-made or natural disturbances tend to keep much of the vegetation in a dynamic state of long-term recovery rather than maintaining a static condition.

Permanent vegetation plots established in 1934 at Coweeta are among the few sets of undisturbed plots that span the period when American chestnut was reduced from a major to a minor component of the forest stand following the chestnut blight. A study was initiated in 1969 (Swank, Coweeta Files) to remeasure woody vegetation on plots which remained undisturbed since establishment. In the period of 1970-1973, 400 of the .08 ha plots were inventoried by measuring the dbh of all stems greater than 0.5 inches in diamter (Figure 8). Data were taken by 1-inch classes and recorded by species. Other data recorded for each plot included percent slope, aspect, elevation, and position on slope. Information for 1934 and 1970's have been keypunched and the first data reduction of stocking and basal area by species has been performed. These data will be used to evaluate changes in forest stand structure over the past 40 years and to describe the major replacement species following the death of American chestnut. Analyses will also provide a basis for the selection of plots and time schedules for remeasurement. This data base provides a unique opportunity to document long-term succession for a variety of forest types in the southern Appalachians and the information will be utilized in several new areas of research.

One aspect that is of particular interest is to examine the change in species composition in areas formerly containing American chestnut. In 1904, the chestnut blight fungus Endothia parasitica was introduced into the United States. By 1952, all the large chestnut trees had been killed (Odum 1971). Areas of Coweeta where chestnut was extant in 1934 have presumably gone through some reorganization of community composition

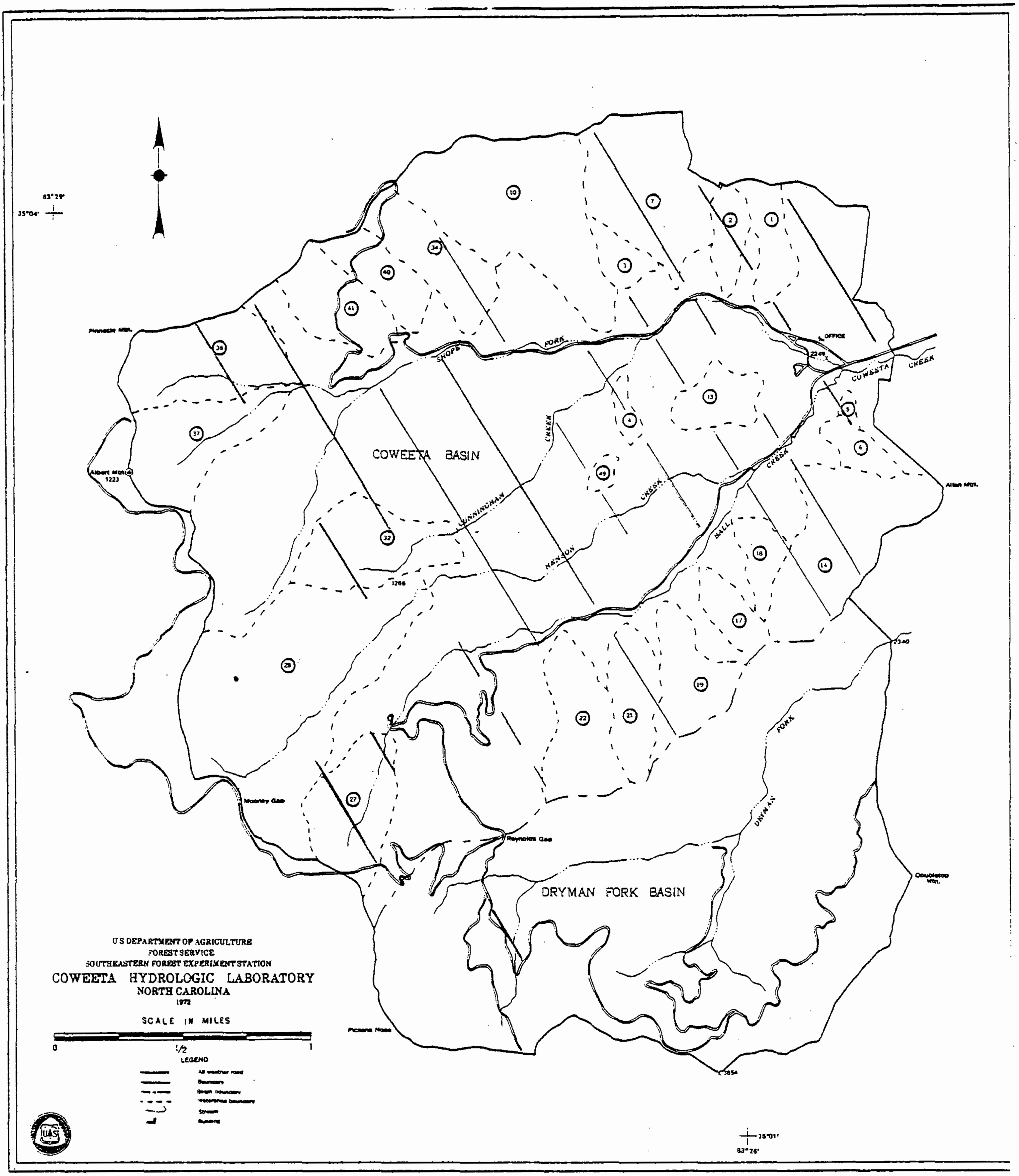


Figure 8. Location of permanent vegetation plots established in 1934.

since that time. The 1934-70 Coweeta plot data will be used to analyse species compositional changes following the demise of American chestnut. Additionally, the plot data will be used to determine the degree of association of species with each other and to determine possible successional relationships among species. To the fullest extent possible, the plot analyses will be integrated with the baseline studies of habitat and plant association.

The question of how the distributions of different species are related to each other can be approached by the use of one of a number of indices of association. Cole's (1949) coefficient of association will be used here. For a pair of species, this method examines the numbers of plots in which they co-occur, mutually exclude each other, or are both absent. The index ranges from 1, indicating maximum co-occurrence, to -1, indicating maximum mutual exclusion. A value of 0 would be expected for species distribution independently of each other. This analysis can be done for each pair of species to determine their distributional similarities.

A number of different methods will be used to determine forest successional trends. The data contain three basic kinds of information on succession. First, there are the temporally separated samples. For each plot, the data from 1934 and the early 1970's can be compared to determine the total amount of species composition change over the 41 year period. Second, both the 1934 samples and the 1975 samples will likely contain temporally separated plots which represent different successional stages of similar series. Third, the size structure of the tree populations within each plot tells something of the history of those populations, and may point out incipient species replacements.

The size or age structure of tree populations are often used to study forest succession (Daubenmire 1968). The relative numbers of individuals in the different size or age classes indicate whether the population is in the process of increasing, maintaining itself, or decreasing within the plot sampled. This type of analysis can suggest successional relationships among the species by showing situations in which one or several species in a stand are being displaced by other invading species. Population size structure will be analyzed for all tree species which are present in sufficient numbers in plots representative of the different vegetation types sampled. Time constraints prevent examining the population structures of all tree species in all 400 plots. Data from both the 1934 and 1970's surveys will be used for the plots chosen in order to examine how the size structures of the populations change over successional time.

Methods of size-association analysis developed by Goff and Zedler (1977) and Zedler and Goff (1973) will also be used to examine successional relationships among the species. This method is used to examine the change in interspecific association with changes in size of the species. One of the two species is divided into size classes, which are then used in the association analysis (described above) as if they were separate species. Coefficients of association are calculated for each size class of one species (i) with the other species taken as a whole. Several patterns might be expected. One such pattern is that as one looks at successively larger size classes of species i, species j becomes associated to a greater degree. This may occur if species j is invading stands in which species i is already present. For example, oaks may tend to invade stands where a pine canopy has previously been established. This relationship might be corroborated by doing the analysis the alternative way, examining the association between size classes of species j with species i as a whole. If successively larger size classes of j become less associated with species i, this might suggest eventual elimination of species i (e.g., pine) once species j (e.g., oak) becomes established. If no consistent differences are found in the degree of association of the different size classes, then no direct successional relationship between the two species is indicated. If both species increase in the degree of association with increasing size, this might indicate the tendency for the two species to establish populations in the same area; beech and sugar maple constitute a possible example. Alternatively, both species might decrease their degree of association with increasing size, which would denote a tendency toward mutual exclusion.

Further, Goff and West (1975) have suggested that the commonly-applied negative exponential function of density-diameter distribution (plotting numbers of stems in equal diameter intervals as a frequency histogram) commonly applied to "all-aged" stands may be deficient if several rather specific conditions are not met (e.g., large tract size containing local even-aged stands of approximately equal area). Rather, for natural medium and old growth stands -- such as might be expected to occur over much of the Coweeta basin -- they suggest that the appropriate function is a "rotated sigmoid" form which more aptly suggests the biological realities of canopy-subcanopy interactions and associated patterns of vigor and relative mortality.

West and Johnson (1976) have subseuqently suggested that relative "tolerance" and hence relative successional or replacement status of individual species is related to the relative convexity/concavity of the resulting density-diameter curves (concave curve = climax spp., convex curve = pioneer spp.). Deviation from a straight-line form of the relationship (log no. of stems vs. log age) has been interpreted (Lead, 1975) as a characteristic of a "declining" (convex) or an "increasing" (concave) species population. Consequently, given information from the 400 permanent plots established on the Coweeta site, the relative roles of species (whether declining or increasing) can be evaluated in a straightforward fashion (controlling, of course, for slope and elevational differences as noted subsequently).

The use of size classes instead of age classes in any kind of population structure analysis has been criticized by some (Harper 1977). The relationship between size (DBH) and age is often not as tight as one would like. Variation in this relationship throws a degree of error into successional analyses based on size. However, when dealing with large numbers of plots, it is not possible to determine ages instead of sizes for each tree. Time constraints and the risk of damage to the tree by increment boring prevent this. One of the main causes of variation in the size-age relationship is the difference in environmental conditions between sites. In the Coweeta Hydrologic Laboratory, the 400 plots occur on different slope-aspects and at different elevations, both of which may significantly affect growth. To control for some of this variability plots will be grouped according to similar elevation and slope-aspect in all analyses.

Examination of compositional changes on the plots between 1934 and the 1970's may also reveal some common successional trends. Of particular interest is the examination of plots which contained chestnut in the earlier survey, in order to determine what species have taken its place. Potentially stable communities may also be recognized by the lack of significant change over this 41-year period.

7. White pine stand dynamics

A study of forest stand dynamics was started in 1967 in young plantations of eastern white pine on WS1 and 17. The original objectives of this research addressed hypotheses concerning the relationships of plant community structure, evapotranspiration, and the amount and timing of streamflow (Swank and Helvey 1971, Swank and Miner 1968, Swank and Douglass 1974). Twenty .08 ha permanent plots were established in each pine plantation on WS 1 and 17 when the stands were 10 years old. Plots were remeasured for stocking and basal area in 1969, 1972, 1975, and 1980. The population was sub-sampled four times during this period to obtain estimates of foliage, branch, and stem surface area and biomass. Samples were also analyzed for 13 elements. A more complete description of the early stages and results of this research appears elsewhere (Swank and Schreuder, 1973, 1974). The stands are not yet of sufficient age to test all of the original hydrologic hypotheses and furthermore, the vegetation data has proved valuable to other ecosystem process research conducted on the watersheds. Thus, we propose to continue the study of stand dynamics and obtain estimates of previously measured parameters in 1983.

8. Temporal change in spatial distribution of tree species in relation to hydrological response following clearcutting of deciduous forest ecosystems

Clearcut harvesting of the eastern deciduous forest began in the 1930's. While there have been several studies of successional change following clearcutting few have been of sufficient duration to determine which species actually dominate at maturity (Oliver 1978). Published research relating spatial shifts in tree species in relation to hydrological response following clearcutting is lacking.

Oliver (1978) found that black birch and red maple dominate old field sites in central New England the first few years after agricultural abandonment. At 25 years northern red oak begins to dominate these sites. He hypothesized this shift may be due to the norther red oaks' deeper root system and larger vessels which would allow more efficient utilization of soil moisture.

The same pattern which Oliver found may also occur at Coweeta. Mesic species such as tulip poplar and red maple occupy sites following clearcutting which were dominated by xerix species such as oaks and hickories (unpublished data, Coweeta Hydrological Laboratory, U.S. Forest Service). Day and Monk (1974) found tulip poplar to be negatively correlated with distance from the stream channel while chestnut oak and scarlet oak were positively correlated with distance on an old-growth watershed at Coweeta. It is not known whether the spatial pattern on clearcut watersheds will gradually shift to that of the old-growth watershed.

Hydrological data from clearcut watersheds indicates a large increase in streamflow following the cut and a gradual return to precut flow with regrowth of the forest. Precut streamflows are reestablished approximately 25 years after cutting (Swank and Helvey 1970). This increased streamflow following cutting indicated there is also an increase in soil moisture throughout the watershed allowing spatial expansion of mesic species. As regrowth occurs soil moisture should become more limiting resulting in a return of tree species to precut spatial patterns.

