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**Long-term Studies of Disturbance and Environmental Heterogeneity as They
Affect Ecological Processes in Landscapes of the Southern Appalachians**

Project Summary

We propose research on the extent and complexity of natural and human-caused disturbances, and how they interact with ecological processes along environmental gradients in the landscape. This work builds upon extensive long-term studies of landscape processes in the southern Appalachians and spans four levels of resolution (plot, watershed, landscape, and region) in the Little Tennessee and the French Broad River basins.

Individual and interacting effects of disturbance and environmental heterogeneity on populations, communities, and ecological processes forms the unifying theme of our proposed LTER research. We will focus our research in three areas: 1) characterization of disturbance and environmental heterogeneity in the southern Appalachians, 2) effects of disturbance and environmental heterogeneity on populations and communities, and 3) effects of disturbance and environmental heterogeneity on biogeochemical cycling and ecosystem processes.

We will build on our extensive understanding of disturbances occurring within the Coweeta basin and continue to characterize environmental heterogeneity, maintaining continuity in our 60+ year record for some variables. As we expand our focus to the southern Appalachians region, we will also consider the historical fire

regime and socio-economic drivers of land use change. The effects of disturbance and environmental heterogeneity on plant and animal populations will be assessed at a range of scales (i.e. plot to region) and we will address key questions on the effects of resource variability on terrestrial and aquatic biodiversity. Using a combination of new studies and continued long-term measurements, we will examine the role of environmental heterogeneity and disturbance in regulating ecosystem pools and processes in streams, riparian zones, and forests. Our research approach utilizes an integrated program of long-term field measurements, experiments, and modeling.

I. RESULTS FROM PRIOR NSF SUPPORT

LTER research at Coweeta focuses on studies along complex environmental gradients to examine response to disturbance in a landscape perspective. We are exploring the causes and consequences of land-use change in the southern Appalachian region and examining ecological processes in three linked components of the landscape: upland forests, riparian zones and streams. These studies are based on our legacy of information about Coweeta, dating back to 1934. Results of the first half century were described in a book (Swank and Crossley 1988), and the following is an overview of our current research results organized under three main themes: A) long-term response to disturbance, B) ecological processes along environmental gradients in forests, canopy gaps, riparian zones, and streams, and C) regional analyses of causes and consequences of land-use change.

I.A. Long-term response to disturbance

I.A.1. Long-term disturbance history

The Coweeta basin has been occupied by humans for over 6000 years, from early Archaic peoples through the Cherokees and early European settlers; the latter two cleared the land for agriculture and stock grazing. Logging in the basin continued through the mid 1920s. Paleoecological analyses indicate 20th century "recovery" forests differ substantially from presettlement forests (Lynch and Clark, in preparation). Whether increased burning from 1450 to 1650 reflects Cherokee activities requires further analysis, but it did not appear to have large impacts on forest composition ([Figure 1](#)). Large changes in composition and increasing charcoal accumulation corresponds with the rise in European agriculture since the 19th century. Declining chestnut coincided with transient increases in maple and longer term increases in elm, hornbeam, hemlock, birch and pine. These taxa all appear to play a greater role in recovery forests than they did in presettlement forests.

I.A.2. Long-term hydrologic and biogeochemical cycling studies

We recently completed a 40-year summary of changes in water yield and timing of streamflow and a 20-year summary of stream chemistry following two hardwood to pine conversions (Swank and Vose 1994). After 10 years, annual streamflow from the pine watersheds was less than expected from mixed hardwoods, and by age 15 water yield reductions were about 20 cm. Annual streamflow reductions frequently

exceeded 25 cm with significant flow reductions in every month. Conversion to pine reduced the frequency of both high and low flows by 33 to 60%. Nutrient budgets showed net accumulations of 1.2 to 4.4 kg ha⁻¹yr⁻¹ for Ca, Mg, K, and Na in pine ecosystems compared to hardwoods. These findings have significant implications for water resource management in the eastern US.

Long-term hydrologic and solute responses to the 1977 commercial clearcut, cable logging experiment showed significant increases (>20 cm) in annual water yield with large increases in streamflow during the low flow months but with only small changes (10%) in storm hydrograph characteristics (Swank 1994). Streamflow returned to pre-treatment levels by year 6. There was minor leaching of soil nutrients as shown by small changes (<3 kg/ha) in solute exports and rapid recovery to baseline stream chemistry. This study significantly altered management practices in the region: within 2 years, a quarter of timber sales on National Forest lands required cable logging.

I.A.3. Long-term atmospheric chemistry effects

Atmospheric chemistry influences forest ecosystem processes and continues as an important research topic at Coweeta. High ozone levels reduced basal area increment, induced premature senescence and loss of foliage, stimulated pine seedling germination, and produced small but measurable increases in NO₃ and K⁺ concentrations in a white pine plantation (Swank and Vose 1990/91). Oxidant (O₃, SO₂, HNO₃) concentrations increase over the elevational gradient, which could have important consequences for forest biogeochemical cycles and for forest growth and health.

I.A.4. Long-term changes in soils

Because soil chemical properties (% C and cation content) directly influence site productivity, we have monitored their changes in reference and managed watersheds over two decades (Knoepp and Swank 1994). On reference watersheds soil C levels remained stable. Changes in exchangeable soil cation content varied with aspect: concentrations decreased in a N-facing slope but were stable on a S-facing slope. The impact of forest management practices varied considerably. Soils in a white pine plantation showed stable C levels, but cations declined. Commercial sawlog harvest resulted in large increases in soil C and cation concentrations, which remained elevated for 17 years. Whole-tree harvest resulted in decreased soil C for the next 14 years. Clearly soil response to harvest varies with type of harvest and site. Long-term studies like these have proven useful in guiding ecosystem management projects in the Southern Appalachians (Meyer and Swank, in press).

I.A.5. Long-term studies of forest succession

We have examined the role of dominant early successional species in forest recovery and identified longer term patterns in composition, diversity, and richness of herbaceous and woody species (Elliott and Swank 1994, Elliott et al., in review). After two successive clearcuts, overstory diversity was highest in the early establishment stage of stand development, then declined at the intermediate stage with canopy closure (Elliott and Swank 1994). On a SW-facing watershed, woody species diversity was relatively stable through succession, although tree species

richness increased (Elliott et al., in review). Ground flora diversity declined through succession.

I.A.6. Vegetation responses to climate

Relationships between annual wood tissue $\delta^{13}\text{C}$, growing season soil water potential and basal area growth were studied in a mature white pine (*Pinus strobus*) stand at Coweeta by extracting wood cores spanning the 1980s (McNulty and Swank 1995). Some of the hottest, driest and wettest years were recorded during this decade. The $\delta^{13}\text{C}$ of annual wood tissue was positively correlated with average growing season soil water potential and average annual basal area growth. Wood tissue $\delta^{13}\text{C}$ appears useful in estimating historic changes in soil water potential and interpreting patterns of basal area growth in mature forests.

I.A.7. Long-term research on streams

We continue to assess long-term recovery of a stream after clearcutting its watershed. Litterfall, leaf decay rates, benthic organic matter, stream geomorphology, nutrient and DOC concentrations, and invertebrate community structure and production have been measured periodically since 1975 (Webster et al. 1992). Benthic invertebrate abundance was 3 times higher and biomass and production were 2 times higher in the disturbed stream even 16 years after disturbance (Stone 1995). The proportion of scrapers decreased and shredders increased over the period. Invertebrate assemblages in the disturbed stream 16 years after clearcutting were similar to those in the reference stream.

Export of coarse particulate organic matter (CPOM) from 3 headwater streams was quantified for nearly a decade (Wallace et al. 1995). Annual CPOM export varied by 9- to 16-fold among years, much greater than the 3- to 5-fold variation in stream discharge. Annual export was poorly correlated with annual discharge but related to storm frequency and magnitude.

Stream geomorphology and biology changed in response to experimental additions of woody debris: depth increased, current velocity decreased, cobble substrate was covered by sand and silt, and benthic FPOM and CPOM standing stock increased (Wallace et al., in press). Solute uptake lengths did not change dramatically, but invertebrate community structure did. We continue to follow changes in geomorphology and invertebrates in this long-term experiment.

I.B. Ecological processes along environmental gradients

I.B.1. Forest disturbance and stress along an environmental gradient

Five intensive research plots have been established along an latitudinal gradient to investigate long-term forest ecosystem responses to stress and disturbance ([Figure 2](#) and [Figure 3](#), and [Table 1](#)).

I.B.1.a. Macro and micro climatic gradients

Large differences exist in macro-climatic regimes: upper elevation plots received 24% more precipitation ([Figure 4](#)), and average annual air temperature was 5°C

lower. Climate was mediated by site factors such as topography, soil water holding capacity, and vegetation characteristics (leaf area index and water use efficiency) that regulate plant water use (see growing season soil moisture, [Figure 4](#)). Hence, at the plot level, micro-climatic gradients did not necessarily follow macro-climatic gradients.

I.B.1.b. Vegetation

Biomass ranges from 150 to 236 Mg ha⁻¹yr⁻¹ with lowest biomass in the xeric oak-pine site and highest in the cove site. Low biomass appears to reflect moisture and nutrient limitations. We have begun to identify the factors limiting recruitment of trees through analysis of seed rain, models of seed dispersal, and seedling demography. Short dispersal distances limit the availability of *Quercus*, *Cornus*, *Carya*, *Fraxinus*, *Pinus rigida*, and *Nyssa*, but not *Acer*, *Liriodendron*, *Tsuga*, or *Betula* (Clark et al., in review). Seed production and dispersal appears much less limiting than are germination success due to seed predators and other factors.