The hypothesis to be tested in this research is that shifts in spatial pattern of tree species following major perturbation of ecosystems is related to hydrological response to those perturbations. There should be an expansion of spatial distribution in mesic species immediately following the perturbation and then a gradual return to predisturbance spatial pattern as the hydrological cycle changes. This research will therefore attempt to relate an ecosystem structural response to a functional process.

This research will be conducted on WS 13, which was last clearcut in 1962. Streamflow of this watershed has been monitored since 1936. In addition, six vegetative surveys were made between 1934 and 1977 (Swank and Helvey 1970). Population shifts in tree species should progress rapidly over the next 5-10 years.

Transects extending from the stream channel to the topographical divide of the watershed will be established for detailed analysis of tree species spatial patterns. Each transect will be mapped for topographical and soil textural change. Topographical and soils data will be used to position 100 m^2 permanent quadrats along the transect for detailed analysis of tree species population dynamics. Diameter and heights of all individuals 5.1 cm at 1.37 m above ground for each species will be measured on each quadrat. Each individual will be tagged for annual remeasurement and for determination of mortality. All standing dead stems on each quadrat will be cut at ground line for age and growth measurement to determine the year of mortality previous to the initial survey.

Change in diameter, height, and mortality of individual species will be compared with stream discharge from the watershed to determine if there is differential response between tree species to the gradual reduction in stream discharge. Correlations between monthly, seasonal, and annual stream discharge will be made with species stratified by distance from the stream channel and/or topographical divide.

9. Woody growth following fall cankerworm defoliation on watershed 27

As part of our research on the effects of defoliation by the fall cankerworm on forest nutrient cycles of WS 27, tree core samples were collected (June, 1977) to examine possible reductions in rates of woody growth. Cores were taken along three transects across a range of tree sizes for the following tree species: *Acer rubrum* (40 cores), *Quercus prunus* (32 cores), *Q. rubra* (27 cores, *Carya* spp. (26 cores), *Betula lutea* (8 cores) and *B. lenta* (6 cores). We measured total periodic wood increment over a five-year period both before (1965-69) and during (1971-75) defoliation.

Data analyzed so far indicate roughly a 33% reduction in growth of hickory, 28% in chestnut oak, and 10% in northern red oak. We will soon complete analyses of these samples for nutrient concentrations for the two five-year periods.

A third set of tree cores for the five-year period 1978-1983 will be taken on WS 27 in the spring, 1983, in order to evaluate the long term effects of the fall cankerworm defoliation. These tree cores will be analyzed for total increment and nutrient concentrations over the 1978-1982 growth period. An additional set of cores may be taken after 1983 depending on results obtained from the analysis of the 1983 cores.

10. Above- and below-ground vegetation processes during recovery of cable-logged watershed 7

The overall objective of this research is to characterize the recovery of plant production and element cycling processes following a commercial clear-cut with cable logging. Here we propose to extend the characterization of the recovery process by 10 years. The revegetation study on WS 7 is comprised of a correlation phase and a process phase. Changes in net primary productivity and rates of element accumulation in the biomass are being correlated with studies of element input, element output, litter deposition, litter decomposition, changes in element storage in litter and on soil exchange sites, and changes in litter and soil solution chemistry. Process studies focus on the role of successional species in nutrient retention within the watershed.

Pre-clearcut, baseline production rates and the standing stocks of elements were estimated from standing stocks on WS 7 and the nutrient data of Day (1974). The clearcut of WS 7 was performed between January and June 1977. The rapid initial recovery of net primary production (NPP), leaf area index (LAI) and element standing stocks were characterized during the summers of 1977, 1978, and 1979 (Boring 1979, Boring et al. 1980). A successional N-fixing legume, Robinia pseudo-acacia, dominated early succession and rapidly accumulated large standing stocks of N, P, and K (Boring 1979).

We propose to extend characterization of above ground recovery by 10 years with sampling at years 5, 7, 10, and 13 after the clearcut. Year 5 will be 1982 and will fall within the budget period of this LTER proposal. During each of the sampling years we propose to characterize NPP, LAI and element accumulation in the vegetation.

The emphasis on successional species is important because of their dominant roles in initial revegetation and element accumulation. Robinia pseudo-acacia will receive particular research emphasis because of its high rate of N-fixation, biomass accretion (Boring 1979), and its ability to fix N (Chapman 1935, Ike and Stone 1958).

Sampling for above-ground vegetation processes will be performed using 24 pairs of permanent plots which have been established on the watershed. Four additional pairs of plots will be located in Robinia pseudo-acacia clones. Plots will be evaluated for species stem densities, NPP, biomass, LAI and element accumulation. Field data of species composition and stem diameters will be coupled with regression equations to estimate NPP and biomass for the plots. Herbaceous NPP and biomass will be estimated by destructive field sampling. Leaf weight to surface area ratios permit estimates of LAI to be made from leaf biomass. Element standing stocks will be estimated from biomass data in conjunction with element concentrations reported by Boring (1979).

The effects of clearcutting and revegetation on below-ground processes is presently under investigation. We also propose to extend root sampling by 10 years to estimate root standing stock for post-clear-cut years 5, 7, 10, and 13. These sampling years will coincide with the sampling of solution chemistry and above-ground biomass.

Pre-clearcut root biomass was evaluated by McGinty (1976) who established 5 plots on WS 7. Samples have been collected at depths of 0-30, 30-60 and at selected locations from 60-90 cm. Fifteen cores were taken from each site on each date. Roots were washed free from soil, sorted and weighed. Sampling has continued to the present except during 1978.

IV. Plan of research

C. Consumers

In this section we describe long-term ecological research proposed for consumers whose activities are directly related to terrestrial primary production. Consumers involved in soil processes and consumers in streams are discussed in the appropriate sections of the proposal.

While consumers normally do not process a major fraction of energy or nutrient flow in ecosystems, they perform regulatory functions and their activities may directly or indirectly regulate rates in other ecosystem components (Kitchell et al. 1979). The nature of such regulation is the subject of current research in a variety of ecosystems, including forested ones (Mattson 1977). Long-term ecological research on consumer activities is a necessary component for the understanding of consumer regulation. Some long-term population records exist for certain animals, and these have made major contributions to ecological understanding (e.g. the Kiabab Plateau deer population, Rasmussen 1941; rose thrips at Adelaide, Australia, Davidson and Andrewartha 1948). However, interpretations of these results is controversial, in part because of lack of concurrent measurements of other ecosystem components. Long-term ecological research proposed here for consumers will have the advantage of being able to relate consumer dynamics to those of process- and ecosystem-level phenomena.

At this stage, it would not be feasible to propose long-term ecological research for all animal groups in forested watersheds of the Coweeta basin. We recognize the need for long-term research efforts on a variety of animal groups and will add animal groups as expertise and resources become available. Currently we propose research on canopy arthropods, long-term ecological research projects on small and large mammals, birds, amphibians and reptiles.

Canopy Arthropods

Quantitative studies of arthropods in forest canopies are few, probably because of sampling difficulties. Considerable information has been developed on the biology of defoliating insect species but little is known of canopy arthropod communities during non-outbreak phases (Futuyma and Gould 1979). Some introduced (i.e. gypsy moth) or native (fall cankerworm, elm spanworm) insects are capable of destructive defoliations, and were doing so even prior to colonial settlement in North America (Josselyn 1672, according to Stephens 1976). It is not clear how some population explosions are initiated or how important vegetation factors may be in initiating insect outbreaks.

Existing data sets from canopy arthropod studies at Coweeta are listed in Table 12. The more significant data sets include biomass estimates and nutrient standing crops for canopy arthropods in four watersheds: two hardwood controls (2 and 18), a successional pine stand (17) and an early successional watershed (7). Biomass estimates are available for a twenty-compartment system, in which the compartments combine arthropod species of similar biology (Crossley et al. 1975). Differences in allocation of biomass among the 20 compartments were noted between the early successional watershed (7) and its adjacent control (2). Also, allocation of canopy arthropod biomass on WS 2 differed from the previously measured values (1972) on the hardwoods WS 18. The estimates of consumption rates have been based on leaf area

Table 12. Available data sets for canopy arthropod biomasses, abundances or feeding rates at Coweeta Hydrological Laboratory.

Year	Watershed					
	2	7	13	17	18	27
1969			a	a		
1970						
1971						
1972				b	b	
1973						
1974					c	c
1975					c	c
1976		d			c	c
1977	e,c	e,c				c
1978	e,c	e,c				c

[a] Relative sampling with identifications to species. Coulson et al. 1971, Crossley et al. 1973.

[b] Biomass estimates, nutrient standing crops. Crossley and Gist 1980.

[c] Frass drop and/or consumption rate estimates. Unpublished.

[d] Biomass estimates, nutrient standing crops. Unpublished.

[e] Biomass estimates, nutrient standing crops. Schowalter et al. 1980.

removed by arthropod feeding. Major comparisons have involved clear-cut versus control watersheds (7 vs. 2) and recovery of WS 27 from an outbreak of the fall cankerworm.

Objectives of the canopy arthropod long-term research include: (1) measurement of arthropod biomass and pertinent vegetation parameters in watersheds of various developmental stages through time; (2) shifts in relative importance of feeding guilds during recovery from watershed disturbance, and (3) development of long-term data bases to allow evaluation of hypotheses relating arthropod outbreaks to ecosystem level nutrient cycling behaviors. The 20 compartment biomass model for canopy arthropods permits evaluation of responses of arthropods groups with contrasting biologies (Crossley and Gist 1980, Schowalter et al. 1980). Within a season, canopy arthropod biomass on different hardwood tree species were generally similar. Differences were marked for arthropod biomasses between recently disturbed versus control watersheds. But, differences measured between years reveal shifts in total biomass and in relative importance of compartments. For example, the compartment "caterpillars" had important biomass in control WS 18 in 1972, due largely to contribution from dogwood. By 1977, the "caterpillars" compartment had increased in relative importance as measured in control WS 2 (on the disturbed WS 7, "caterpillars" were of less importance). The increase of "caterpillars" during this 5-year period coincided with an outbreak of fall cankerworm (<u>Alsophila pometaria</u>) in high elevation watersheds 27 and 36 (Waide et al., unpublished data), and thus may have been a basin-wide phenomenon. A long-term data base would have permitted us to distinguish gradual, basin-wide changes from acute responses to disturbance. The relation of canopy arthropod biomasses to nutrient dynamics in vegetation, or ecosystem-level nutrient dynamics, are not at all clear. It is still debated whether nutrient-rich vegetation is more heavily consumed than nutrient-poor vegetation (the latter presumably poor in feeding deterents as well (Price 1973)). Results in forest fertilization experiments have yielded contradictory results as regards canopy arthropod populations (Shigo 1973). In WS 2 and 18, canopy arthropod biomasses were not correlated with foliar nutrient contents of different tree species. Still, there are recurring observations that insect outbreaks occur in vegetation with high concentrations of N, P and K (Cooke et al. 1978). We observed high nutrient concentrations in foliage under defoliating attack by fall cankerworm (WS 27 and 36, Waide et al. unpublished). Long-term measurement of canopy arthropods and foliage nutrient dynamics, across several successional watersheds, may help to elucidate the contribution of foliage nutrients to insect outbreaks.

The research plan includes 500 samples annually (summer) on each of WS 2, 7, 17, 18 and 6 or 27, using a net-bag procedure (Crossley et al. 1975). Samples will be sorted to arthropod guilds (compartment model of Crossley et al. 1975, Crossley and Gist 1980, Schowalter et al. 1980), weighed, and stored. Eventually, samples will be analyzed for nutrient contents (N, P, K, Ca, Mg, Na). An additional 100 samples per watershed will be collected, sorted and stored for later taxonomic verification. Of the WS scheduled for sampling, 2 and 18 are controls for which we have some previous data, WS 7 is the clear-cut currently under study, and WS 17 is a white pine plantation. Both have been sampled previously and provide a comparison with the two control watersheds for the detection of long-term trends. We will sample WS 6 and 27 in alternate years. WS 6, a grassland successional WS, has not been sampled previously. WS 27 has just recently recovered from an outbreak of fall cankerworm (Waide et al. unpublished).

IV. Plan of research

D. Decomposition

1. Introduction.

Throughout our research program at Coweeta we have emphasized research on rates, patterns, and mechanisms of organic matter decomposition and accumulation within forest ecosystems. Decomposition processes represent important components of forest biogeochemical cycles. Decomposer organisms in litter and soil horizons process organic matter inputs, and thus remineralize contained nutrients which then may be taken up by plants or by microorganisms, or leached from the system. Decomposition of organic inputs depends on complex interactions among microbial and faunal components of forests which are regulated both by substrate quality parameters and by climatic factors. Our research has attempted to integrate all of these complex aspects of the decomposition process. In the subsections which follow, we discuss our work in this area, both what we have accomplished and what we propose to undertake as part of a program of long-term ecological research at Coweeta.

2. Leaf litter inputs, standing crops, and decay rates.

Throughout our research at Coweeta we have expended considerable effort in understanding what factors regulate the inputs, standing crops, and rates of decomposition of leaf litter in southern Appalachian forest ecosystems. We propose to continue our heavy emphasis in this area of research in the future. Below we describe our work in these three areas.

Litterfall Inputs

Inputs of litter to the forest floor have been measured for a variety of Coweeta watersheds, using litter traps 0.4045 m^2 in area (Table 13). The number of traps has varied from 10 to 24, depending upon watershed size. Samples were collected weekly or biweekly during leaf fall, sorted to species, and oven-dried. Leaf biomass was thus estimated by tree species, and leaf area indices were derived from subsamples by using an optical planimeter (Gist and Swank 1974). Samples were analyzed for cations (plasma emission spectrography), total N (autoanalyzer methods), and lignin (spectrophotometric analysis).

Litter trap collections provide measures of leaf primary production, nutrient and organic inputs to the forest floor, and leaf area removed by canopy consumers. Our collections have been spread over a number of watersheds and years (Table 13), but except for the defoliated WS 27, we lack a sustained long-term effort on any watershed. We propose to initiate annual litterfall measurements on WS 2, 6, 7, 13, 17, 18 and 27. Our previous experience suggests that 20-24 traps per watershed, emptied biweekly during the periods of leaf fall, will yield adequate estimates. Six watersheds were chosen to support the canopy arthropod and the decomposition studies, and allow for comparison of disturbed with undisturbed, control watersheds.

Litter Standing Crops

Standing crops of decomposing litter represent important storages of organic matter and nutrients within forest ecosystems, as well as important substrates for microbial processes and soil-litter arthropods.

Table 13. Measurement of leaf litter input to the forest floor: available records and data sets.

	Watersheds									
Year	1	2	7	13	17	18	27	36	37	48
1969				x						
1970	x				x	x				
1971				x	x	x				
1972	x			x				x	x	
1973										
1974			x				x			
1975							x			
1976							x			
1977		x	x	x			x			
1978			x				x			
1979		x	x				x		x	

Amounts of litter in forests result from the integration of processes of leaf litter inputs and decomposition. We have measured standing crops of litter and associated nutrients in separate 01 and 02 horizons on a variety of watersheds (WS 2, 6, 7, 13, 17, 18, 27) at biweekly, monthly and seasonal frequencies.(Table 14).

Because knowledge of litter standing crops ties in with so many other projects we propose to continue at Coweeta, because forest floor litter pools represent important components of forest nutrient pools, and because standing crops of litter accumulate slowly associated with long-term successional processes in forests, we propose to continue our measurements in the area. Specifically, we propose annual sampling of litter standing crops on WS 2, 6, 7, 13, 17, 18, and 27. We will take between 10 and 20 0.25 m^2 samples on each watershed, depending on size. Samples taken just prior to and again at the completion of annual litterfall, separated into 01 and 02 horizons, and dried, weighed, and analyzed for nutrient concentrations.

Leaf Litter Decomposition

The decomposition of organic matter on the forest floor permits regeneration of nutrient elements bound in dead organic materials. Dead organic matter forms a major nutrient reservoir, significant at Coweeta and at other forest sites. Rates of decomposition are altered following disturbance, and such rate changes constitute a major nutrient cycling response to disturbance in watersheds. Decomposition rates vary between tree species and between habitats. Species differences in decomposition and rates of element loss may be predicted from various substrate quality factors (C:N ratio, lignin content, cation content)

Table 14. Measurements of litter standing crops in forest ecosystems at Coweeta.

	Watersheds						
Year	2	6	7	13	17	18	27
1969		x		x	x	x	
1970		x		x	x	x	
1971		x		x	x	x	
1972		x		x	x	x	
1973							
1974			x				x
1975			x				x
1976			x				x
1977	x		x				
1978	x		x				
1979	x		x				

(Alexander 1978, Cromack 1972, Cromack and Monk 1975). Such substrate quality parameters have been shown to change as plant species replace one another in a successional sequence (Pancholy and Rice 1973). Following clear cutting on WS 7, decomposition rates declined the clear-cut WS 7 for some tree species; however, decomposition for herbaceous successional species was more rapid on WS 7 than on the control WS 2 (Waide et al. unpublished).

Superimposed upon habitat or species variables are factors associated with ecosystem type or climatic regime (Meentemeyer 1978) which further serve to predict decomposition rates. Disturbances such as clear-cutting, which alter microclimatic regimes, may produce significant changes in decomposition rates owing to modifications of abiotic variables. Such changes may be expressed as changes in rates of litter decomposition or as changes in the shape of the decomposition curve (Waide et al. unpublished).

At Coweeta, we have measured leaf litter decomposition using litter bag techniques (Olson and Crossley 1963, Crossley and Hogland 1962) in a variety of watersheds (Table 15). Leaves have been collected from trees at the time of senescence, air dried, and placed in 10 x 10 cm or 20 x 20 cm nylon mesh bags. After being weighed, bags were placed in various habitats in the field. Upon collection, some replicates were extracted in Tullgren funnels for microarthropod analysis. Nutrient analyses were performed on all bags. Leaf litter species were chosen to represent dominant species at Coweeta or species representing a range of substrate qualities.

In all, we have documented rates of litter decomposition and nutrient release from major leaf species and in a variety of watersheds

Table 15. Data sets on leaf litter decomposition.

	Watersheds			
Year	2	7	17	18
1969			a	a
1970			a	a
1971			a	a
1972				
1973				
1974	b	b		
1975	b,c	b		
1976	c			
1977	c,d	d		
1978	d	d		
1979	e	e		
1980	e	e		

a mixed litter species, Cromack 1972

b 16 leaf species, habitat comparisons, Waide et al. (unpublished)

c 7 leaf species, xeric and mesic comparisons, habitat comparisons, Waide et al. (unpublished).

d 15 leaf litter species, clear-cut vs. control comparison, habitat comparisons, Waide et al. (unpublished)

e 9 leaf species, successional species comparions, habitat comparisons, Waide (unpublished) (undisturbed and manipulated) and habitat types. However, these results consider at most two years' decomposition and usually consider but one year. Typically 25% to 50% of weight remains when the experiment is terminated. A major objective of research proposed here is to make a prolonged set of measurements over a 5-year period. These measurements are necessary to specify the value of our short-term measurements (and comparable measurements by others). Our hypothesis is that decomposition (weight loss) will become progressively slower (Olson 1963). Further, measurements of litter inputs and losses through decomposition should enable us to predict the standing amount of dead organic matter on the forest floor. Annual estimates of dead organic matter (see below) will permit an evaluation of the adequacy of our measurements of decomposition rates (evaluation to be based upon a simple balance model relating standing crop to differences between inputs and losses). A second objective of the research is the documentation of the recovery of predisturbance decomposition rates on WS 7 in comparison with the successionally more advanced WS 13 (18 years post-cut) and two hardwood controls (WS 2, 18). Such long-term studies may also help us to understand better the process of soil organic matter genesis in southern Appalachian forests. Finally, continued documentation of decomposition rates and nutrient loss rates on control watersheds (WS 2 and 18) will provide a data base against which long-term regional trends, possibly resulting from diffuse antropogenic influences (increasing industrialization), might be evaluated.

The experimental design calls for five leaf litter species (dogwood, tulip-poplar, hickory, red maple, chestnut oak) chosen to represent a range of substrate types, importances, and previous data sets. Litter bags will be placed at mid-elevations in mesic sites on six watersheds (WS 2, 6, 7, 13, 17, and 18). Our previous experimentation (Waide et al. unpublished) suggests that variation within watershed types at Coweeta can be minimized provided xeric sites or unusual exposures are avoided. Thus, we propose to spread our effort over several watersheds rather than measure within-watershed variation. The experiment will be initiated with sufficient litterbags for quarterly collections, three replications of each leaf species, over a 5 year period (a grand total of 1800 litterbags). In the fifth year (1985) we will begin a 1-year experiment on WS 17 and 18 for comparison with our earliest measurements of litter decomposition.

3. Woody litter

In contrast to leaf litter decomposition, much less effort has been directed at examining woody litter standing crops, inputs, and decay rates at Coweeta. Cromack (1972) obtained preliminary estimates of rates of woody litter inputs to forest floor compartments on WS 18, as well as estimates of woody litter standing crops by size class and decay state. Cornaby and Waide (1973 and unpublished) obtained data on densities, nutrient contents and rates of nitrogen fixation and denitrification in decaying chestnut logs, also on WS 18. Following cable logging of WS 7, Waide and Swank (unpublished) estimated amounts of logging slash remaining by size class (0-1, 1-3, 3-5, and > 5 cm) and species (>5 cm only). Data on wood density, total surface area of decomposing woody litter, and nutrient contents were also obtained. Under separate funding from the Department of Energy, Swank and Waide (unpublished) also obtained similar data for woody litter on WS 4 prior to cutting and residue removal. We do not presently have the manpower to initiate a separate detailed study of woody litter inputs and decay rates at Coweeta. However, we do propose to initiate a limited study taking advantage of the large amount of woody litter remaining on WS 7 following logging. In this study we hope to obtain initial information on rates and processes of wood decomposition in Southern Appalachian hardwood forests, and thereby partially to fill a major gap in our understanding of long-term nutrient cycling processes within these forested systems. Beginning in 1982-1983, and every 2-3 years thereafter for 3-4 sample periods, we propose to sample woody litter > 5 cm diameter in 18 4-m^2 plots located on WS 7. These will be located contiguous to the plots we initially sampled the material from in 1978. Samples will be separated into 3 size fractions (0-1, 1-3, 3-5 cm), dried, weighed, and analyzed for nutrient content. Since we do not expect significant inputs of woody litter to litter-soil pools for some time, that should allow us to estimate decay rates for this material.

For logs (i.e., woody litter >75 cm diameter), we will utilize a different sample regime. Sample logs will be located, permanently marked, and remeasured over a fairly long time period. Logs will be stratified by species, size class, and location in the watershed. We will locate, mark, and initially sample all logs in 1980-81. Sampling will then proceed at 3-5 yr intervals, depending on the rate and extent of decomposition. On each sampling date we will remove replicate samples from each permanently marked log. Each sample will be analyzed for rates of ca 2 production and nitrogen fixation, for density, and for nutrient content.

4. Gaseous nitrogen transformations

Introduction

Gaseous transformations of nitrogen have been identified as principal components of the nitrogen cycle in forest ecosystems (Todd et al. 1975a). Moreover, changes in the N cycle may in large measure regulate the response of the entire forest ecosystem to perturbations such as defoliation or cutting (Swank and Waide 1980). But, since denitrification depends upon the process of nitrification to supply NO_3^-, studies of nitrification and mineralization are of equal importance. Despite the importance of the nitrogen cycle to all ecosystems, the response of these gaseous transformations of nitrogen to disturbance, the time required to recover to predisturbance conditions, and the factors regulating this recovery remain unknown. This section describes research which addresses these questions.

Previous Results at Coweeta

Research on gaseous components of the forest nitrogen cycle have been conducted on a variety of watersheds at Coweeta. In the early phase of our work, we measured rates of nitrogen fixation and denitrification, and numbers of nitrifying bacteria, in two litter and four soil horizons on WS 6, 13, 17, and 18 (Todd et al. 1975a, 1975b, 1978). We also measured rates of nitrogen fixation and denitrification in woody litter on WS 18 only (Cornaby and Waide, 1973; Todd et al. 1978). In more recent work we measured all three processes in two litter and two soil horizons on WS 2, 7, and 27.

Dramatic increases in rates of nitrogen fixation were seen on WS 7 following cutting (Table 16). This increase may be largely

Table 16. Rates of nitrogen fixation and numbers of nitrifying bacteria in soil and litter layers in clearcut (WS 7) and control (WS 2) watersheds at the Coweeta Hydrologic Laboratory.

		WS 7		WS 2
Process	Depth	Pre-cut	Post-cut	
Nitrogen Fixation ($g N/m^2/yr$)	01 litter	0.024	0.185	0.006
	02 litter	0.041	0.135	0.008
	0-10 cm soil	0.486	4.229	0.104
	10-30 cm soil	0.599	2.679	0.080
	Total	1.150	7.228	0.198
Nitrosomonas	01 litter	$1.50 \times 10^{4*}$	4.11×10^4	1.17×10^4
Type Bacteria	02 litter	1.28×10^5	6.86×10^4	8.50×10^3
($number/m^2$)	0-10 cm soil	2.83×10^6	4.17×10^7	7.01×10^6
	10-30 cm soil	4.32×10^6	4.56×10^7	1.76×10^7
	Total	7.30×10^6	8.74×10^7	2.46×10^7
Nitrobacter	01 litter	$1.50 \times 10^{4*}$	2.24×10^4	8.41×10^3
Type Bacteria	02 litter	1.28×10^5	1.22×10^5	2.77×10^3
($number/m^2$)	0-10 cm soil	2.83×10^6	3.44×10^7	3.59×10^6
	10-30 cm soil	4.32×10^6	2.25×10^7	6.90×10^6
	Total	7.30×10^6	5.70×10^7	1.05×10^7

---

*Pre-cut methodology did not distinguish between these two groups of nitrifying bacteria; a common estimate is given for both.

attributable to the increase in soil temperatures. A portion of this increase may also result from an increase in the population of black locust on WS 7 following cutting. However, the full extent of this contribution to forest N dynamics can not be stated since routine sampling techniques include nodules only by chance. Similarly, an increase in numbers of both types of nitrifying bacteria were observed (Table 16), but an increase in numbers does not necessarily mean an increase in activity (Belser 1979).