A recently completed vegetation map based on over 400 permanent plots ([Figure 5](#)) combined with continued basin-wide climate modeling will enable us to apply our plot-level data to the larger landscape. Vegetation diversity decreases as elevation increases, but is neutral to changes in landform. Productivity responds to both landform (increasing from ridge to cove) and elevation (increasing from high to low). Species composition changes predictably in response to landform and elevation-mediated environmental variation ([Figure 6](#)). Linear modeling, when combined with digital elevation data, proved as effective as typic diagrams in mapping this variation ([Figure 5](#)), and both were superior to geostatistical techniques (Bolstad et al. in review). Landscape or regional models based on relatively high resolution and often-used DMA data may be significantly undersampling terrain-related variation in vegetation composition.

We identified significant differences in the physiological responses of dominant overstory tree species, including responses to light, temperature, air vapor pressure deficit, and soil moisture. Light-saturated photosynthetic rates (Pnet) ranged over two-fold (Sullivan et al., in press) ([Figure 7](#)), indicating that species composition as determined by environmental gradients can have a considerable effect on forest productivity. Much of the variation in Pnet among species was related to leaf N ($r^2 = 0.6$), which increases with increasing elevation within a species (Griffith 1993). This emphasizes the importance of linking C with nutrient cycles.

Litterfall along the elevational gradient ranged from 2653 to 3823 kg ha⁻¹ yr⁻¹. This variation was not related to elevation, basal area or productivity. Maximum leaf area index (LAI, m²/m²) generally followed litterfall mass patterns and ranged from 3.3 (xeric oak-pine) to 9.0 (low elevation mixed oak), and vertical distribution and light attenuation varied considerably among community types (Vose et al. 1995). The high LAI value reflects the contribution of *Rhododendron maximum* -- a major component of both mixed oak stands.

Root biomass was determined for all plots with root coring, and phenology (growth and turnover) was determined with root observation boxes. Total summer root biomass ranged from 13 to 21 Mg ha⁻¹ with the lowest value on the cove site and highest on the high elevation mixed oak site. Root:shoot ratios generally declined with increasing average annual soil moisture.

I.B.1.c. Canopy herbivory

Herbivory was measured from 3 canopy walkways coincident with the gradient plots. Percent leaf area removed by herbivory decreased significantly as elevation increased (Reynolds 1995, Reynolds and Crossley 1995, [Figure 8](#)). Arthropod guild structure was significantly different for *Acer rubrum* at all sites, but was similar for *Quercus rubra*.

I.B.1.d. Forest floor

Forest floor mass ranged from 9 Mg/ha in the cove site to 33 Mg/ha in the high elevation mixed oak site. Although decomposition rate varied along the gradient, the variation was unrelated to macro-climatic variation (Hoover and Crossley 1995). The lower elevation cove site had the lowest decomposition rate despite the fact that it was warmer and more moist. Microarthropod abundance was generally lowest on the northern hardwood site and highest on the high elevation mixed oak site. Microarthropod diversity is extremely high at Coweeta with over 45 oribatid mite genera and 160 species collected in a 1 m² plot.

I.B.1.e. Soils

Soils were analyzed for most cations and anions. Variation in extractable Ca is large (29 mg/kg to 441 mg/kg); soil C ranges from 3.33 to 9.87% ; soil N ranges from 0.09 to 0.7%; and soil C:N ratios ranges from 39 to 14. Soil pH is less variable and ranges from 3.9 to 4.2. Soil N cycling processes (especially N mineralization) varied greatly among years and plots. Most notably, the northern hardwood site had extremely high N mineralization rates. In a dry year (1993), N mineralization rates decreased substantially. Soil S cycling analyses show greater S immobilization in the northern hardwood site (Stanko-Golden et al. 1992).

I.B.1.f. Mammals

We are determining patterns of distribution, diversity, and abundance of small mammals along altitudinal and vegetational gradients at Coweeta using traps (Laerm et al., in press). *Soricid* (shrew) abundance is correlated with coarse woody debris, soil type, and past watershed disturbance. Two rare shrew species (*Sorex palustris* and *S. dispar*) occur at Coweeta.

I.B.1.g. Synthesis

Macroscale climatic data indicate a strong gradient in precipitation and temperature among the plots, with high elevation plots receiving more precipitation and experiencing lower air temperatures. Topography, soils, and vegetation mediate these macro-climatic factors such that plot-level micro-climatic gradients differ from macro-climatic gradients. Watershed-scale nutrient budgets and plot-level responses do not necessarily agree: e.g., at the watershed scale, N budgets indicate very similar N fluxes on high versus low elevation watersheds; however, N mineralization rates are much greater at high elevation northern hardwoods site, but this elevated N availability is not being stored in the vegetation. It appears that at the watershed scale, plot-level responses are being dampened by subsurface processes occurring in other vegetation types on the watershed ([Figure 5](#)).

I.B.2. Succession in canopy gaps

In the southern Appalachians, formation of small (<300 m²) canopy gaps is the primary mechanism by which forest structure, composition, and diversity are maintained. A recent region-wide severe drought led to overstory tree mortality and provided an opportunity to characterize canopy gap formation (Clinton et al. 1993) and to monitor long-term successional dynamics within permanent canopy gap plots (Clinton et al. 1994). In addition, we have experimentally created canopy gaps with and without evergreen understory at both high and low elevations ([Figure 2](#)) by girdling trees after gathering 2 years of pre-treatment data. Changes in microclimate following overstory mortality have been characterized using automated instrumentation (Clinton 1995) and combined with results from seed predator exclusion fences to form the basis for understanding seedling recruitment and success.

I.B.3. Riparian zone

I.B.3.a. Long-term changes in evergreen understory

Over a 17-year period (1976-93) area of rhododendron increased by nearly 15% (66 ha) (Dobbs 1995). Evergreen understory distribution shows little relation to elevation, slope or soils, but is correlated with aspect, distance from stream, and precipitation.

I.B.3.b. Experimental rhododendron removal

Rhododendron is the dominant understory species in riparian zones. To test the hypothesis that rhododendron alters patterns of organic C and nutrient flux, we experimentally removed near-stream rhododendron in August 1995 after collecting 2.5 years of baseline data ([Figure 15](#)). Transects on both a treatment and a reference slope were instrumented with tension lysimeters, TDR (time domain reflectometry) sites ([Figure 2](#)), and piezometer transects (near the stream). Concentrations of nutrients and DOC were measured in lysimeters, piezometers, and streamwater. A hillslope water flux model has been parameterized and calibrated using water levels in near-stream saturated zones, soil moisture from TDR transects, streamflow, and topographic and soil distribution data (Yeakley et al. 1994).

No significant differences have been observed in processing of precipitation-borne sulfate in riparian soils with vs. without rhododendron. Added sulfate was largely immobilized by physicochemical adsorption, although longer term storage was as organic S. During most seasons, ester sulfate was the major organic form synthesized, but immediately after leaf fall, sulfonate-S formation dominated as a consequence of increased fungal activity.

We are also monitoring soil microbial communities on reference and treatment hillslopes. In both areas microbial biomass peaked in December and in April prior to experimental removal (Maxwell and Coleman 1995). Omnivore-predator populations of nematodes were maximal in December and June and were positively correlated with microbial biomass N.

I.B.4. Streams

Our stream studies are designed to determine the longitudinal patterns of key ecosystem processes as they are controlled by longitudinal changes in geomorphology and habitat patch frequency. We have sampled at 4 locations along Ball Creek selected to represent different stream sizes and geomorphic types ([Figure 2](#)), and for some components have extended our sampling well beyond the Coweeta Basin to the Little Tennessee River and Fontana Lake, a 60 km gradient. The sites in Ball Creek differ strikingly in physical parameters such as stream discharge (29X variation), size of transient storage zones (28X) (D'Angelo et al. 1993), and standing stock of woody debris (12X). There is less variation in litter input (1.3X), gross primary production (3X), and fish production (4X). Other ecological processes (invertebrate production, leaf decay rate, benthic respiration) vary less than 1.5X. Hence, as observed along the environmental gradient in Coweeta forests (above), the physical template appears more variable than ecological functions. In contrast, biological communities change along the gradient. Greatest faunal replacement occurred in mid-order reaches, and biomass- and production-based analyses indicated large changes in functional groups along the gradient as well as among different habitats (Grubaugh et al., in press). These changes followed patterns predicted by the River Continuum Concept.

We have also investigated the ability of indices of benthic community structure (North Carolina Biotic Index and EPT Index) to track changes in ecosystem level processes after experimental alteration of a stream invertebrate community (Wallace et al., in press). Indices tracked the disturbance regime throughout the 6-year experiment, while indices for the reference stream showed little variation. Our results demonstrate the potential of such indices to detect and monitor stream ecosystem changes during and following disturbance.

I.C. Regional analyses of causes and consequences of land-use change

Our goal is to develop a predictive understanding of the social, economic and environmental factors that drive land cover change in the Southern Appalachians and the ecological consequences of those changes for regional C cycles and for terrestrial and aquatic biodiversity. We began this research in November 1994 funded by an LTER augmentation grant. We have focused our attention on two watersheds ([Figure 8](#)), Little Tennessee (LT) and French Broad (FB) Rivers, because these offer a contrast in the pattern of land-use change. LT retains large areas of forested land, while FB has a longer history of forest fragmentation. We are using aerial photographs to analyze changes in land-use in this region over the past 5 decades and have documented significant differential disturbance related to landform and topographic position. Prior to the mid- 1950s permanent vegetation alteration was concentrated in low-elevation coves and flats and near urban areas. Current disturbance is much more likely at mid-to higher-elevation steeper sites, and farther from urban centers.

The socioeconomic component seeks to determine and model social and economic drivers of land-use change building on research already completed in the LT basin (Turner et al., in press). We selected 5 counties in the FB basin for intensive study ([Figure 8](#)) and have randomly located 100 sample blocks in which to estimate the impact of social/economic conditions on land-use. We are determining the accessibility of blocks to road systems and markets, land values for differing land-

uses, and ownership. Information on production markets, transportation systems, second home development, and site productivity will serve as variables in models of land-use change.