Rice and Pancholy (1972) have suggested that climax ecosystems inhibit nitrification; clear-cutting would remove such inhibition mechanisms resulting in an increase in populations of nitrifying bacteria. Mineralization rates are not known, but the absence of root exudates would tend to result in a decreased C:N ratio in the soil, which should stimulate mineralization rates. With more available substrate (from fixation and/or mineralization), an increase in numbers of nitrifying bacteria would be expected. Thus, no inferences can be made as to the validity of the theory of inhibition by climax ecosystems.

Recent studies have been initiated to measure losses of nitrogen from Coweeta soils via denitrification. Rates were determined from Phase I curves as described by Smith and Tiedje (1979), which are essentially an assay of the amount of denitrifying enzymes present within soil at the time of sampling. Results indicate the existence of both Phase I and Phase II rates for Coweeta soils, and that the transition occurs after 2 hours of incubation. Thus, this technique may be used to estimate denitrification rates for Coweeta soils. Based on only 4 months of data, the amount of gaseous N lost appears to be 9.6 kg/ha/yr on WS 2 and 6.3 kg/ha/yr on WS 7. Although these data are too sparse to permit reliable interpretation, the apparent decrease in the denitrification rate following clear-cutting would not be surprising.

Recent reports that N_2O (nitrous oxide) is produced during oxidation of NH_4^+ to NO_2^- by nitrifying bacteria prompted a series of experiments to determine the significance of this mechanism of N loss at Coweeta. That nitrification was the source of the N_2O was confirmed using acetylene and nitropyrin as inhibitors (Bremner and Blackmer 1979; Walter et al. 1979). The data collected over the last 4 months indicate that this source accounts for 0.8 kg N/ha/yr lost on both WS 7 and WS 2. This is at least 10% of the amount lost via denitrification.

Objectives

During the three years since clear-cutting WS 7, the observed increases in N fixation and nitrifier numbers have persisted, suggesting that changes in rates of other N cycle reactions also continue in a disturbed condition. As regrowth continues and mechanisms operating during succession are manifested, the perturbed N cycle processes will move toward the reestablishment of pre-cut rates. The overall goal of the proposed research is to determine how long this disturbed state will continue and to examine the role of the N cycle in forest succession. The mechanisms of a proposed inhibition of nitrification by climax ecosystems are unclear. However, as succession progresses, such mechanisms should first be exerted in the simplest system possible and may be easier to identify. These questions provide the basis for the long-term study of individual N cycle processes and their relation to ecosystem development during regrowth. Therefore, the following objectives may be stated:

(1) To identify all the principal N-fixing components and to assess their contribution to the annual N-fixation budget.

(2) To measure the amounts of gaseous N lost annually through the activity of nitrifying and denitrifying bacteria.

(3) To determine the rates of mineralization in order to assess the relatedness of the responses of N-fixing and nitrifying organisms.

(4) To combine the measurements of the microbially mediated processes of the N cycle with estimates of the N flux and content in other compartments of the ecosystem to assess the efficiency of the cycle within the system.

Research Design and Methodology

Measurements of the various components of the N cycle will be made on samples collected from the 01 and 02 litter layers and 0-10 cm and 10-30 cm layers of mineral soil on 16 previously established plots on WS 7 (12 sites) and WS 2 (4 sites). Sampling will be expanded to include 4 sites each to be established on WS 6 and WS 13. Samples will be taken monthly for the first two years. After this period, analyses will be performed seasonally for two years and then monthly every third year thereafter. Since microbial transformations occur on a more rapid time scale than other components, a more frequent sampling schedule at periodic intervals will allow detection of small-scale changes that otherwise might be overlooked. These several watersheds all represent different stages of succession. (See earlier description of watersheds). We will also measure these same processes on six plots on WS 27, the defoliated watershed, but only seasonally for a single year (1981-82).

Nitrogen-fixation will be measured using acetylene reduction assays (Nardy et al. 1973), nitrification by short-term activity measurements of NO_2^- production in the presence of chlorate (Belser 1979) and by enumeration (Rowe et al. 1977), mineralization plus nitrification according to the method of Guthrie and Duxbury (1978), denitrification with Phase I rates as described by Smith and Tiedje (1979), and N_2O production by nitrifying bacteria according to the procedure of Bremner and Blackmer (1979).

In addition to these basic measurements, a systematic survey for nitrogenase activity will be conducted on the four watersheds (WS 2, 6, 7, 13) to identify the major types of fixation occuring. Once they are identified, the sampling regime will be modified as necessary to provide a more complete picture of the annual amount of N fixed. This survey will include evaluation of soil, soil surface, and above-ground activity. Such a survey should also reveal patterns of fixed N contributions by the various components. Early spring contributions may be dominated by lichens, growing season contributions by soil organisms, and autumnal fixation by leaf litter or soil surface organisms.

Estimates of N flux from measured rates and N concentrations reveal only net reactions. A tracer is necessary to measure accurately the movement of N through a system. Three plots (0.1 ha each) in triplicate will be established and receive the following treatment each year for three years: controls - no treatment, unlabelled control - N fertilizer at a rate of 100 kg N/ha, experimental plot - ^{15}N fertilizer at a rate of 100 kg N/ha. Such treatment will raise the background ^{15}N content of the plots. By measuring the concentrations of the various forms of N on a monthly basis, the flow of N through the system can be measured as each pool is diluted or enriched. Such a technique has been successfully used to measure simultaneous rates of mineralization, nitrification, and denitrification (Tiedje 1980).

5. Fungal sporocarps.

Introduction

Recently, emphasis has focused on the roles of microbial symbionts in nutrient uptake by plant roots. Free-living fungi have been demonstrated to accumulate and concentrate nutrients above levels found in their respective soil or litter substrates (Ausmus and Witkamp 1974, Ausmus et al. 1976, Cromack et al. 1975, Harley 1971, Stark 1973, Witkamp and Barzansky 1968). Mycorrhizal or plant root symbiotic fungi selectively absorb ions and increase the rate of ion absorbtion by their host plant (Skinner and Bowen 1973, Sihanonth and Todd 1977).

Most non-symbiotic and mycorrhizal fungi produce large aboveground reproductive structures or sporocarps. Large quantities of nutrients are contained within the sporocarp structure (Byrne et al. 1976, Cromack et al. 1975, Hinnerie 1975, Muncie et al. 1975, Stark 1972, Ramage 1930).

Recent investigations at Coweeta on nutrient cycling processes by forest floor inhabiting fungi has lead to the hypothesis that fungi selectively capture and concentrate nutrients from within the soil-litter matrix and transport these nutrients to the soil surface via sporocarp production (Todd and Biever 1979, 1980). Sporocarp production and nutrient concentrations have been demonstrated to be a significant elemental transport and recycling mechanism within the forest ecosystem (Table 1).

Objectives

The research cited above demonstrates the role of fungal sporocarps in concentrating mobile and non-mobile nutrients in forest floor systems. Analyses of sporocarps for nutrients include heavy metals, pesticides and radionuclides would refer to the status of these substances within the forest floor system. Monitoring of these elements as a function of time concentrated within the sporocarp would reflect the status of these elements in forest ecosystems. Therefore, the objectives of this research are:

1) To perform chemical analyses of sporocarps to reflect chronic environmental impacts. These impacts may appear as changes in sporocarp production before such stresses may be demonstrated by monitoring of classic ecosystem parameters (i.e. streamflow, fauna or flora analyses).
2) To monitor rates of sporocarp production and nutrient translocated concurrently with vegetation monitoring.

Experimental Procedures

Five permanent plots (2 x 50 m) were established to monitor sporocarp production on each of two watersheds (WS 2 and 17) in 1977 (Todd and Biever 1979, 1980). In this study five additional plots will be added at the two locations. Ten plots will also be located on WS 7 (clear-cut). Analyses at the three sites will provide a comparison of two vegetation types and in addition two stages of successional development for the hardwood vegetation.

Sporocarp collection will be carried out at quarterly intervals during 1980 and 1982 and our long term plans include continuing collections at two year intervals past 1982. The data collected in 1977 and the new work described in this proposal will produce a data base covering five years.

Chemical analyses of the sporocarps will include the 20 elements listed in Table 17 (Nitrogen, micro-Kjeldahl; Sulfur, Leco sulfur Analyzer; Carbon, weight loss following ashing; and the remaining 17 cations by double acid extraction and argon plasma-emission spectrography). Radionuclide and pesticide analyses will be performed on pooled samples from the fall collection period for each vegetation type.

6. Other microbial processes

In addition to measurements of sporocarp production and the microbially mediated transformations of N fixation, denitrifcation, and nitrification, we have also measured several other aspects of microbial processes at Coweeta. Specifically, we measured ATP concentrations in 2 litter and 2 soil horizons on WS 2 (1977-1979), 7 (1974-1979) and 27 (1974-1976). We have also measured rates of CO_2 production separately for litter and soil horizons by trapping evolved CO_2 in dilute alkali. CO_2 evolution rates were measured on WS 6, 13, 17 and 18 over 1971-1973, on WS 27 over 1974-1976, on WS 7 during 1974-1980, and on WS 2 for the period 1977-1980.

Further measurements of ATP concentrations on soil or litter

Table 17. Elemental determinations for samples of Sporocarps collected at Coweeta Hydrologic Laboratory. Values expressed (g/ha) are means ± standard error (Todd and Biever 1980).

Element	White Pine	Hardwood
C	2489.33 ± 581.89	2650 ± 680.10
N	113.22 ± 26.82	112.54 ± 28.83
S	4.96 ± 1.25	8.84 ± 2.83
P	11.59 ± 2.56	12.36 ± 2.68
K	65.84 ± 15.38	74.83 ± 18.43
Ca	2.49 ± 0.80	3.17 ± 0.89
Mg	4.92 ± 1.18	5.42 ± 1.22
Fe	2.30 ± 0.87	1.88 ± 0.51
Mn	0.43 ± 0.13	0.47 ± 0.13
B	0.0091 ± 0.0023	0.0084 ± 0.0024
Cu	0.13 ± 0.04	0.12 ± 0.04
Zn	0.28 ± 0.07	0.30 ± 0.07
Na	0.30 ± 0.07	0.29 ± 0.07
Al	4.63 ± 1.95	4.21 ± 1.11
Si	2.28 ± 1.00	1.57 ± 0.36
Co	0.0037 ± 0.0015	0.0053 ± 0.0018
Cr	0.0059 ± 0.0015	0.0040 ± 0.0011
Ni	0.0050 ± 0.0012	0.0041 ± 0.0008
Pb	0.11 ± 0.04	0.07 ± 0.02
Cd	0.0046 ± 0.0015	0.0058 ± 0.0016
Sr	0.02 ± 0.01	0.03 ± 0.0089

horizons are not relevant to our long-term research goals at Coweeta, at least with our current interpretations. We do feel, however, that further measurements of rates of CO_2 respiration are important, especially as they relate to research on litter decomposition and accumulation. Thus, we propose monthly measurements of respiration rates in 1982-83, 1984-85, 1987-1988, and 1990-1991 on the following watersheds: WS 2, 6, 7, 13, 17 and 18. We will measure CO_2 evolution separately for soil and litter layers via trapping in soda lime. From 10-24 measurements will be taken on each watershed depending on size.

7. Soil organic matter and nutrient pools

Standing crops of organic matter and nutrients within soil horizons result from the integration of a variety of processes acting simultaneously within forest ecosystems. These include organic matter inputs, especially via root death and exudation, organic matter decomposition, leaching, weathering of geologic materials, and nutrient uptake by microbes and plants. Direct measures of soil pool sizes integrate these various processes, and provide direct information on soil fertility, important in studies of forest biogeochemistry. Such studies also reveal important aspects of an ecosystem's response to perturbation.

In our work at Coweeta we have accumulated a large amount of research data on nutrient and organic matter pool sizes in various soil horizons. During the period 1970-1973, we obtained such data in 5 soil horizons on WS 6, 13, 17 and 18 (Yount 1975, Todd unpublished). In our study of forest defoliation on WS 27, soil pools were measured in 2 horizons during 1974-1976. Over the period 1974-1980, we have also measured soil pool sizes in 2 horizons in conjunction with our study of forest response following cable logging. Results of the latter study have shown distinct and dramatic increases in organic matter and nutrient pool sizes in soil horizons. How long such elevated levels persist, and the factors responsible for recovery to predisturbance levels, remain major questions to be addressed over the long-term. Organic matter contents have been determined via Walkley-Black titrations; NO_3^- and NH_4^+ by autoanalyzer methods following extraction with 2M KCl; exchangeable cations on either an atomic absorption spectrophotometer or a plasma emission spectrograph, following extraction either with neutral NH_4Ac or the North Carolina double acid extraction procedue (.075N mixture of H_2SO_4 and HCl); and N by autoanalyzer methods following microjeldahl digestion procedures.

We propose to continue these measurements on the following watersheds: WS 2, 6, 7, 13, 17, 18, and 27. Samples will be taken annually in the fall just prior to litterfall, in the following years: 1980, 1981, 1982, 1984, 1987 and 1990. Depending on watershed size, 10-20 samples will be taken on each watershed from 3 soil horizons: 0-10 cm, 10-30 cm, and 50-70 cm. Existing methods will be used to analyze these samples for organic matter content (Walkley-Black), NO_3^- and NH_4^+ (KCl extraction, autoanalyzer), total N (microjeldahl digestion, autoanalyzer), and exchangeable cations (North Carolina double acid extraction, plasma emission spectrograph). We will also measure cation exchange capacity and % base saturation on these same samples using standard techniques.

8. Soil animals

The breakdown and decomposition of dead organic matter on the forest floor is strongly influenced by soil animals, a fact recognized by biologists such as P. C. Muller and Charles Darwin in the 1800's. American pioneer soil biologists such as A. P. Jacot considered soil animals to play important functional roles. Recent experimental studies (see Lohm and Persson 1976) confirm the significance of soil animal activities in soil processes. Long-term ecological studies on a large variety of soil animal groups is desirable, but must necessarily be restricted initially. We propose here to begin with studies of macro- and microarthropods in decomposing litter and associated mineral soil. In subsequent years we intend to add long-term research on annelids, enchytraeids and earthworms, subject to availability of expertise and resources.

Previous research at Coweeta has studied the relation of arthropods to leaf litter and woody litter decomposition in five watersheds. Gist (1972) and Cornaby (1973) compared arthropod influences on Ca and K flows during decomposition on WS 18 (hardwood control) and WS 17 (adjacent pine plantation) (Cornaby et al. 1975). Crossley (unpublished) measured soil arthropod biomasses on WS 27 during its period of peak defoliation. Seastedt (1979) demonstrated stimulation of nutrient immobilization by soil arthropods, in studies in clearcut (WS 7) and control hardwood (WS 2) systems. Abbott (1980) studied arthropods related to woody litter decomposition in WS 7 and WS 2. Other work with soil arthropods includes collembolan community structure on WS 7 (Reynolds 1976), relative indices of macroarthropod abundance on WS 7 using pitfall traps (Crossley and Reynolds, unpublished), and various tullgren extractions of soil and litterbags by Crossley. Abbott et al. (1980) summarize distribution and microhabitat information for oribatid mite species identified from the Coweeta basin.

Long-term ecological research on microarthropods has the objectives of (1) quantifying arthropods (especially mites and collembolans) associated with leaf litter decomposition processes being measured with litterbags, (2) measuring response of soil microarthropods to recovery from disturbance in some watersheds, and (3) developing a long-term data base describing soil microarthropod abundances. Objective (1) parallels the long-term objectives proposed for litterbag measurement of leaf litter decomposition. The seasonal objective extends the existing data base on clear-cut, defoliated, and white pine watersheds. We are now suggesting (Seastedt and Crossley, MS) that the response of soil microarthropod communities to disturbance can be viewed as a set of shifts in vertical distribution of species and shifts in the mix of r and K specialists. Documentation of changes in microarthropod abundance and community structure will allow us to evaluate these and other hypotheses relating soil microarthropods to the decomposition process.

To accomplish these objectives, watersheds 2, 7, 17, 18 and 27 will be studied using litterbag, soil core and .5 x .5 M plot sampling methods. Microarthropods will be extracted from litterbags used to measure decomposition and nutrient loss rates from: dogwood, chestnut oak, red maple, tulip poplar and hickory species, sampled quarterly. Concurrently, three soil cores will be collected at each litterbag site and extracted in a high efficiency extractor (Merchant and Crossley 1970). The litter plot samples will be collected concurrently with, and in close proximity to, the litterbag and soil core samples. Initial separation of the arthropods into major taxonomic groups will be performed, but we anticipate that species identification will eventually be made.

IV. Plan of research

E. Ecological research in stream systems

1. Introduction

Stability characteristics of stream ecosystems are dependent upon the maintenance and predictability of inputs from outside the system -- e.g., solar, hydrologic, and biotic inputs. A prime example of dependence of one ecosystem on another is that of headwater streams in forested regions. Such streams may be characterized as having low resistance to perturbation and high resilience following perturbation (Webster et al. 1975, O'Neill 1975, Webster and Patten 1979). However, recent studies of the response of Big Hurricane Branch to the clear-cutting of the surrounding watershed have suggested that the resilience characteristic of the stream cannot be fully realized in the face of continuing perturbation of the surrounding watershed (Gurtz et al. 1980). That is, until the quantity, quality, and timing of allochthonous inputs have been restored to pre-disturbance conditions, the stream will be in a state of flux beyond the temporal fluctuations of undisturbed streams. This finding contrasts with results of some studies showing rapid recovery of benthic fauna following droughts, floods, and dredging. For example, Fisher (personal communication) has shown that the algae and benthic fauna of desert streams reach a maximum within a few weeks following major storms which eventually denude the streambed.

The growing information base on the chemical, biological, and hydrologic characteristics of stream ecosystems at Coweeta make long-term studies particularly attractive. Studies of long-term biological recovery of streams have already begun through a recent comparison of disturbed and undisturbed watersheds to their ecological characteristics of ten years ago (Woodall 1972, Haefner 1980). We are now comparing DOC in streams with measurements made in 1969-1971 (Meyer unpublished). Intensive studies (Gurtz 1980) of the short-term (i.e., 1-3 years) impacts of a major perturbation have laid the groundwork for periodic assessment of changes. The proposed research will allow analysis of stream recovery on two time scales and two stream orders simultaneously. Further, the value of long-term research on undisturbed streams should not be understated. Our proposal to continue study of adjacent first- and second-order undisturbed streams will allow an improved assessment of response to long-term environmental changes in the surrounding terrestrial ecosystem and in atmospheric conditions.

2. Site description

This proposed research will be conducted on four streams at Coweeta (Table 18). Sawmill Branch on WS 6 has been subjected to the greatest disturbance. Stream-bank vegetation (12% of WS area) was removed for 5 m on either side of the stream channel in 1942. Regrowth was allowed until 1958 when the forest was clear-cut and converted to fescue. Heavy applications of lime and NPK were used during the fescue conversion. Applications of herbicides were made on the WS in 1966-67 excluding a 3 m strip on either stream bank. A series of logging and herbicide treatments to the watershed began in 1942 and ended in 1968. The vegetation has subsequently been allowed to regrow naturally and is now dominated by black locust (<u>Robinia pseudoacacia</u>). Further details of this stream and its watershed are given in Woodall and Wallace (1969), Johnson and Swank (1973), Webster and Patten (1979) and Haefner (1980). We will use Grady Branch, on WS 18, a control for studies of Sawmill

Table 18. Characteristics of streams at Coweeta Hydrologic Laboratory

	Watershed			
	6	18	7	14
Stream Name	Saw Mill Branch	Grady Branch	Big Hurricane Branch	Hugh White Creek
Strahler Stream Order	1	1	2	2
Watershed area (ha)	8.9	12.5	58.7	61.1
Main Channel Length (m)	370	345	1225	1077
Main Channel Gradient ($m \cdot m^{-1}$)	0.234	0.200	0.191	0.161
Average Annual Discharge ($l \cdot s^{-1}$) (predisturbance)	---	3.1	17.7	19.0
Vegetation	regrowth from herbicide in 1967	hardwood	regrowth from clearcutting in 1977	hardwood

Branch. WS 18 has remained undisturbed since at least 1924. Vegetation is dominated by oaks, hickories, and yellow poplar. Rhododendron is an important understory species, especially along the stream.

Vegetation on WS 7, drained by Big Hurricane Branch, was clearcut in 1977. An additional significant perturbation to this stream was construction of logging roads in 1976. Further details of the stream, watershed, and logging operation can be found in Gurtz et al. (1980). Regrowth of vegetation on the watershed is occurring primarily as sprout regrowth (details in Section IV B of this proposal). Hugh White Branch, on WS 14, will be used as a control for studies on Big Hurricane Branch. This watershed has not been disturbed since at least 1924 and the vegetation is similar to that on WS 18.

3. Evidence for long term recovery

Seston transport in Big Hurricane Branch and Hugh White Creek was studied intensively from July 1977 - July 1978 (Gurtz et al. 1980). Increased levels of both inorganic and organic seston were found in Big Hurricane Branch, especially beginning one year after clearcutting (two years after construction of logging roads). Subsequent samples have shown that seston levels are decreasing but still remain substantially elevated (based on samples in December 1979).

Prior to clearcutting WS 7, streamside vegetation provided 259.2 g m^{-2} y^{-1} direct litterfall to Big Hurricane Branch and an additional 115.6 g m^{-1} y^{-1} lateral movement or blow-in (Webster and Waide, in manuscript). Tree species comprising more than 5% of this allochthonous stream input were hickories, 12.8%; rhododendron, 12.7%; oaks, 21.8%; birches, 6.2%; and yellow poplar, 5.7%. Following clearcutting (fall 1978-79), leaf fall became reduced to 4.2 g m^{-2} and lateral movement as 38.6 g m^{-1}. In addition to the quantitative changes in leaf inputs, there have been significant qualitative changes. Species composition of leaf input following cutting was dominated by red maple, rhododendron, birches, yellow poplar and dogwood, with a conspicuous absence of oaks. Additionally, measurements of leaf breakdown rates indicated qualitative changes in the leaves themselves (Webster and Waide, in manuscript). Though breakdown of dogwood leaves subsequent to clearcutting was not significantly different from breakdown prior to clearcutting, both oak and rhododendron leaves broke down significantly faster after the clearcut. All leaves used in the studies were collected on the watershed prior to each study. We attribute the accelerated breakdown rates primarily to differences in the quality of leaves rather than in-stream factors.

Measurements of leaf fall to Sawmill Branch were made four years after the disturbance in 1972-73 (Webster and Patten 1979). These collections indicated a low level of input, 285.8 g m^{-2} compared to 353.2 g m^{-2} in Grady Branch. WS 6 litterfall consisted primarily of black locust and blackberry leaves. Thus, evidence suggests that while allochthonous inputs quantitatively recover in 5-10 years following cutting, qualitative recovery is a much longer term phenomenon. We are currently investigating the effect of leaf quality (different leaf species) on shredder insect assimilation efficiencies.

Current studies on dissolved organic carbon in Big Hurricane Branch and Hugh White Creek have documented consistently lower DOC concentrations, more rapid uptake of experimentally-added DOC, and greater seasonal variation in concentration in the disturbed stream. In addition, DOC concentrations have been followed in Sawmill Branch (WS 6) and Grady Branch (WS 18) during 1979-1980, and they can be compared with DOC concentrations measured during 1969-1971 in these streams (P. Falco, unpublished data). DOC concentration is highest in spring and autumn in both streams during all years, and these within-year variations are greater than any changes in mean DOC concentration over the ten year period. During this decade, there has been a reduction in the within-year variation in DOC concentration in Sawmill Branch.

Short term response of aquatic invertebrates to perturbations associated with clearcutting have been studied on WS 7 and WS 14 (control) (Gurtz 1980). A stratified random sampling regime was selected to include four common habitats: rock face (moss covered boulders or outcrops), cobble riffle (primarily rocks 64-256 mm diam.), pebble riffle (16-64 mm), and sandy reach. Initial results show that dominant leaf-shredders have decreased in Big Hurricane Branch (WS 7) relative to the control stream, Hugh White Creek (WS 14). Dramatic increases occurred in the predominantly grazer and collector-gatherer mayfly taxa Baetidae and *Ephemerella* spp. as well as riffle beetles, Elmidae. The greatest increases occurred in the most stable rock face habitats and least in sandy reaches. These changes did not occur in the control stream. But, we do not have the evidence to know how long these changes will persist.

Benthos on WS 6 and WS 18 (control) were studied intensively in 1968-69 (Woodall and Wallace 1972). The vegetation of WS 6 at that time was primarily grass and annual plants. High numbers of individuals and species wre present in WS 6 at that time, but there were very significant differences between WS 6 and WS 18. These differences were primarily related to higher standing stocks of "grazer" organisms and low standing crops of shredder detritivores (particularly Peltoperla) on WS 6 (Woodall and Wallace 1972). Webster (1975) again sampled the benthic fauna (1972-73) and Haefner (1980) did a follow-up study in 1978-79. Results of these studies show a continual decline of grazers and an increase of shredder-detritivores on WS 6 compared with WS 18. However, grazer organisms are still significantly higher and shredder-detritivores significantly lower on WS 6 compared to WS 18. These results suggest that recovery of stream benthos with respect to trophic structure and function is a long-term process dependent on recovery of terrestrial vegetation.

We have documented changes in the stream ecosystem which have occurred 10- and 20- years following deforestation (WS 6) and we have studied intensively the changes which occur during the first 2½ years following clear cutting on WS 7. However, as concluded by Gurtz et al. (1980), recovery of the stream ecosystem is dependent on recovery of the surrounding watershed. Thus, long-term changes will continue to occur. At Coweeta, we have a unique opportunity for examining such long-term recovery. Although both short (WS 7) and longer term (WS 6) changes have been examined, we cannot yet document the sequence of changes on the same stream. Until recently we have not had the opportunity to study short-and long-term changes in the same stream. Continued studies on WS 7 will allow us to do this. Conversely, WS 6 offers us the advantage of studying even longer term changes in streams following disturbance.