I.C.1. Impacts of land-use change on regional C cycles

We are establishing sites in 3 regions of the southern Appalachians (LT, FB and southwestern Virginia). Sites are in early successional forest (<30 yr), mature forest (80-150 yr), old-growth forest (>150 yr), and pasture ([Figure 9](#)). In forested sites, plots are located in cove, slope, and ridge positions. At each site we are quantifying C pools (soil, forest floor, and plant), measuring flux rates, and will develop net ecosystem C budgets. We will determine the impacts of land-use change on C budgets by combining our small scale measurements with landscape-level C budget modeling.

Large differences exist in woody biomass pools among land-use types: e.g., woody biomass in the old growth forest is 2- to 8-fold greater than early and mid-successional sites. Variation across topographic positions is also evident, although of lesser magnitude than across land-use types. There are also large differences in the distribution of biomass among species across topographic positions. If there are large differences in respiration rate among species, then species distribution could directly influence C balance among and within land-use types. Hence we are measuring tree stem CO₂ flux attributable to both growth and maintenance respiration. Soil CO₂ flux measurements were greatest in June when soils were warmest and lowest in early spring and late fall when soils were coolest ([Figure 10](#)). There appear to be large differences in C cycling among land-use types. The roles of litter and soil temperature, soil moisture, fine and coarse root mass, root and soil N and C, and litter mass N and C that regulate these differences are currently being analyzed.

I.C.2. Impacts of land-use change on terrestrial and aquatic biodiversity

We have sampled vascular plant and bird diversity at 22 sites ([Figure 11](#)) in a study of the effects of forest fragmentation in the FB and LT basins. Bird diversity declined with forest patch size; however, patch size had no effect on plant species richness, although it did affect community composition. Smaller patches have a greater proportion of edge species and a smaller proportion of forest-interior species, although small patches still harbor some forest interior species ([Figure 11](#)). A spatially explicit model has been written to simulate population dynamics in landscapes with different fragmentation patterns and is being used to explore interactions between life-history strategies and landscape pattern.

We are examining the effects of different land cover types on fish and aquatic invertebrate diversity and abundance and stream geomorphology in a series of 24 small vs. large streams draining either agricultural or forested watersheds in the FB and LT basins ([Figure 12](#)). In the LT, agricultural watersheds have higher fish diversities and densities regardless of stream size ([Figure 12](#)). Agricultural sites are dominated by drift-feeding fishes, whereas a greater diversity of foraging types are represented in forested streams. Trout are found only in forested streams, and sites with large numbers of trout have low diversities and densities of other species. Adverse impacts of sediments on species composition are more apparent in FB than LT sites. Invertebrate density in the LT does not differ significantly among land-use

types or stream size, although larger pasture streams appear to have fewer taxa. There are no significant differences in diversity indices, but there are fewer sensitive species (e.g. Plecoptera) in pasture streams.

I.D. Synopsis

During the current funding period we have melded long-term aspects of previously established LTER research with newly-initiated studies on ecological processes along environmental gradients and expanded our efforts to a regional scale. Scientific dividends have been substantial from our long established (20-60 years) studies, and new insights are emerging when these studies are coupled with the recently initiated research. It is clear that to understand ecological responses to disturbance in the southern Appalachians, one must consider gradients of both natural and anthropogenic disturbances as they are superimposed on gradients of environmental factors. This is the theme of our proposed research.

II. PROPOSED NEW RESEARCH

9; II.A. Overall theme of the research

The southern Appalachians are characterized by steep environmental gradients which exert a profound influence on both terrestrial and aquatic ecosystems. For example, variation in elevation, topography, and aspect result in large differences in environmental conditions, and hence forest community composition over relatively short distances ([Figure 13](#)). Superimposed on these naturally occurring gradients is a complex and often subtle pattern of current (i.e. decades to centuries) and historic (i.e. centuries to millennia) disturbances. Individual and combined effects of disturbance and environmental heterogeneity on populations and ecological processes forms the unifying foundation for our proposed six-year LTER renewal. Quantifying the relative impacts of these influences for particular processes is crucial for understanding the complex forces shaping southern Appalachians ecosystems.

Our proposal includes: (1) continued study of ecological processes within the Coweeta basin, and (2) continued expansion of the scope of our research to the southern Appalachian region. Our approach will be to assess the response of population and community dynamics and ecological processes (i.e. biogeochemical cycling and ecosystem function) to environmental heterogeneity and disturbance at several spatial scales: in plots, in watersheds, in landscapes (Coweeta basin), and in the southern Appalachian region ([Figure 14](#)). This will be accomplished through an integrated program of long-term measurements, short- and long-term experiments, and modeling. We address three major research areas.

II.A.1. Characterizing disturbance and environmental heterogeneity in the southern Appalachians

Building on our extensive understanding of disturbances occurring within the Coweeta basin, we will continue to characterize temporal and spatial variation in environmental condition from the plot to the region, retaining continuity in measurements that extend over a 60+ year record for some variables. In addition, we will continue to quantify the effects of natural (e.g. drought, insects, hurricanes) and anthropogenic disturbance (e.g. clearcutting, acidic deposition) on populations and ecosystems. As we expand the temporal and spatial focus of our research, we

will consider the historical fire regime and the socioeconomic drivers of land-use change.

II.A.2. Effects of disturbance and environmental heterogeneity on populations and communities

We seek to understand how plant and animal populations respond to biotic and abiotic variation at spatial scales ranging from the plot to the landscape, how the biota may generate heterogeneity that is ecologically significant and how human disturbance alters those patterns. We address key questions of current interest in ecology by exploring the effects of resource variability on herbivores, and effects of within-habitat heterogeneity on stream fishes, terrestrial animal communities, and tree seedling dynamics. We examine the consequences of land-use change to terrestrial and aquatic communities in the region.

II.A.3. Effects of disturbance and environmental heterogeneity on biogeochemical cycling and ecosystem processes

Understanding biogeochemical cycles and ecosystem processes in both terrestrial and aquatic ecosystems has been a key element of Coweeta's LTER and related research activities. In the most recent grant period, we investigated the role of environmental heterogeneity, disturbance/stress, and their interaction in regulating ecosystem pools and processes in streams, riparian zones, and forests. The research proposed here includes continuation of measurements of select topics initiated in previous LTER grants and new research which builds on past studies. We propose to use a combination of continued long-term measurements on established plots, initiate new experiments, and use modeling to scale from the plot to the region.

The following sections provide elaboration of the research areas described above, list questions and hypotheses to be addressed, and provide research plans for answering questions and testing hypotheses.

II.B. Characterizing disturbance and environmental heterogeneity in the southern Appalachians

Disturbance is the major factor influencing species composition, diversity, biomass, and productivity of southern Appalachian ecosystems. Disturbance intensity and impacts vary at a range of spatial and temporal scales. Primary natural disturbances in the southern Appalachians are fire, drought (Clinton et al. 1993), floods, hurricanes (Douglass and Hoover 1988), icestorms (Whitney and Johnson 1984), pathogens, and insects (Schowalter and Crossley 1988). On a longer time scale, debris avalanches and landslides are the major natural disturbances influencing land forming processes in the area (Grant 1988, Velbel 1988). Ecosystems often respond strongly to these disturbances. For example, amphibian survival, species richness, and abundance may be reduced in gaps (Petranka et al. 1993). Vegetation and vertebrate assemblages may change depending on disturbance intensity, forest age, and structure (Shugart 1984); and seston and biotic characteristics are influenced by changes in near-stream forests (Webster et al. 1988, 1992).

In combination with these natural disturbances, southern Appalachian ecosystems have been substantially influenced by humans for at least the last 6,000 years. On a regional basis, humans have permanently changed the landscape from a few to over

fifty percent of the area. Human activities have also altered the atmospheric environment (i.e. acidic deposition and ozone) which has affected both aquatic and terrestrial ecosystems (Swank and Waide 1988, Swank and Vose 1988). Fire exclusion, the extirpation of large predators, the introduction of non-native species, and direct and indirect manipulations to increase and maintain high populations of game species such as deer, grouse, turkey and trout, have further changed these ecosystems.

Superimposed on these disturbed landscapes, are strong environmental gradients which occur in response to variation in elevation, topography, aspect, and soils. For example, at Coweeta, mean annual temperature decreases by almost 5 °C from lower to higher elevations, while precipitation increases by 30 percent (Swift et al. 1988). These gradients lead to a partitioning of forest communities along topographic and elevational gradients ([Figure 13](#)). Biota also respond to medium and smaller-scale topographic variation, with species composition changing from ridge to sideslope to coves (Day et al. 1988), or along and within stream order gradients (Grubaugh 1994). At even finer scales, microsite variation in nutrient and water availability can greatly influence microflora and fauna. Temporal variation can also be substantial. For example, in the mid-1980's Coweeta experienced a record drought (Swift et al. 1988) which resulted in substantial mortality of canopy trees (Clinton et al. 1993, Smith 1991). Taken together, spatial and temporal variation in environmental driving variables creates a complex mosaic. Environmental heterogeneity interacts with disturbance through space and time. Some sites, because of their position along environmental gradients, are more prone to certain disturbances (i.e. ice damage occurs more frequently at cooler and higher elevations, windthrow is more likely on exposed slopes, drought mortality is more frequent on ridge sites and on coarse textured soils, and fires are more likely on dry, warm, low-elevation southern exposures). Disturbances also often have a direct effect on environmental heterogeneity by altering microclimatic conditions. For example in gaps created by overstory mortality, light increases in the forest floor. Some disturbances alter future probabilities of subsequent disturbances at the same or adjacent site. For example, intense fire reduces fuel loads and standing biomass, thereby decreasing fire likelihood for > 30 years. Fire probability will decrease not only on the burned site, but also for adjacent stands because recently burned stands serve as partial firebreaks for up to several decades.

To understand how this variation effects populations and ecosystem processes, we will continue to use a combination of long-term measurements, experiments, and modeling to characterize temporal and spatial variation in environmental conditions and interactions with disturbance from the plot to the region ([Figure 14](#)). As we continue to expand our research effort to the entire southern Appalachian region, we must also understand causes and consequences of historic and contemporary landscape change. At this scale, we hypothesize that land use is more important than environmental heterogeneity in influencing populations and processes. We will study factors influencing landscape change in the southern Appalachians at two temporal scales. At the scale of centuries to millennia, dramatic changes in species composition occurred in the region in response to changes in climate and, we hypothesize, in the regional fire regime. At the scale of decades during the last 50 years, landscape change reflects the effects of intensive human land-use, ranging from forest regeneration after widespread clearcutting early in this century to the recent changes in settlement patterns due to a decrease in agriculture and an increase in vacation/retirement home development. The ecological implications of this land-use change will be addressed in Sections IIC-D.

II.B.1. Historical fire regimes (Clark)

Fire may have long been an important control on vegetation composition, structure, and ecosystem function (e.g. C storage) in southeastern forests (Garren 1943, Quarterman and Keever 1963, Komarek 1968, Abrams 1992). Fire suppression is believed responsible for large changes in forest composition in the southern Appalachians (Abrams et al. 1995), including the expansion of *Rhododendron* that appears to have affected tree recruitment patterns (refer to II.C.2.c.). Unfortunately, we have little more than anecdotal evidence of pre-Contact fire importance (e.g. Pyne 1982, Silver 1990), because fire scars on trees (Harmon 1982, Harmon et al. 1983) have limited extent. It is thus impossible to assess how recent fire differs from that of the past and how sensitive fire regimes may be to climate variability, another focus of this proposal. We propose to build on analyses completed under initial support from the Augmentation grant to examine temporal and geographic variability in fire importance, from relatively low intensity cultural influences of pre-Cherokee times to the present. Analysis of sediment charcoal will contrast fire importances of cultural settings outlined below, and it will determine temporal and geographic variability for pre-Cherokee times. We will use pollen analysis to compare composition of 20th century "recovery" forests with presettlement forests. Together, fossil pollen and charcoal will be used to assess how representative are estimates of land use changes analyzed by (II.B.2.) and (II.B.3.), how changing fire importances may have affected C cycles analyzed in (II.D.3.a.), and how these recent influences depart from pre-Contact forests.

The paleo component of our proposal is motivated by recognition that modern vegetation dynamics and ecosystem function in our region play out against a backdrop of frequent and intense change. The southern Appalachians have been subjected to broad scale climate changes since the Pleistocene (Watts 1970, 1980, Delcourt and Delcourt 1984a, 1984b, Kneller and Peteet 1994). The long history of cultural exploitation includes low impact agriculture of DeSoto's time. By Contact, Cherokee had penetrated and rapidly expanded to become one the largest and most important North American tribes with a capital town situated just north of Coweeta at the mouth of the Little Tennessee (Rights 1991). Eighteenth century accounts describe the Little Tennessee Valley and surrounding areas as highly impacted by agriculture (Bartram 1792) and autumn burning for game (Rights 1991). Regional upheaval of the 18th and early 19th centuries were followed by increasingly intense agriculture, employing methods borrowed from Europeans. Census data and descriptions indicate broad-based agriculture shortly before Cherokee removal in 1838 (Swanton 1979). Subsistence agriculture, mostly by Europeans, and then logging was followed by 20th century forest recovery, the "wooded setting home market" (see II.B.3) and fire suppression.

Climate- (Clark et al. 1996) and human- (Clark and Royall 1995b, 1996) induced changes in fire importance can be traced with stratigraphic data and used to establish geographic patterns of past burning ([Figure 1](#)) and to show patterns of C release to the atmosphere (Clark and Royall 1994, 1995b, Clark 1996, Clark et al., in review). We have recently developed a semi-automated method of macroscopic particle characterization using image analysis that improves our estimates of mass fluxes of particles from the atmosphere (Clark and Hussey 1996). We developed and applied the method under our Augmentation award, demonstrating that good records of vegetation and climate change exist in the many peatlands scattered throughout our study region (e.g. [Figure 1](#)) (Lynch and Clark, in preparation). We propose to

expand our analysis to twelve peatlands in the southern Appalachians, where we will concentrate pollen and charcoal analyses on the last several millennia. Coring, pollen, charcoal, and ^{14}C analysis is underway. The limited budget requested for regional paleo analysis in this proposal will be supplemented by funds from Clark's Principal Young Investigator award. That award will provide ^{210}Pb dating of sediment cores and supplement pollen and charcoal analysis we propose for new cores here.

II.B.2. Human-caused landcover change during the last half-century (Bolstad)

Humans have become the single largest disturbance agent in most landscapes, altering more vegetation and moving more soil than natural biotic and physical processes combined. The primary direct human disturbances in the southern Appalachians are forest harvesting for wood products and land conversion to agricultural or urban/suburban landuses. We hypothesize that the frequency, intensity, and extent of these two types of disturbance have changed over the last 50 years, due to both physical/biotic conditions and to policies, politics, and laws established during this time period. Furthermore, impacts of these changes in land-use cascade through both terrestrial and aquatic ecosystems in the southern Appalachians. Land-use change data are crucial for developing and validating socio-economic models of factors causing land-use change (II.B.3) but also provide key sampling frames and data for other initiatives in this proposal, including research on carbon, nutrient, and water cycles (II.D.3), terrestrial ecosystem fragmentation and biotic diversity (II.C.1), and aquatic ecosystem response to disturbance (II.C.2). We have three objectives in this research: (1) obtain decadal time series of detailed land-use/landcover data from the 1940s until present, which include classes for forest (young and old), agriculture, old fields, and urban/suburban areas, (2) digitize time series and overlay to identify the range of land conversion/land-use characteristic size, location, and configuration, and to estimate conversion frequencies, and (3) identify land-use trajectories and identify key sampling frames for related studies within this proposal. We will use a combination of historical and current aerial photographs and satellite imagery to map landcover/land-use changes over the last 50 years. Photointerpretations of archival photographs for study areas will be digitized, registered to a standard coordinate system, and combined with terrain, soils, climate, and other environmental, infrastructure, and socio-economic data in a GIS. Time-series overlays will be used to calculate transition matrices and probabilities, and allow statistical characterization and modeling of land-use transitions, causes, and impacts.

II.B.3. Socio-economic drivers of land-use change (Arthaud, Wear, and Newman)

Historic and current land and resource uses are among the most direct and the most important forces affecting the composition and productivity of southern Appalachian ecosystems. Land uses are determined by both broad scale factors such as market prices for timber and agricultural products and local factors such as the topography, soil type, and location of a site. All of these factors are the basic inputs to landowners' decision making, through which they interact to define land use and vegetative patterns that vary over both space and time (Wear and Flamm 1993, Turner et al., in press). Understanding how these human decisions define landscape structure is essential for (1) identifying ecosystem risks and (2) defining strategies for achieving ecosystem level goals (Wear et al., in press).

Our current work focuses on explaining patterns of land use in the southern Appalachians using classical land use models, i.e. von Thunen-type land allocation models (Hall 1966, Samuelson 1983; this will be extended to explicitly address spatial factors. This work addresses the modern era of land-use dating to the 1940s and compares land use patterns across time periods. We propose to extend this work to:

II.B.3.a. Test how land use options at one point in time are influenced by the history of human endeavors at a site

We hypothesize that certain land uses may constrain options available in the future; e.g. an agricultural practice may result in a short-run depreciation of "natural capital" that may or may not be restored over time. Tests will be constructed by extending static land-use choice models to a dynamic framework that addresses the history of land uses at individual sites. We will model the probability of a land-use change as a function of several variables that define the time a site has been dedicated to its current use and previous uses, as well as its locational and market attributes. Models will be estimated using limited dependent variable approaches (e.g. multinomial logit, see Maddala 1983) and hypothesis tests will be completed using standard chi-squared tests for full and constrained models. Historical data will be developed from intensive sampling at "legacy" sites, i.e., ones which have been identified for intensive analyses of human use over the past century. These sites will also be used to study the effects of land-use history on terrestrial biodiversity (II.C.1).

II.B.3.b. Test for recent structural changes in patterns of land-use related to increased recreational and aesthetic values and the relative importance of market and nonmarket factors in land-use choice

Previous work indicates significant changes in patterns of choices for "wooded setting" home locations that are not entirely explained by topography and location relative to market and service centers (Turner et al., in press). We posit that these changes may also be related to proximity of parcels to aesthetic resources, e.g. mountain views, and to public lands and that these factors may be increasingly important for determining where future development will occur in the region. Hypothesis tests will require expanding logit models of land use states to incorporate these variables. Estimates of marginal effects coefficients will provide a means of comparing the relative effects of market (central place) proximity and aesthetic attributes. We will focus this analysis on the Little Tennessee and French Broad River Basin sites defined through the augmentation research.

II.B.3.c. Develop predictive models to forecast the likely location of future land-use changes

By focusing attention on that portion of the landscape that is most likely to change due to, for example, their proximity to markets as well as to aesthetic resources, we may be able to define where landscape conditions may become limiting for providing essential habitats and environmental services. We will apply land-use state models developed under objective 2) to parcels described in the regional GIS to estimate the probability of a change to a different land use. Probabilities of change will then be mapped.

The goal of all the projects described above is to link historic land uses in the southern Appalachians to current day terrestrial and aquatic diversity. In addition, predictive models of future land use change will be linked with both population and C cycling studies/models to predict the potential effects of future land use change on biodiversity and C storage, respectively (Sections II.C and II.D).

II.C. Effects of disturbance and environmental heterogeneity on populations and communities

This part of the research focuses on four key issues: 1) the effects of disturbance, specifically land use change, on terrestrial and aquatic diversity, 2) the effects of environmental heterogeneity (biotic and abiotic) on the population ecology of animal and plant species, 3) the potential for heterogeneous animal and plant populations to generate further environmental variability of ecological significance, and 4) the effects of human disturbance superimposed on environmental heterogeneity at landscape scales. We attempt to link these issues with ecosystem processes at watershed and regional scales (II.D).