4. Objectives

Our overall objective is to assess long-term recovery of southern Appalachian streams with respect to restoration of trophic structure and function following clearcutting. Attributes examined in each of two disturbed streams will be compared with those of undisturbed streams of similar size. The following are specific objectives to be addressed during this study:

1. Measure long-term recovery of organic and inorganic seston output as indicated by changes in particle size distribution and quantity.
2. Measure long-term changes in DOC concentration during natural regrowth.
3. Assess long-term changes in the quality and quantity of allochthonous inputs.
4. Measure aquatic primary production during natural succession.
5. Assess long-term recovery of benthic invertebrate communities with respect to the restoration of trophic structure and function.
6. Assess long-term changes in secondary production of selected species of benthic invertebrates.

5. General long-term sampling plan

Our long-term sampling plan is to collect three more years data from Big Hurricane Branch and Hugh White Creek in 1981-82, 1984-85, and 1988-89. We propose two more annual collections from Sawmill Branch and Grady Branch, 1984-85 and 1988-89. Table 19 lists years of sampling with appropriate watersheds for various types of long-term research in streams.

Table 19. Past and future sampling schedule for stream studies.

	Sawmill Br. WS 6	Grady Br. WS 18	Big Hurricane Br. WS 7	Hugh White Creek WS 14
1968-69	1,2	1,2		
1969-70	7	7		
1970-71	7	7		
1971-72				
1972-73	1,2,3	1,2,3		
1975-76			1,2,3,4	
1976-77			1,2,3,4	1,2
1977-78	1,2	1,2	1,2,3,5	1,2,5
1978-79			1,2,3,4,5,6	1,2,3,5,6
1979-80	7	7	3,5,7	5,7
1980-81			3,5,6	5,6
1981-82	7	7	1 - 7	1 - 7
1982-83				
1983-84	1-4,7	1-4,7		
1984-85			1 - 7	1 - 7
1985-86				
1986-87				
1987-88				
1988-89	1-4,7	1-4,7	1 - 7	1 - 7
1989-90				

1 Benthic invertebrates
2 Benthic detritus
3 Litterfall and lateral movement
4 Leaf breakdown
5 Seston transport
6 Primary production
7 Dissolved organic carbon

Samples taken from Sawmill Branch and Grady Branch will be used to evaluate continuing differences in benthic fauna and detritus quality of allochthonous inputs, quality of detritus as measured by breakdown rates, and DOC concentrations. These same measurements will also be made in Big Hurricane Branch and Hugh White Creek where, in addition, we will measure seston transport and primary production.

6. Methods

All methods will follow those used in previous studies at Coweeta.

a. Benthos and benthic detritus

Benthic sampling on WS 7 and WS 14 (control) will be conducted using (similar to the) 1977-79 methods. This method involves a stratified random design based on four abundant habitat types: Rock Face (moss-covered boulder and granite outcrop), Cobble Riffle, Pebble Riffle, and Sandy Reach (mixed sand and gravel). Sixteen Surber samples (4 of each type) have been collected monthly in Big Hurricane Branch and 12 (3 of each type) in Hugh White Creek. Ancillary measurements made for each sample include dry weight of detritus (wood, twig, and leaf fractions), current velocity, and approximate proportions in each sampled area of inorganic substrate size classes (Boulder, Cobble, Pebble, Gravel, and Sand). These data help us interpret much of the variability normally encountered with Surber samples. In addition, a limited number of debris dam samples will be collected from each watershed.

Benthic samling on WS 6 and WS 18 (control) will be made according to procedures used previously (Haefner 1980). These involve 6 random samples collected monthly from each watershed. Current velocity and approximate proportions in each sampled area of inorganic substrate size class are made as above. These samples are also used for detritus dry weight (wood, twig and leaf fractions).

All benthic sampling has been conducted with a fine meshed (mesh size - 250 um^2) Surber net. Samples are preserved in the field with a 6% formaldehyde solution. In the laboratory each sample is washed through a series of sieves and organic matter decanted from inorganic material. Invertebrates are sorted using a binocular microscope.

We will perform production calculations for selected groups of organisms on each watershed. This will involve additional collections for biomass determination. Production will be calculated using either the Hynes methods as modified by Hamilton (1969) or the removal summation methodology. Similar procedures are being used by Haefner (1980) and Gurtz (1980) for these four watersheds.

b. Litterfall and lateral movement

Litter and lateral movement will be measured each year using 10 litterfall traps located over the stream and 10, 40 cm wide lateral movement traps placed on the stream bank.

c. Leaf breakdown

Rates of leaf breakdown will be measured using 3 mm mesh bags. We will incorporate a control stream (WS 18 or WS 14) for each study. Leaf species will be selected according to vegetation on the watershed at the time of study.

d. Particulate transport

Particulate material in suspension (seston) will be studied using a wet filtration system (Gurtz et al. 1980). Particles are measured in the following size classes: 5.0 mm (C), 5.0-0.864 mm (L), 864-234 um (ML), 234-105 um (S), 105-43 um (F), 43-25 um (VF), and 25-5 um (UF). Samples will be collected on a seasonal basis during both storm and non-storm periods.

e. Primary production

Rates of uptake of ^{14}C will be measured in situ by confining natural substrates within recirculating chambers. Solar radiation, water temperature, and pH will be monitored during each measurement.

f. Dissolved organic carbon

Biweekly DOC samples will be collected from WS 6, WS 7, WS 18 and WS 14 during the years indicated on Table 19. All DOC samples will be filtered through precombusted glass fiber filters, stored frozen in glass, and analyzed on a Dohrmann DC-54 Organic Carbon Analyzer. The precision of this instrument is ± 10 ug C/1 or ± 2%.

7. Reference collections, data storage and retrieval

We have developed a rather extensive collection of stream benthos from Coweeta. These collections have been developed over a 10 yr period and are housed in the Museum, Department of Entomology, at the University of Georgia (James B. Wallace is an Associate Curator). Benthic abundance data is stored on both computer cards and in tabulated form. In addition, for earlier benthic abundance data this information is available in theses and/or published form.

IV. Plan of research

F. Interpretation of process research

Our major research strategy in formulating this program of long-term ecological research at Coweeta remains unchanged from previous and on going studies (Monk et al. 1977, Swank and Waide 1980). That is, our research is largely designed to focus on a series of process-level studies. Our objectives in these process studies are described in detail above, and are related to past accomplishments in over a decade of intensive research on forest ecosystem dynamics at Coweeta.

However, we feel strongly that the main thrust of long-term research such as that proposed here must remain at the level of the ecosystem. Unless conscious and specific efforts are made to integrate details of process-oriented research in the context of ecosystem concepts and hypotheses, such process-oriented studies may become inefficient and disorganized. We have utilized two broad conceptual models - of the ecosystem as a hierarchical system (Monk et al. 1977, Webster 1979, Schiadler et al. 1980, Waide et al. 1980), and of resistance and resilience as two components at an ecosystem's response following disturbance (Webster et al. 1975, Waide and Swank 1976, Monk et al. 1977, Swank and Waide 1980) - to achieve integration among specific process studies. Integration is also achieved by relating process results to the integrated responses of intact watershed ecosystems, measured as net nutrient budgets. Moreover, we have employed both compartment and computer simulation models (Mitchell et al. 1975, Waide and Swank 1976, 1977, Webster and Patten 1979, Swank and Waide 1980) in our work to summarize and to integrate our past research results, as well as to focus on future research initiatives. Thus, both conceptual and simulation models have been useful to us in our continuing program of research in forest ecosystem dynamics. Both types of model serve as evolving hypotheses about the dynamical behavior of forest ecosystems, useful at any instant in time to make specific predictions or interpretations, but also flexible as new data or understandings become available.

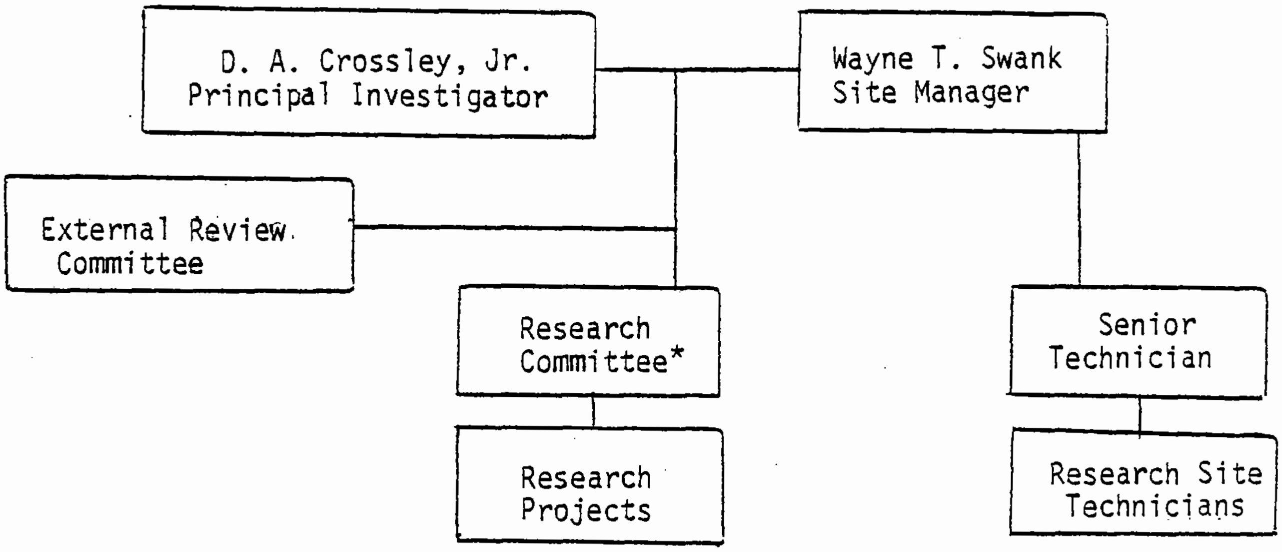
We will thus continue to focus upon process-level research, but always within the context of ecosystem-level objectives. Long-term research results will never be fully appreciated unless interpreted as the integrated response among components of ecosystems. Such a philosophical approach will remain central to our program at Coweeta.

V. Project administration

The long-term ecological research program at Coweeta will be administered through two interacting groups (Figure 9) comprised of an on-site research directorate (the Research Committee) and an external program Review Committee.

The program will receive an annual review by the external committee. The duties of this committee will be (1) to review all aspects of the research project, including data collection, analysis, storage and evaluation, (2) to make recommendations concerning improvements in the development and evaluation of data sets, (3) to advise project management concerning data compatability with other long-term ecological research sites, and (4) to advise project management concerning future directions for research. We propose that the committee membership consist of two representatives from regional institutions, two representatives from other long-term ecological research projects, and one representative from the U.S. Forest Service.

The on-site research directorate (Figure 10) will meet frequently to provide the following functions: (1) to insure that information exchange occurs between site investigators and that data sets become accessible as soon as they are developed, (2) to monitor progress in research projects and provide adjustments needed to attain goals, (3) to evaluate and make recommendations on all new research or other manipulations proposed for watersheds in the site, and (4) to maintain communication and facilitate information exchange with other long-term ecological research sites. In the event of unresolved conflicts on land use, the Southeastern Forest Experiment Station Director will make final decisions. The membership of the on-site research directorate is listed



*Research Committee

D. A. Crossley, Jr. (Chairman)
James E. Douglass, Project Leader, Coweeta Hydrol. Lab., USFS
Bruce Haines
H. L. Ragsdale
Wayne T. Swank
R. L. Todd
J. B. Waide
J. B. Wallace
J. R. Webster

Ex Oficio:
James B. Cooley, Exec. Director, Inst. Ecology, Univ. Georgia
Senior Technician

Figure 9. Organization of project administration.