The re-emergence of metapopulation dynamics, the development of spatially-explicit population models, and the importance of spatial distributions for conservation ecology are key issues in the ecological literature (Pulliam 1988, Stewart-Oaten and Murdoch 1990, Gilpin and Hanski 1991, Doak and Mills 1994). At the regional scale (II.C.1 and II.C.2), we focus on how human land use affects diversity of terrestrial and aquatic communities and we propose to develop predictive models of potential future changes. For studies of environmental heterogeneity we focus on the Coweeta basin because: a) it has a well-defined elevation gradient with established gradient sampling plots; b) there are a series of nested watersheds that vary in elevation and aspect; c) histories of recent natural and anthropogenic disturbances are well documented; and d) a large data base exists that includes distributions and abundances of many key organisms.

The following proposed studies are linked by the common goal of understanding the causes and consequences of disturbance and environmental heterogeneity for the population and community ecology of animals and plants in both terrestrial and aquatic ecosystems. These studies incorporate spatial variation in factors as diverse as soil moisture, foliage chemistry, forest community composition, and stream substratum disturbance. They further measure the responses to disturbance and environmental heterogeneity in organisms as diverse as small mammals, fish, birds, insect herbivores, oribatid mites, vegetation, and stream invertebrates. There are fundamental questions in common to all of these projects, and together they address the overall importance of a spatially-complex environment for the population and community ecology of species in general, within the overriding theme of natural and anthropogenic disturbance.

II.C.1. Disturbance history, land-use, and impacts on biodiversity at various spatial scales

(Bolstad, Pearson, and Turner)

The importance of human land-use for explaining the patterns of biotic diversity observed in today's landscapes has been recognized recently (e.g. Glitzenstein et al. 1990, Foster 1992, Turner et al., in press). The field studies we initiated in 1995 with the augmentation funding focused on one effect of human land-use activities: the fragmentation of native habitats into smaller patches, on vascular plants and breeding birds in mesic cove forests. Two other factors are likely to explain substantial variability in the plant and animal communities. First, even within small forest fragments, the natural sources of environmental heterogeneity are important. Second, the past use(s) of the forest (e.g. logging, agriculture, pasture) or the occurrence of natural disturbances appear to have a strong influence on both biotic and abiotic components of the environment at a variety of spatial scales. We will continue our studies of the effects of land-use on the native biota, expand our work to other taxa (arthropods, mammals and salamanders, in conjunction with Laerm and Crossley) and explore the mechanisms underlying the effects of habitat fragmentation and land-use on the plant communities. Using a combination of field and modeling studies, we will investigate interaction between life-history strategies and habitat fragmentation that affect species diversity and abundances.

Our study addresses four questions: 1) How does the legacy of land-use affect community composition in forest patches? 2) Do land-use practices change the spatial scale of heterogeneity of the biota within forest patches as compared to undisturbed forest patches? 3) In forest fragments, how do within- and between-patch heterogeneity interact with species life-history traits to determine presence and abundance of forest herbs? and 4) How does species abundance and diversity vary in naturally occurring patches in relatively undisturbed portions of the forest landscape? Coweeta offers unique opportunities to address these questions because of the detailed (and growing) knowledge of disturbance history at the site. Previous land-use data from both within and beyond the Coweeta drainage basin (logging, farming, etc.) will be used as a template on which to superimpose current plant assemblages, to compare the variance in assemblages within and among disturbance categories, and as the basis for predicting how environmental perturbation influences recruitment and mortality processes.

During the coming six years, we will establish study areas within 10 forest patches of similar size in which the land-use history can be determined back to the late 1800's (legacy sites). Five sites will have remained in a forested state since the late 1800's (although they may have been grazed or selectively logged) and five sites will have been previously cultivated but have returned to forest. Land-use and disturbance history back to the 1930's will be obtained by analysis of historic aerial photographs. County records (e.g. family histories, tax records, deed descriptions) will be used to extend the history back as far as possible. Vascular plants and birds will be sampled in these 10 "legacy" sites by using the same sampling techniques being used under the augmentation work. This sampling includes characterization of the environmental heterogeneity (soils, slope, aspect, elevation) within the patches. The data obtained from these legacy sites will provide a detailed understanding of how past land-use interacts with natural patterns of heterogeneity to structure the present-day communities.

An essential complement to our field studies is the development of spatially-explicit models of how populations respond to landscape-scale habitat changes. We have already developed rule-based models that describe the spatial distribution of suitable habitat across the landscape for individual species (Pearson et al., in preparation). A

model developed under current funding integrates species' life-history characteristics in a spatial context to permit dynamic simulation of populations across heterogeneous and changing landscapes. The model provides a broader-scale context for our field studies and will permit evaluation of impacts on species of alternative land-use and fragmentation patterns overlaid on natural environmental heterogeneity. Especially in the Little Tennessee drainage, where development is presently much less extensive than in the French Broad, this work provides a mechanism to evaluate plausible development scenarios. This work complements the efforts on understanding the effects on environmental heterogeneity on communities (II.B.2) and on understanding and predicting human land-use dynamics in the region.

II.C.2. Land-use and long-term change in aquatic ecosystems of the southern Appalachians

(Benfield, Helfman, Meyer, Pringle)

We propose to determine how land-use affects aquatic biota in the southern Appalachians, and to predict how future alterations to the landscape are likely to affect the form and function of its aquatic ecosystems. We will accomplish this by investigating current and historical patterns in land-use and aquatic biota in the French Broad (FB) and Little Tennessee (LT) River Basins, by examining the relation between current patterns of land-use and stream ecosystem function, and by experimentally manipulating sediment and its interaction with macrofauna and algae. Our hypotheses are 1) land-use affects aquatic biota in adjoining fluvial systems and responses are proportional to degree of disturbance (length and intensity); and 2) the impact of land-use on aquatic diversity results from sediment inputs. Changes in land-use practices that increase sedimentation in streams cause greater shifts in species composition and ecological function than do changes that stabilize or reduce sediment input. We propose four research approaches: 1) assessments of species composition and ecosystem function in streams draining regions with well-defined land-use types, 2) experiments to examine interactions among macrobiota, sediments and algae in streams draining regions with well-defined land-use types 3) an historical component involving resampling sites identified by searching museum and other records to determine the time-course over which changing land-use practices have an impact, and 4) experimental manipulation of sediment inputs.

II.C.2.a. Faunal assemblages and ecosystem function in streams draining regions of different land-use

This project extends current sampling of benthic macroinvertebrates and fishes and characterization of sediments in streams in the LT and FB basins, involving three small (3-4 order) and three large (5-6 order) streams draining either forested or agricultural watersheds in each basin (total = 24 streams). One rapidly expanding land-use type in the southern Appalachians is suburban, brought about by extensive construction of vacation and retirement homes. We have not addressed suburban impacts in our current sampling. Hence we propose to sample macroinvertebrates and fishes and characterize sediments in 6 streams draining suburban watersheds in each basin during years 1 and 2 using our current sampling protocol ([Table 2](#)). This will provide us with a data set on land-use and aquatic biota in 36 streams.

Our sampling involves stream reaches that flow through extensive patches of land cover types. However, we do not know how extensive a land cover patch must be to influence a stream. We propose to determine the areal extent and relative influence of different amounts of a land cover type. We will choose three watersheds with distinct forest/agriculture boundaries. We will sample twice annually a 50 m reach beginning 200 m upstream of this margin (forested region) and then successively at points beginning at the margin and at 100 m, 250 m, 500 m, and 1 km below the forest/agriculture boundary. GIS-based maps will help determine the agricultural acreage draining into the stream at the sampling points, allowing us to regress assemblage characteristics (e.g. density and diversity of fishes and invertebrates, proportions in different functional groups) against land cover area.

Stream biota are particularly vulnerable to sediment moving along the bottom as bedload, yet we have no measure of this. At the 36 sites described above, we will measure bedload movement seasonally using deadfall traps (Shen and Julien 1993). The amount of material collected in small containers placed in the stream bottom is a measure of bedload transport.

An integrative ecosystem function is one that involves interaction over several trophic levels. Organic matter decomposition in streams is such a response because it may involve fungi, bacteria, and macroinvertebrates. We have found leaves, woody debris, and various species of shredders in all streams sampled, indicating that allochthonous organic matter contributes to the energetics of these streams. We propose to measure stick decomposition as an integrated functional response to land-use in the 36 streams ([Table 3](#)). This is a natural extension of past LTER research on leaf and wood decay in Coweeta streams (Benfield et al. 1991, Tank et al. 1993). Sticks are preferable to leaves because sticks decay more slowly and are less susceptible to removal.