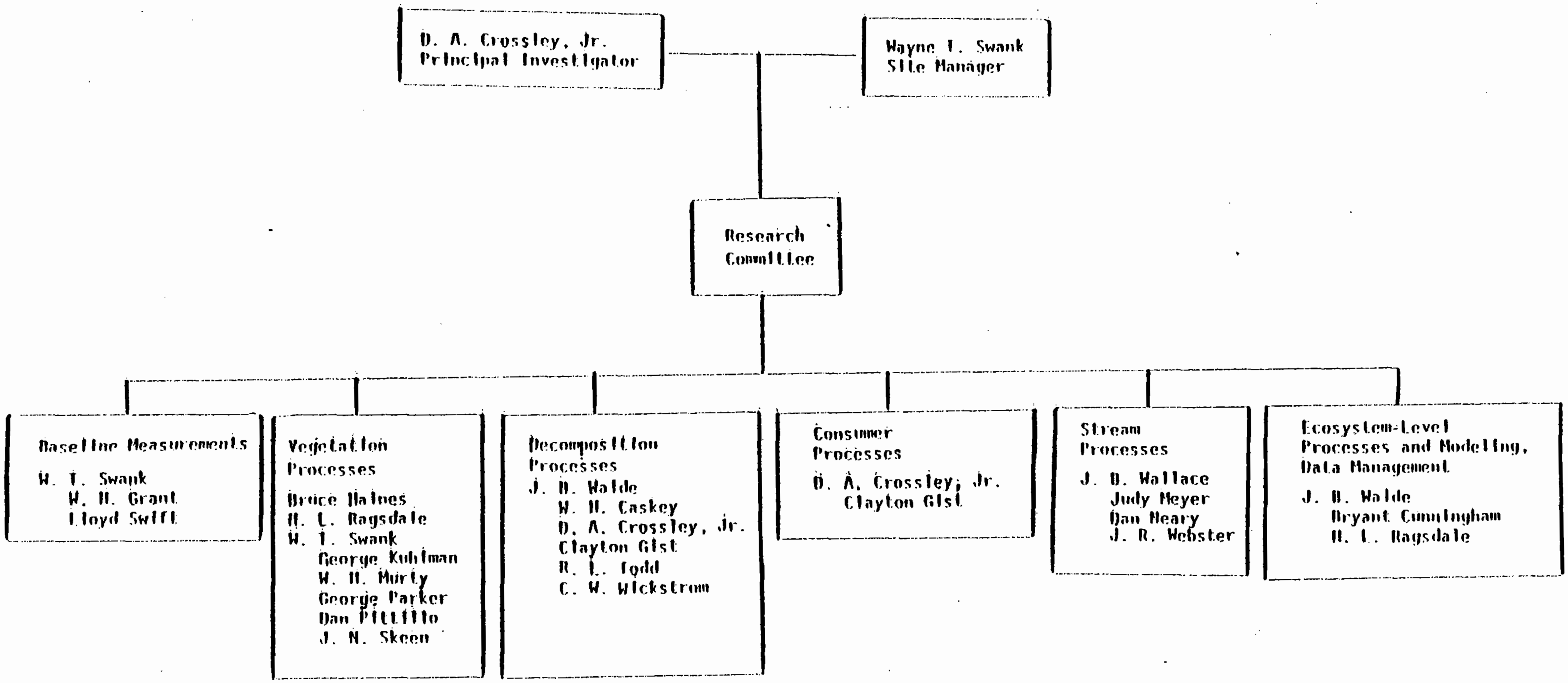


Figure 10. Organization of research responsibilities.

in Figure 10, and encompasses the major components of the proposed research.

Continuity of leadership in this research is assured through the joint participation of scientists at the University of Georgia's Institute of Ecology and U.S. Forest Service scientists at Coweeta Hydrologic Laboratory itself. These two units have cooperated in a continuous research program at Coweeta since 1968. Crossley (Principal Investigator) and Swank (Site Manager) were among the original investigators when work was initiated twelve years ago. Other participants (Gist, Todd, Waide, Wallace and Webster) have been involved with the research for eight years or more. These evidences of long-term commitment, plus the dedication of Georgia's Institute of Ecology and the U.S. Forest Service's Coweeta Laboratory to long-term ecological research, assure the continuity of leadership necessary for such research to be successful.

VI. Literature Cited

Abbott, David T. 1980. Woody litter decomposition at Coweeta hydrologic laboratory, North Carolina. Ph.D. Dissertation, University of Georgia.

Abbott, David T., T. R. Seastedt and D. A. Crossley, Jr. 1980. The abundance, distribution and effects of clear-cutting on Cryptostigmata in the Southern Appalachians. MS.

Alexander, M. 1978. An Introduction to Soil Microbiology, 2nd Ed. Wiley & Sons, New York, N.Y.

Anagnostakis, S. L. 1979. Testing Endothia parasitica strains for vegetative incompatibility. In Proceedings of the American Chestnut Symposium, pp. 101-102. (W. L. MacDonald, F. C. Cech, J. Luchok, and C. Smith, Eds.) West Virginia University Book.

Ausmus, B. S., N. T. Edwards and M. Witkamp. 1976. Microbial immobilization of carbon, nitrogen, phosphorus and potassium: implication for forest ecosystem processes. In: The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. (J. M. Anderson and A. Macfayden, eds.) pp. 397-416. Blackwell Sci. Publ., Oxford.

Ausmus, B. S. and M. Witkamp. 1974. Litter and soil microbial dynamics in a deciduous forest stand. Eastern Deciduous Forest Biome - IBP No. 73-10. Univ. Tennessee, Oak Ridge.

Baes, C. F. and H. L. Ragsdale. 1980. Age specific lead distribution in xylem rings of three tree species in Atlanta, Georgia. (Manuscript submitted to Environmental Pollution).

Beale, Richie H. 1979. Procudures for chemical analyses at the Coweeta Hydrologis Laboratory. Coweeta Publication Files.

Belser, L. W. 1979. Population Ecology of Nitrifying Bacteria. Ann. Ren. Microbiol. 33: 309-333.

Boring, L. 1979. Early forest regeneration and nutrient conservation on a clearcut southern Appalachian watershed. MS thesis, University of Georgia.

Boring, L. R., C. D. Monk and W. T. Swank. 1980. The role of successional species in early forest regeneration. Manuscript.

Bremner, J. M. 1978. Effects of soil processes on the atmospheric concentration of nitrous oxide. In Nitrogen in the Environment. D. R. Nillsen and J. G. MacDonald (eds.), pp. 477-491. Academic Press, New York.

Bremner, J. M. and A. M. Blackmer. 1979. Effects of acetylene and soil water content on emmission of nitrous oxide from soils. Nature 280: 380-381.

Byrne, A. R., V. Ravnik and L. Kosta. 1976. Trace elements concentration in higher fungi. The Science of the Total Environment 6: 65-78.

Chapman, A. G. 1935. The effects of black locust on associated species with special reference to forest trees. Ecol. Mono. 5: 39-60.

Cole, L. C. 1949. The measurement of interspecific association. Ecology 30: 411-424.

Cook, J. C., Mark W. Houseweart, H. M. Kulman and L. C. Thompson. 1978. Foliar mineral differences related to sawfly defoliation of white spruce. Env. Ent. 7: 780-781.

Cornaby, B. W. 1973. Population parameters and systems models of litter fauna in a white pine ecosystem. Ph.D. dissertation, Univ. of Ga. 98 p.

Cornaby, B. W., C. S. Gist and D. A. Crossley, Jr. 1975. Resource partitioning in leaf litter faunas from hardwood and hardwood-converted-to-pine forests. P. 588-597 in F. G. Howell, J. B. Gentry and M. H. Smith (eds.). Mineral Cycling in Southeastern Ecosystems. ERDA, Technical Information Service.

Cornaby, B. W. and J. B. Waide. 1973. Nitrogen fixation in decaying chestnut logs. Plant and Soil 39: 445-448.

Cromack, K. 1973. Litter production and litter decomposition in a mixed hardwood watershed and in a white pine watershed at Coweeta Hydrologic Station, N. C. Ph.D. Dissertation, Univ. of Ga.

Cromack, K. and C. D. Monk. 1975. Litter production, decomposition and nutrient cycling in a miced hardwood watershed and a white pine watershed. In Mineral Cycling in Southeastern Ecosystems, F. G. Howell, J. B. Gentry and M. H. Smith (eds.), ERDA Symp. Series (CONF-740513).

Cromack, K. Jr., R. L. Todd and C. D. Monk. 1975. Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. Soil Biol. Biochem. 7: 265-268.

Crossley, D. A. Jr., Callahan, Gist, J. R. Maudslay, J. B. Waide. 1975. Compartmentalization of arthropod communities in forest canopies at Coweeta. J. Ga. Ent. Soc. 11: 44-49.

Crossley, D. A. Jr. and Clayton S. Gist. 1980. Canopy arthropod biomasses and nutrient element contents in a hardwood forest at Coweeta. MS.

Crossley, D. A. Jr. and M. P. Hoglund. 1962. A litter-bag method for the study of microarthropods inhabiting leaf litter. Ecology 43: 571-574.

Davidson, J. and H. G. Andrewartha. 1948. Annual trends in a natural population of Thrips imaginalis (Thysanoptera). Jour. Anim. Ecol. 17: 193-199.

Daubenmire, R. 1968. Plant communities, a textbook of plant synecology. Harper and Row, New York. 300 pp.

Day, F. 1974. Primary production on nutrient pools in the vegetation on a southern appalachian watershed. Ph.D. dissertation, Univ. of Ga.

Day, Frank P. and C. D. Monk. 1974. Vegetation patterns on a southern Appalachian watershed. Ecol. 55: 1064-1974.

Elliston, J. E. and R. A. Jaynes. 1977. Biological control of chestnut blight - a progress report. 68th Annu. Rept., Northern Nut Growers Assoc., pp. 84-90.

Futuyma, Douglas J. and Fred Gould. 1979. Associations of plants and insects in a deciduous forest. Ecol. Mono. 49: 33-50.

Gist, C. S. 1972. Analysis of mineral pathways in a cryptozoan food web. Ph.D. dissertation, Univ. of GA., Athens.

Gist, C. S. and W. T. Swank. 1974. An optical planimeter for leaf area determination. Am. Midl. Nat. 92(1): 213-217.

Goff, F. G. and P. H. Zedler. 1972. Derivation of species succession vectors. Amer. Midl. Natur. 87: 397-412.

Goff, F. G. and D. West. 1975. Canopy-understory interaction effects on forest population structure. Forest Science. 22: 98-108.

Grente, M. J. 1965. The hypovirulent forms of Endothia parasitica and the hope of fighting against the canker of chestnut. Compte Rend. Hedb. Scances Acad. Agr. France 51: 1033-1037.

Grente, J. and S. Berthelay-Sauret. 1979. Biological control of chestnut blight in France. In Proceeding of the American Chestnut Symposium, pp. 30-34. (W. L. MacDonald, F. C. Cech, J. Luchok, and C. Smith, Eds.) West Virginia University Book.

Gurtz, M. E., J. R. Webster and J. B. Wallace. 1980. Seston dynamics in southern Appalachian streams. Effects of clear-cutting. Can. J. Fish. Aquat. Sci. In press.

Gurtz, M. E. 1980. Distributional ecology of aquatic invertibrates in disturbed and undisturbed southern Appalachian streams. Ph.D. Thesis, Univ. of Ga. In prep.

Guthrie, T. F. and J. M. Duxbury. 1978. Nitrogen mineralization and denitification in organic soils. Soil Sci. Soc. Am. J. 42: 908-912.

Haefner, J. D. 1980. Effects of old field succession on stream insects in the southern Appalachians, and production of two net-spinning caddisflies. M.S. Thesis, Univ. of Ga. In prep.

Hamilton, A. L. 1969. On estimating annual production. Limnol. Oceanogr. 14: 771-82.

Harden, J. W. and A. W. Cooper. 1970. Floristics and vegetation of the gorges in the southern Blue Ridge Escarpment. pp. 291-330. In: P. Hold (ed.) The distributional history of the biota of the southern Appalachians: Part II Flora. Va. Polytechnic Inst. and State Univ. Monogr. No. 2.

Hardy, R. W. R., R. C. Burns and R. D. Holsten. 1973. Applications of the acetylent-ethylene assay for measurement of nitrogen fixation. Soil Biol. Biochem. 5: 47-81.

Harley, J. L. 1971. Fungi in Ecosystems. J. of Ecol. 59: 653-668.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York.

Henderson, G. S., W. T. Swank, J. B. Waide and C. C. Grier. 1978. Nutrient budgets fo Appalachian and Cascade region watersheds: A comparison. For. Sci. 24: 385-397.

Hinneri, S. 1975. Mineral elements of macrofungi in oak-rich forests on Lenholm Island, inner archipelogo of SW Finland. Ann. Bot. Fennici 12: 135-140.

Ike, A. F. and E. L. Stone. 1958. Soil nitrogen accumulation under black locust. Soil Sci. Soc. Amer. Proc. 23: 346-349.

Jaynes, R. A. and J. E. Elliston. 1979. Control of *Endothia parasitica* cankers on American chestnut sprouts with hypovirulent strains. *In* Proceedings of the American Chestnut Symposium, pp. 110-114. (W. L. MacDonald, F. C. Cech, J. Luchok, and C. Smith, Eds.) West Virginia University Book.

Johnson, P. L. and W. T. Swank. 1973. Studies of cation budgets in the Appalachians on four experimental watersheds with contrasting vegetation. Ecol. 54: 70-80.

Kershaw, K. A. 1973. Quantitative and Dynamic Plant Ecology. 2nd ed. American Elsevier Publishing Co., Inc. N.Y. 1-20.

Kitchell, James F., Robert V. O'Neill, David Webb, George W. Gallepp, Steven M. Bartell, Joseph Koonce, and Beverly S. Ausmus. 1979. Consumer regulation of nutrient cycling. BioScience 29: 28-34.

Leak, W. B. 1975. Age distribution in virgin red spruce and northern hardwoods. Ecology. 56: 1451-1454.

Lohm, U. and T. Persson. 1977. Soil organisms as components of ecosystems. Ecol. Bull. no. 25, Swedish Soil Scinece Soc. (Uppsala). 614 p.

Mattson, W. J. (ed.). 1977. The role of arthropods in forest systems. Springer-Verlag (New York, Heidelberg, Berlin). 104 p.

McGinty, D. 1976. Comparative root and soil dynomics on a white pine watershed and in a hardwood forest in the Coweeta basin. Ph.D. dissertation, Univ. of Ga.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59: 465-472.

Mitchell, J. E., J. B. Waide and R. L. Todd. 1975. A preliminary compartment model of the nitrogen cycle in a deciduous forest ecosystem. In Mineral Cycling in Southeastern Ecosystems. F. G. Howell, Jr., J. B. Gentry, and M. H. Smith (eds.). ERDA Symp. series (CONF-740513).

Mittempergher, L. 1979. The present status of chestnut blight in Italy. In Proceedings of the American Chestnut Symposium, pp. 34-37. (W. L. MacDonald, F. C. Cech, J. Luchok, and C.Smith, Eds.) West Virginia University Book.

Monk, C. D., D. A. Crossley, Jr., R. L. Todd, W. T. Swank, J. B. Waide, and J. R. Webster. 1977. An Overview of nutrient cycling research at Coweeta Hydrologic Laboratory. In Watershed Research in North America. D. L. Correll (ed.) Chespeake Bay Center for Environmental Studies, Edgewater, Maryland. p. 35-49.

Muncie, J. G., F. M. Rothwell and W. G. Kessel. 1975. Elemental sulfur accumulation in *Pisolithus* Mycopathologia. 55: 95-96.

Odum, E. P. 1971. Fundamentals of ecology. 3rd ed. Saunders, Philadelphia, Pa. 574 pp.

Oliver, C. D. 1978. The development of northern red oak in mixed stands in central New England. School of Forestry and Environ. Studies, New Haven, Conn.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecol. 44: 322-331.

Olson, J. S. and D. A. Crossley, Jr. 1963. Tracer studies of the breakdown of forest litter. pp. 411-416 in Radioecology, Reihnold (New York).

O'Neill, R. V., W. F. Harris, B. S. Ausmus and D. E. Reichle. 1975. A theoretical basis for ecosystem snaysis with particular reference to element cycling. In Mineral cycling in southeastern ecosystems. F. G. Howell, J. B. Gentry, and M. H. Smith (eds.). ERDA Symposium Series (CONF-740513).

Pancholoy, S. K. and E. L. Rice. 1973. Soil enzymes in relation to old field succession: Amylase, cellulase, invertase, dehydrogenase and urease. Soil Sci. Soc. Amer. Proc. 37: 47-50.

Phillips, E. A. 1959. Methods of Vegetation Study. Holt, Rinehart & Winston. N.Y.

Price, Peter W. 1975. Insect Ecology. Wiley (New York, London, Sidney, Toronto). 514 p.

Ramage, H. 1930. Mushrooms-mineral content. Nature 126-279.

Rasmussen, D. I. 1941. Biotic communities of the Kaibab Plateau, Arizona. Ecol. Monogr. 11: 230-275.

Reynolds, Lee J. 1976. Relative abundance of forest floor collembola as influenced by leaf litter decomposition rate. MS thesis, University of Georgia.

Rolfe, G. L. 1974. Lead distribution in tree rings. Forest Science. 20: 283-286.

Rowe, R., R. Todd and J. Waide. 1977. Microtechnique for Most Probable Number Analysis. Appl. Environ. Microbiol. 33: 675-680.

Schindler, J. E., J. B. Waide, M. C. Waldron, J. J. Hains, S. P. Schreiner, M. L. Freedman, S. L. Benz, D. R. Pettigrew, L. A. Schissel, and P. J. Clarke. 1980. A microcosm approach to the study of biogenchemical systems: 1. Theoretical rationale. In: Giesy, J. P., ed. Microcosms in Ecological Reserach. ERDA Sump. Series (in press).

Schowalter, T. D., J. Warren Webb and D. A. Crossley, Jr. 1980. Nutrient cycling in canopy arthropod communities in clearcut and uncut forest ecosystems. MS.

Seastedt, T. R. 1979. Microarthropod response to clearcutting in the Southern Appalachians: Effects on decomposition and mineralization of litter. Ph.D. dissertation University of Georgia.

Shanks, R. E. 1954. Climates of the Great Smoky Mountains. Ecology 35: 354-361.

Sheppard, J. C. and W. H. Funk. 1975. Trees as environmental sensors monitoring long-term heavy metal contamination of Spokane River, Idaho. Environmental Science & Technology. 9: 638-642.

Shigo, Alex L. 1973. Insect and disease control: forest fertilization relations. p. 117-121 In Forest Fertilization Symposium Proceedings, USDA Forest Service General Technical Report NE-3. 246 p.

Sihanonth, P. and R. L. Todd. 1977. Transfer of nutrients from ectomycorrhizal fungi to plant roots In Soil Organisms as Components of Ecosystems. Ecol. Bull. (Stockholm) 25: 392-397.

Simon, H. A. 1973. The organization of complex systems. In Hierarchy Theory. H. H. Pattee (ed.). Georgia Braziller, New York.

Skinner, M. F. and G. D. Bowen. 1974. The uptake and translocation of phosphate by mycelial strands of pin mycorrhiza. Soil Biol. biochem. 6: 62-8.

Smith, M. S. and J. M. Tiedje. 1979. Phases of denitrification following oxygen depletion in soil. Soil Bio. Biochem. 11: 261-267.

Stark, N. 1973. Nutrient cycling in a Jeffrey pin forest ecosystem. Montana Forest and Conservation Experiment Station Univ. of Montana, Missoula. 389 p.

Stevens, George R. 1976. The Connecticut forest. pp. 21-30 in Perspectives in Forest Entomology. Academic Press (London). 428 p.

Swark, W. T. 1967. The dynamics of changes in water yield on related to white pine plantation development. Coweeta Files. 4.01.

Swank, W. T. 1969. Changes in stream flow associated with hardwood coppice development. Coweeta Files. 4.01.

Swank, W. T. 1969. Succe-sional trends of forest stands following the death of American chestnut. Coweeta Files. 4.01.

Swank, W. T. 1979. Atmospheric contribution to forest nutrient cycling: Some Considerations. Presented at Symposium on Impact of Intensive Harvesting on Forest Nutrient Cycling. Aug. 13-16, 1979, State University of N.Y., Syracuse, N.Y.

Swank, W. T. and J. E. Douglass. 1974. Streamflow greatly reduced by converting deciduous hardwood stands to pine. Science 185: 857-859.

Swank, W. T. and J. E. Douglass. 1975. Nutrient flux in undisturbed and manipulated forest ecosystems in the southern Appalachian Mountains. Proceedings of the Tokyo Symposium on the Hydrological Characteristics of River Basins and the Effects on These Characteristics of Better Water Management: 445-456.

Swank, W. T. and J. E. Douglass. 1977. Nutrient budgets for undisturbed and manipulated hardwood forest ecosystems in the mountains of North Carolina. In Watershed Research in Eastern North America: A workshop to compare results. Vol. 1, p. 343-363. David L. Correll (ed.). Smithson. Inst., Edgewater, Md.

Swank, W. T. and T. D. Helvey. 1970. Reducation of streamflow increases following regrowth of clearcut hardwood forests. IASH-UNESCO-Symposium on the results of research on represenative and experimental basins, Wellington, New Zealand.

Swank, W. T. and F. S. Henderson. 1976. Atmospheric input of some cations and anions to forest ecsystems in North Carolina and Tennessee. Water Resour. Res. 12: 541-546.

Swank, Wayne T. and N. H. Miner. 1968. Conversion of hardwood-covered watersheds to white pine reduces water yield. Water Reserv. Res. 4: 947-954.

Swank, W. T. and J. B. Waide. 1980. Interpretations of nutrient cycling research in a management context: Evaluating potential effects of alternative management strategies on site productivity. In: R. W. Waring, ed. Forests: Fresh Perspectives From Ecosystem Analysis. Oregon State Univ. Press, Corvallis. (in press).

Szopa, P. S., E. A. McGinnes and J. O. Pierce. 1973. Distribution of lead within the xylem of trees exposed to airborne lead compounds. Wood Science. 6: 72-77.

Tiedje, J. M. 1980. Assimulatory and dissinulatory nitrate reduction: Perspectives and methodology for simultanesus measurement of several nitrogen cycle processes. In Terrestrial Nitrogen Cycles: Processes, Ecosystem Strategies, and Management Impacts. Bull. Swed. Ecol. Soc. (in press).

Todd, R. L. and L. J. Biever. 1979. Fungal sporocarp production as a mechanism of nutrient recycling in forest ecosystems. Abst. Amer. Soci. of Microbiology.

Todd, R. L. and L. J. Biever. 1980. Fungal sporocarp production on a mechanism of nutrient recycling in forest exosystems. Manuscript submitted to Science, January 1980.

Todd, R. L., R. D. Meyer and J. B. Waide. 1978. Nitrogen fixation in a southeastern United States deciduous forest. In U. Granhall (ed.) Environmental Role of Nitrogen-Lixing Blue-green Algae and Asymbiotic Bacteria, Ecol. Bull. (Stockholm) Vol. 26: 290-291.

Todd, R. L., J. B. Waide and B. C. Cornaby. 1975. Significance of biological nitrogen fixation and denitrification in a deciduous forest ecosystem in Mineral Cycling in Southeastern Ecosystems. F. G. Howell, J. B. Gentry and M. H. Smith. (eds.). ERDA Symp. Series (CONF-740513) p. 729-735.

Van Alfen, N. K., R. A. Jaynes, S. L. Anagnostakis, and P. R. Day. 1975. Chestnut blight: Biological control by transmissible hypovirulence in Endothia parasitica. Science 189: 890-891.

Waide, J. B., J. E. Schindler, M. C. Waldron, J. J. Hains, S. P. Schreiner, M. L. Freedman, S. L. Benz, D. R. Pettigrew, L. A. Schissel, and P. J. Clarke. 1980. A microcosm approach to the study of biogeochemical systems: 2. Responses of aquatic laboratory microcosms to physical, chemical, and biological perturbations. In: Giesy, J. P., ed. Microcosms in Ecological Research. ERDA Symp. Series (in press).

Waide, J. B. and W. T. Swank. 1975. Nutrient cycling and the stability of ecosystems: Implications for forest management in the Southeastern U.S. Proc. Nat. Amer. Foresters (1975): 404-424.

Waide, J. B. and Swank, W. T. 1976. Nutrient recycling and the stability of ecosystems: Implications for forest management in the Southeastern U.S. In America's renewable resource potential 1975: The turning point. Natl. Conv. Soc, Am. For. Proc. 1975:. 404-424.

Waide, J. B. and Swank, W. T. 1977. Simultion of potential effects of forest utilization on the nitrogen cycle in different southeastern ecosystems. In Watershed Research in Eastern North America: A workshop to compare results. Vol. II, p. 767-789. David L. Correll (ed.). Smithson. Inst., Edtewater, Md.

Walter, H. M., D. R. Keeney and I. R. Fillery. 1979. Inhibition of nitrification hyacetylene. Soil Sci. Soc. Am. J. 43: 195-196.

Ward, N. I., R. R. Brooks and R. D. Reeves. 1974. Effect of lead from motor-vehicle exhausts on trees along a major thoroughfare in Palmerston North, New Zealand. Environmental Pollution. 6: 149-158.

Waters, T. F. and G. W. Crawford. 1973. Annual production of a stream mayfly population: A comparison of metnods. Limnol. Oceanogr. 18: 286-296.

Webster, J. R. 1975. Analysis of potassium and calcium dynamics in stream ecosystems on three southern Appalachian watersheds of contrasting vegetation. Ph.D. dissertation, Univ. of Ga., Athens, Ga. 232 p.

Webster, Jackson R. and Bernard C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecol. Mono. 49: 51-72.

Webster, J. R., J. B. Waide and B. C. Patten. 1975. Nutrient cycling and stability of ecosystems. In Mineral Cycling in Southeastern Ecosystems. F. G. Howell, J. B. Gentry and M. H. Smith, eds. ERDA Sumposium Series (CONF-740513).

West, D. and W. C. Johnson. 1976. The density-diameter distribution as an expression of tolerance. Unpub. ms. ORNL

Whittaker, R. H. 1978. Classification of Plant Communities. Dr. W. Junk Publishers. The Hague, The Netherlands. 1-31.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs. 26: 1-80.

Witkamp, M. and Barzansky B. 1968. Microbial immobilization of 137 Cs in forest litter. Oikos 19: 392-5.

Woodall, W. R., Jr. 1972. Nutrient pathways in small mountain streams. Dissertation, Univ. of Georgia.

Woodall, W. R., Jr. and J. B. Wallace. 1972. The benthic fauna of four small southern Appalachian streams. Am. Mid. Nat. 88: 393-407.

Yount, David J. 1975. Florest-Floor Nutrient Dynamics in Southern Appalachian Hardwood and White Pine Platation Ecosystems. In Mineral Cycling in Southeastern Ecosystems, F. G. Howell, J. B. Gentry and M. H. Smith (eds.). ERDA Symposium Series (CONF-740513). p. 598-608.