II.C.2.b. Interactions among biota and sediments in streams draining regions of different land-use

Increased sedimentation is a primary cause of biodiversity changes in streams (Waters 1995). Sediments and macrobiota (fish, shrimp) interact to influence standing crop and composition of algal periphyton assemblages in tropical streams of Puerto Rico and Costa Rica (Pringle et al. 1993, Pringle and Blake 1994, Pringle in press, Pringle and Hamazaki in review). In these streams macrobiota remove sediments and associated algae from benthic surfaces, often reducing total algal standing crop but enhancing the biovolume of understory algal taxa. In southern Appalachian streams, the interactions among macrobiota (fish, crayfish), sediments, and algae are not known, but are likely influenced by changes in land-use because of its impact on both light regime and sediment delivery to the channel. We propose to investigate these interactions in the FB and LT Rivers by excluding macrobiota from small ($\sim 0.5 \text{ m}^2$) patches of stream bottom using an electric exclusion technique (Pringle and Blake 1994) that excludes macrobiota via continuous, non-lethal, electric pulses produced by 6-volt, solar-powered electric fences. Algal periphyton (AFDM, biovolume), sediment cover (DM), and insect densities will be sampled on clay tiles retrieved from treatments every 5 days throughout a 40 day experimental period during the summer. Sediment size fractions and bedload movement will be characterized. The 6-year plan of experiments is summarized in [Table 4](#). In year 1 we will do exclusion experiments at the nine 3-4 order sites in LT. The interactions among sediments, macrobiota, and periphyton probably vary depending on current

regime; therefore, in year 2 we will do an exclusion experiment in each of three habitats [pool (0 cm/s), riffle (25-35 cm/s), and run (2-5 cm/s)] in 3 streams draining pasture in the FB basin. In year 3, we will experimentally alter sediment load in Coweeta Creek to examine its interaction with macroconsumers and algae. In each of 3 runs, 3 replicates of each of the following treatments will be installed in a randomized block design: macrobiota present or absent in treatments with natural sedimentation, artificial sediment removal, and sediment augmentation. Artificial sediment removal will entail daily sediment removal by rapidly dipping tiles in and out of the water; and sediment augmentation will entail sprinkling stream bank sediments onto the surface of tiles daily at the highest rates measured in our bedload samplers. In years 4, 5, and 6 we will assess the interactive effects of nutrient enrichment, sediments, and macroconsumers in pasture or suburban streams in the LT and FB basins by combining electric enclosure experiments with an algal bioassay technique that employs nutrient-diffusing substrata (Tate 1990, Pringle and Triska in press).

II.C.2.c. Long-term patterns of change in aquatic biota

We propose to trace changes in land-use over time to see if changing land-use is important in determining biodiversity (macroinvertebrate and fish species composition and function) in streams. We will find watersheds that have been stable over the last 50 - 100 years (as pasture, rowcrops, and/or forest) and establish what appears to be characteristic, baseline communities. We can then compare these streams with those which have undergone radical land-use change. In addition we address the question of how long an area has to be subjected to a particular land-use type for changes in species or functional group composition to occur by resampling sites that were sampled decades ago and catalogued in museums or other collections. Numerous records of invertebrate collections in the region exist in student theses and state and federal government records. Historical museum records are proving absolutely invaluable for fishes. Using collection data bases from 9 museums, we have located over 30 collection locales (including species lists and relative abundances) in 2 counties that go back as far as 1888, with more frequent records from 1934 to the present. We propose to assimilate these records into a data base that can be combined with land-use records, and resample fauna at sites showing both little and extensive land-use change over the intervening period. If possible, we will include "legacy" sites.

II.C.2.d. Experimental manipulation of sediment inputs

To understand underlying mechanisms creating patterns of diversity and distribution, we propose experimental manipulations examining the influence of sediment load on life history and reproductive characteristics of LT fishes (Burkhead and Walsh 1995, Buckley and Bart 1995). In years 5 and 6, we will test a representative benthic species native to the area that responds to differences in sediment load (e.g. *Etheostoma chlorbranchium*). We will construct 3 paired channels (0.5 m wide x 4 m long) in a Coweeta stream, and use these for experiments with added sediment. Response variables to be measured include direct mortality, growth rate, body condition, feeding rate, and reproductive output (gonosomatic index, egg number, and spawning success). We hypothesize that sediment reduces growth and reproductive rates of darters through 3 major effects: 1) an energy cost by filling in refuge sites, forcing animals to expend more energy to maintain position in the stream, 2) a feeding cost by reducing the amount of available habitat for stream

invertebrates, and 3) a reproductive cost such as silting of spawning sites. If these trials are successful, we will also run them with a species that our data indicate does better in sediment-laden water, such as the mirror shiner, *Notropis spectrunculus*. Mechanistic analyses of the influence of sediment on southeastern fishes are sorely lacking (Waters 1995).

II.C.3. Linkages among spatial variation in plant quality, herbivore population dynamics, and soil processes (Hunter and Crossley)

We propose to investigate environmental heterogeneity at one level generating environmental heterogeneity at a second level by influencing the distribution of key intermediate species. More specifically, we hypothesize that heterogeneity in foliage quality for herbivores determines the spatial distribution of herbivores. The heterogeneous patterns of defoliation that result may influence soil processes by modifying inputs to the forest floor. Herbivory levels on canopy trees at Coweeta vary with elevation (Reynolds, 1995). Two key questions remain to be answered: 1) to what extent does spatial variation in the quality and availability of foliage explain patterns of herbivory along the elevation gradient? and 2) what are the effects of heterogeneous patterns of defoliation on the densities and activities of soil microarthropods?

II.C.3.a. Herbivory and plant quality

Two factors are critical determinants of densities of defoliating insects on oak worldwide. The phenology of oak budburst and leaf-fall influence herbivore densities among individual trees. Trees that leaf out early and drop foliage late often support the highest densities of defoliating insects (Hunter 1992). Second, concentrations of foliar phenolics influence herbivore densities among trees. High tannin concentrations result in low densities of leaf-chewing insects (Hunter 1996). Tree phenology and tannin concentrations for oak insects are unstudied along elevational gradients. Coweeta is ideal for this because: 1) oak foliage remains for four weeks longer at lower elevations than at higher elevations at Coweeta; 2) nutrient availability (which affects foliar phenolic concentrations) is known at five elevation gradient plots, and varies among plots (Griffith 1993); and 3) canopy walkways facilitate estimating herbivore population densities, herbivory levels, and foliage chemistry (Reynolds and Crossley 1995). Such research will be invaluable if and when the gypsy moth (*Lymantria dispar*) arrives in the Coweeta basin (probably before the year 2000). We will use a photographic method, calibrated during 1995 (Hunter, Reynolds) to estimate budburst dates from 10 individual trees of each of 3 important canopy tree species at Coweeta (*Quercus rubra*, *Q. prinus* and *Acer rubrum*). Photographs of expanding buds, taken weekly and scanned from slides onto a computer, can be used to measure bud and leaf expansion and to estimate the date of 50% leaf expansion. Budburst estimates will be made in this way at each of the five gradient plots (10 trees x 3 species x 5 plots = 150 trees photographed each week for 6 weeks during leaf expansion). Measures of phenolic chemistry will be made from the same 150 trees once each month from full leaf expansion to leaf-fall. Briefly, branches will be collected by a combination of shotgun sampling and collection from canopy walkways. Leaf disks will be punched directly from leaves into methanol, and partitioned for analysis by high performance liquid chromatography (HPLC) and by sequential extraction in methanol, ethanol, and acetone. HPLC analysis is used for simple phenolics, depsides, and flavonoids. Sequential extraction provides an estimate of total phenolics, including tannins (Waterman and Mole

1994). Herbivore densities and herbivory will be estimated monthly from a subset of trees that are accessible from canopy walkways (methods in Hunter 1992, 1994). Correlation techniques, within and among gradient plots, will be used to associate herbivore densities and herbivory with budburst and foliar chemistry.

II.C.3.b. Herbivory and soil processes

Canopy defoliation results in a variety of inputs into soils via insect frass, modified stem- and through-fall, and green-fall. For example, Crossley et al. (1988) reported large inputs of ammonium and phosphate to forest floors, and nitrates to a stream following an insect outbreak (*Alsophila pometaria*) at Coweeta. Litter arthropod diversity and abundance may increase following defoliation events (Schowalter and Sabin 1991). Although herbivory may have a dramatic effect on nutrient availability and decomposition in soils, the relationships between canopy herbivory and soil processes are poorly known in forest systems. The elevation gradient at Coweeta provides an opportunity to study the effects of spatial heterogeneity in defoliation levels on soil microarthropod abundance and decomposition. We will collect frass in funnel traps by opening 12 traps at each gradient plot for 4 hours of daylight and 4 hours of darkness once each month from leaf expansion through leaf-fall (12 traps x 5 plots = 60 samples per month). These will be used for estimates of frass fall, and related to herbivore densities (above). An additional 12 through-fall traps, adjacent to the frass traps, will be used to assess the effects of herbivory on ammonium and phosphate concentrations in through-fall (again, correlated with herbivore densities and defoliation). The abundance and diversity of oribatid mites will be measured monthly in 12 individual 1m² quadrats directly adjacent to the frass and through-fall traps in each gradient plot. Litter-fall traps already established at each site will be used to estimate green-fall (portions of leaves dropped during defoliation by herbivores). During the first 3 years of the project, estimates of frass-fall, green-fall, and through-fall will be made for each plot, as described. During the second 3 years of the study, we will manipulate experimentally the frass-fall, green-fall, and throughfall into quadrats (using data from the first 3 years to establish appropriate quantities for manipulation). Quadrats will receive either half or double the average input of frass (group 1), green-fall (group 2), or through-fall (group 3) and compared with controls (group 4). Each treatment (and controls) will be replicated 6 times per plot. The response of oribatid mite density and diversity to experimental manipulation of herbivore-derived inputs will be measured monthly in each experimental quadrat during the second 3 years of the project. Overall, we will use correlation and analysis of variance techniques to establish the effects of natural (sampling) and experimental (manipulated) additions of herbivore-derived inputs for soil arthropod abundance and diversity.

II.C.4. Environmental heterogeneity and community dynamics (Clark, Clinton, Elliott, Grossman, Laerm, McNulty, Swift, and Yeakley)

Questions of spatial scale dominate the current ecological literature (Kareiva 1994, Tilman 1994). The following three studies consider the effects of environmental heterogeneity on community composition at very different spatial scales, and question the degree to which we can generalize about the mechanisms structuring communities among those scales. In addition, the studies have an implicit temporal component; at what rates do communities respond to natural and anthropogenic disturbance (i.e. increased heterogeneity) and does it vary among spatial scales?

II.C.4.a. Effects of spatial and temporal environmental heterogeneity on stream fish assemblages

We propose to measure effects of spatial and temporal environmental heterogeneity on fish assemblage structure. We will continue to monitor assemblage structure in the three 100m gradient sites established previously, and will extend our sampling downstream to at least one site with greater diversity (i.e. > 20 species). Fish samples will be taken once or twice yearly as per Freeman et al. (1988). We will quantify fish abundance, population structure, and physical measurements such as substratum composition, water temperature, and gage height (see Freeman et al. 1988, and Grossman et al. 1995). These data will be used to assess assemblage stability sensu Grossman et al. (1990) and determine the effects of temporal heterogeneity in the physical environment on assemblage stability and population structure of individual species. In addition, because several species (e. g. mottled sculpin, *Cottus bairdii*, longnose dace, *Rhinichthys cataractae*, and rainbow trout, *Oncorhynchus mykiss*) are present in at least two gradient sites with differing physical characteristics (Grossman et al. 1995), we will also assess the potential effects of spatial heterogeneity on population structure of these species. Finally, a second five years of data will enable us to examine the relative importance of density-dependent and density-independent processes on population regulation in these species. This information is almost nonexistent for stream fishes, especially non-game species (Grossman et al. 1990, Grossman et al. 1995). We also propose to use a landscape approach to elucidate factors controlling the distribution and abundance of mottled sculpin in the Coweeta basin. Mottled sculpin numerically dominate many streams across northern North America. This species also has a small home range (<0.5 m², Freeman & Stouder 1989). Although most abundant in riffles, mottled sculpin are microhabitat generalists (Grossman & Freeman 1987). In fact during and after the drought of 1985-1988, the microhabitat distribution of this species did not differ significantly from random (Grossman et al., unpublished data). Sculpin occupied patches that had prey abundances significantly higher than randomly selected patches (Petty and Grossman 1996), suggesting that prey distribution is driving microhabitat use by sculpin. We will expand this approach to broader spatial scales, to determine the relative importance of physical factors and prey abundance on the distribution and abundance of this species across reaches of Shope Fork. We will measure the availability of physical variables in reaches (as defined by Hill and Grossman 1987) using the methods of Grossman & Freeman (1987) and take a minimum of five benthic samples from riffles. We will then test for correlations between sculpin abundances and physical parameters (e.g. depth, velocity, substratum composition, photosynthetically active radiation) across reaches, as well as prey abundance. Both univariate and multivariate statistics will be used to examine these relationships (Grossman and De Sostoa 1994).

II.C.4.b. Disturbance and heterogeneity as determinants of species richness of animal assemblages

Small mammal (soricid and rodent) and amphibian communities at Coweeta and elsewhere in the southern Appalachians differ significantly in species richness, and evenness both within and between representative vegetational cover types (Ford et al. 1994, Laerm et al. 1996, Laerm et al., in press). Perturbation history may also influence richness and evenness. The research proposed here will focus on three aspects of the determinants of regional patterns of biodiversity of small mammal and salamander assemblages: 1) How do richness, and evenness vary within and

between vegetational cover types (spruce-fir, northern hardwood, cove hardwood, oak- hickory, oak-pine, and rhododendron riparian zones)? 2) How does spatial variation in habitat structure influence biodiversity? This will be examined through correlation of habitat characteristics (elevation, aspect, coarse woody debris, soil moisture, soil-type, and vegetation diversity) with patterns of richness, and evenness; and 3) Does perturbation history influence richness, and evenness? This will be tested by comparisons among original growth, mature (80-100 year old), mid-successional (40-60 year) and young (0-10 years) stands of several representative cover types described under 1) and 2) above. We will use standardized Jollie-Siebert mark-release recapture methodology (Ford et al. 1994) for estimating small mammal densities. Amphibians will be estimated by direct observation, based on transects, and visual time-searches. Comparisons of relative abundances will be based on drift-fences, using pitfall sampling.

II.C.4.c. Site factors, plant life-history traits, and gap studies

Most recent explanations for coexistence of diverse forest assemblages invoke tradeoffs between the ability of plant species to colonize sites versus their ability to hold them (Tilman 1994, Pacala and Tilman 1994, Clark and Ji 1995). Both colonization and site retention will depend upon intrinsic attributes of the species and physical factors at the site. Spatial variation in physical factors will interact with species attributes to determine species composition at any point in space and time. This study has two goals: 1) to describe interactions between spatially-heterogeneous site factors and the life history traits of plants at different life stages that ultimately determine the ability of species to colonize and retain sites, and 2) by understanding how environmental variability and life history traits combine to determine forest assemblages, results should allow the prediction of how assemblages might change following modification in the environment by forces such as global change. The elevation gradient at Coweeta is an excellent resource for this study; by determining the life history stages that limit populations of key species at different locations along the gradient, using experimental approaches, such as creating canopy gaps, this study will show both where and how these species are sensitive to changes in the environment.

The three-year pretreatment phase of gap experiments was completed in 1993 and girdling of trees implemented in August/September 1994. Experimental gaps included three with and three without *Rhododendron* understories on both low- and high-elevation mixed oak stands, for a total of 12 gaps. Data collected on temperature, soil moisture, N mineralization, seedling censuses, seedling physiology, and tree growth rates since 1991 constitute the pretreatment baselines for experimental effects that began with the 1995 growing season. Most girdled trees did not leaf out in 1995, so responses of physical factors, N mineralization, and seedling physiology are expected to have begun in 1995/1996. Seedling dynamic responses and tree-growth responses may not be observable until 1996. Following tree recruitment, successful colonization and the species composition that eventually fill a gap may be determined by the species with the greatest resource use efficiency under that particular set of resource availabilities. Differences among species in resource use efficiency may play a significant role in their relative abilities to tolerate variation in the availability of key resources such as nitrogen, water, and light.

To investigate the importance of resource use efficiencies as an adaptive life history strategy, we propose to examine the relationships among resource use efficiencies

and availabilities of four understory tree species (*Acer rubrum* L., *Quercus prinus* L., *Quercus coccinea* Muenchh., and *Quercus rubra* L.) that naturally occur in these artificially created gaps. Because forest gaps can alter resource availability, the temporal and spatial patterns of gaps interact with species strategies for growth and survival. Species response to this change will vary with the magnitude, rate, and persistence of the resource change and with the life histories and resource requirements of the organisms that colonize the gaps. Pre-treatment measurements suggest that high elevation oaks have higher rates of net photosynthesis (P_N : 67, 64, and 77% higher for *Q. prinus*, *Q. coccinea*, and *Q. rubra*, respectively) than low elevation oaks and there is a difference among oaks within an elevation. However, if there is a difference in leaf duration between elevations, then the difference in total carbon gain over a growing season may not be as dramatic as suggested by P_N data alone. In order to evaluate this total carbon gain for understory tree species it is important to understand the phenological development at both the high and low elevation sites. We propose to follow and record dates of important phenological development (i.e. bud swell, bud burst, leaf expansion, leaf color, and leaf abscission) of understory trees through the growing season at both elevations.

Seedling demographic data thus far suggest that seed production and dispersal are much less limiting than is germination success due to seed predators and other, as yet, undetermined factors. Highest percentages of first-yr seedling densities to seed rain densities are for *Acer* and *Liriodendron*, at 0.5 to 4.0% and 0.01 to 0.06%, respectively. The greatest bottleneck for tree recruitment thus appears to lie first in establishment success and, secondarily, in seed arrival (Clark et al., in review).

To investigate seed and seedling predation on tree recruitment, mammal exclosures were installed in gap plots in 1994. Twenty four 1 x 2 m exclosures and 12 control plots were established, in gap (3) and non-gap (3) areas of *Rhododendron* and non-*Rhododendron* locations. Exclosures were of two mesh sizes: 1) to exclude deer but not rodents (hogwire), and 2) impermeable to rodents and deer (hardware cloth). Preliminary experiments on seed predation show complete removal of *Quercus* in all treatments (to squirrels, because all exclosures were open at the top), heavy losses of *Fagus* above and below litter to insect damage, and no effects on *Liriodendron*. These preliminary results suggest recruitment might be strongly limited by seed predation for *Quercus* (squirrels) and *Fagus*, but not for *Liriodendron*. The fraction of removed *Quercus* that are planted elsewhere is not known, but we plan surveys to assess whether new first-year seedlings result from planted vs. surface germinants.

If canopy gaps and presence of *Rhododendron* are important controls of forest dynamics in the southern Appalachians, then we expect these variables to respond to canopy losses that began in 1995. Monitoring of changes in light, moisture, temperature, and mineralization provides the necessary environmental factors that contribute to those responses. During the new funding period we will continue censuses, measurements, and sampling at intervals used for the pretreatment phase. Pre- and post-treatment data are thus comparable, and comparisons with understory controls permit hypothesis tests of gap effects.

II.D. Effects of disturbance and environmental heterogeneity on biogeochemical cycling and ecosystem processes

Understanding biogeochemical cycles and ecosystem processes in both terrestrial and aquatic ecosystems has been a key element of Coweeta's LTER research activities. Early research emphasized the role of severe disturbance (e.g. clearcutting, drought) and the resultant impacts on nutrient, carbon, and hydrologic cycles. In the most recent grant period, we investigated the role of environmental heterogeneity, disturbance/stress, and their interaction in regulating ecosystem pools and processes in streams, riparian zones, and forests. The research proposed here includes continuation of measurements of select topics initiated in previous LTER grants and new research which builds on past studies. Our approach will be to address ecosystem process response to environmental heterogeneity and disturbance/stress at several spatial scales: in plots, in watersheds, in landscapes (Coweeta basin), and in the southern Appalachian region ([Figure 13](#)). This will be accomplished through an integrated program of long-term field measurements, experimentation, and modeling.

II.D.1. Stream ecosystems (Benfield, Meyer, Wallace, Webster)

Most streams in the eastern U.S. begin in forests and are dominated by allochthonous inputs. As width increases downstream, light to the streambed increases, allochthonous inputs are lower, and the stream becomes more autochthonous based (Vannote et al. 1980). Over the past 5 years, much of our effort in the LTER has been directed towards study of the first to fourth order continuum within the Coweeta basin. Our results have not shown strong changes along this continuum that can be attributed to increasing stream size (see I.B.4.). Instead, specific geomorphological characteristics of a site (e.g. pool, riffle, run) are more important in determining functional and community characteristics. Further downstream, stream-size characteristics become much more important (Grubaugh et al., in press); however, even in the Little Tennessee River, there are areas of riffle that have macroinvertebrate communities more typical of riffles in headwaters than mid-order streams. Over a 60-km stream continuum, where annual degree days increased by 50% and discharge increase 3000-fold, habitat-weighted secondary production of benthos increased from < 10 to > 150 g AFDM/m²/yr, among the highest values ever recorded (Grubaugh 1994). In addition to large changes in production, there were large changes in taxa over the gradient. These stream size trends can be overridden by anthropogenic disturbance; e.g., Ward and Stanford (1983) showed that a dam can reset a stream to conditions more similar to those found upstream. In the Little Tennessee River, human land use seems to have the opposite effect; effects of sediment inputs, elevated nutrients, and lack of riparian shading create conditions more typical of larger streams.

The stream research proposed is centered on the observation that there are biotic assemblages associated with habitat types within the stream (Huryn and Wallace 1987, Naiman 1988, Gregory et al. 1991). We recognize several habitat types within any reach of stream: riffles, runs, depositional zones, bedrock chutes, and channel expansion zones (i.e. areas wet only during storms) that characterize small headwater streams. Downstream, areas of specific habitat types get larger, depositional zones become pools, and channel expansion zones become floodplains. New habitat types, such as macrophyte beds, may become increasingly important, and the habitat types found within a reach of stream will also reflect land use in the watershed.

Our new research is designed to answer two questions: How do stream size, in-stream habitat types, and riparian land use vary along a 1st to 7th order stream gradient? How are organic matter sources, in-stream organic matter dynamics and invertebrate communities affected by stream size, habitat types, and riparian land use along this gradient? In addition to this new research, we will continue our ongoing studies that address long-term recovery of stream processes and invertebrate communities from watershed (clear-cutting) and site specific (log addition) disturbances. These studies (II.D.1.b) address the question: what is the long-term (decadal) pattern of recovery from disturbance for organic matter dynamics (inputs, storage and decomposition) and invertebrate communities in southern Appalachian headwater streams? In combination with the regional stream research (II.C.2), these studies will enable us to analyze the long-term response of stream ecosystems to anthropogenic disturbance in the context of longitudinal gradients of change along a stream continuum.

II.D.1.a. Variation in carbon dynamics and use by animal communities along environmental disturbance gradients

Our objective in the following studies is to characterize the habitat types of the Ball Creek - Coweeta Creek - Little Tennessee river system in terms of their functional and community structural characteristics and their relationships to the stream-size continuum, site-specific geomorphological characteristics, and land use. To address the questions outlined above, we propose the following studies:

II.D.1.a.(1). Geomorphological survey of the stream continuum. We have completed a physical survey of over 13 km from Ball Creek to the confluence of Coweeta Creek with the Little Tennessee River. We propose to continue this survey about 50 km down the Little Tennessee to Fontana Reservoir. At 100 m intervals, we will measure width, bankfull width, flood plain width, mean depth, extent of riparian vegetation, substrate composition, and coverage of aquatic macrophytes. This survey will be completed during year 1.

II.D.1.a.(2). Site selection. Intensive studies will be conducted at four sites. The first is a 3rd order site on Ball Creek sampled in our previous research ([Figure 2](#)). The next three will be selected from among the sites previously used by Grubaugh (1994) and will include the 5th order site on Coweeta Creek.

II.D.1.a.(3). Riparian inputs of allochthonous organic material. During year 2, litterfall inputs to small streams will be sampled by suspending litter traps over the stream. At the larger river sites we will place litter traps in the riparian area and use the fraction of the annually inundated area covered by riparian vegetation to estimate allochthonous input. The estimates will vary depending on the extent and timing of floods within a particular year.

II.D.1.a.(4). Primary production . We will measure primary production at each site using the upstream-downstream diurnal oxygen change technique (e.g., Bott 1996). This technique has been extensively used in larger streams in eastern US (reviewed by Webster et al. 1995) and has recently been modified for use in smaller streams (Marzolf et al. 1994). This technique will allow us to measure both primary production and community respiration. Measurements will be made at each site five times per year during year 3.

II.D.1.a.(5). Seston transport. Other than direct allochthonous inputs and in-stream primary production, the other source of organic matter to heterotrophic organisms in a stream is organic matter transported from upstream. During year 4 of the study, we will estimate seston transport at each site. Samples will be collected every two weeks for non-storm transport. Seasonally we will collect samples during storms and determine both organic and inorganic particle transport. Streamflow at non-gaged sites will be estimated from drainage area and flow at gauged sites.

II.D.1.a.(6). Trophic basis of secondary production. Benthic macroinvertebrates will be collected seasonally at each site and foregut contents mounted on slides, identified, digitized and summarized as described by Wallace et al. (1987). We will examine how resources (seston composition, benthic organic matter, and primary production) vary seasonally along the stream size and elevational gradient. With gut analyses, we can determine how food resources (i.e., detritus, fungi, algae, and animal) ingested by the dominant taxa within various functional groups vary seasonally over the gradient. Using the procedure of Benke and Wallace (1980) and our measures of secondary production at these sites (Grubaugh 1994), we will be able to assess how the trophic basis of production varies over the gradient.

*II.D.1.a.(7). Role of the aquatic macrophyte *Podostemum* in structuring the invertebrate community.* Secondary production of aquatic invertebrates within dense growths of *Podostemum ceratophyllum* at downstream sites in the LittleTennessee River are among the highest reported for aquatic invertebrates. We will investigate the importance of *Podostemum* to invertebrate community structure by comparing seasonal benthic abundances and biomass of taxa in functional groups on cobble and bedrock substrates where *Podostemum* has previously been manually removed (by scraping and brushing) with substrates containing unmanipulated *Podostemum*. We predict distinct shifts in benthic abundances and biomass of taxa (i.e., from filterers to predominantly scrapers) and lower abundances and biomass of benthos in areas where the *Podostemum* has been removed.

II.D.1.b. Long-term studies of disturbance in Coweeta streams

The following ongoing studies address long-term responses to disturbance. We have been following recovery of a stream from clear-cut logging for two decades. We have also begun a long-term woody debris manipulation (Wallace et al., in press) where we continue to follow changes in abiotic factors and invertebrate community structure and biomass.

II.D.1.b.(1). Recovery of streams from watershed logging. Since 1975 we have been studying the effects of logging on Big Hurricane Branch (e.g. Webster et al. 1992). During year 5 we will remeasure the following processes in Big Hurricane Branch and Hugh White Creek (reference stream): litter inputs, leaf decomposition, benthic organic matter, stream invertebrates, and seston transport.

II.D.1.b.(2). Long-term studies of large woody debris addition to a stream ecosystem. We propose to continue our annual sampling for benthic invertebrates at 3 experimental sites (large woody debris addition) and 3 reference sites (cobble riffles) on Cunningham Creek (Wallace et al., in press). These sites were sampled seasonally from 1988 until 1992, when an annual sampling regime was initiated. These data are providing valuable long-term records of invertebrate abundances and biomass at manipulated and reference sites.

II.D.2. Riparian ecosystems (Yeakley, Coleman, Fitzgerald, Haines, Knoepp, Meyer)

Riparian zones represent the linkage between terrestrial and aquatic ecosystems in the landscape; however, little is known about the delineation and function of riparian zones at Coweeta. Water and nutrients exported from the upslope areas pass through the riparian zone and hence, riparian zone nutrient cycling processes are inextricably linked to stream water chemistry. In addition, riparian zones at Coweeta are dominated by rosebay Rhododendron (*Rhododendron maximum*) which we hypothesize exerts a major influence on riparian zone function. This component of the proposal addresses two questions: (1) How do riparian zone nutrient cycling and hydrologic processes vary with elevation, topography, stream order, and soils? and (2) What is the impact of Rhododendron removal on carbon, nutrient, and water dynamics?

II.D.2.a. Riparian zone delineation and nutrient cycling

Objective criteria for delineating the hydrologic basis of riparian zones in mountainous watersheds from terrain and soil features have yet to be determined. Riparian zones in streams in the Coweeta basin grade from narrow areas confined by steep hillslopes in headwater catchments to shallow sloped areas in the broader valley floor of the 5th order stream beyond the basin. Expansion and contraction of near-stream saturated areas has long been depicted as the primary mechanism of streamflow generation at Coweeta (Hewlett and Hibbert 1963). Bi weekly measurements along 4 piezometer transects on the headwater riparian experimental site, however, have shown a surprisingly stable phreatic surface, with all 4 upslope piezometers (1-3 m from stream) having free water surface levels varying no more than 10 cm each during 1995 (Figure 15). Soilwater zones on those steep sites are apparently uncoupled from streamwater and unlikely to experience saturated conditions on timescales longer than the duration of an infiltration front from a high intensity storm. We will test if this result applies generally to headwater catchments at Coweeta. We further hypothesize that phreatic surfaces in the riparian zone expand with stream order, becoming broader, more responsive to seasonal precipitation variation (i.e. to timescales longer than an isolated storm event), and more interactive with soilwater in 5th order streams such as Coweeta Creek.

Shallow soils and steep slopes at higher elevations have a profound effect on nutrient processing. Prior work at Coweeta has shown that the dominant anion in streamwater varies from SO_4 at high elevations to HCO_3 at lower elevations (Swank and Waide 1988). Recent storm studies have shown that SO_4 and SiO_2 can be partitioned to determine relative contributions of rainwater, soilwater, and groundwater within streams during storms at Coweeta (Figure 16) (Webster and Yeakley, unpublished data). We propose to establish piezometer transect pairs from hillslope to stream in each of four 1st order watersheds (high elevation WS27 and WS36; low elevation WS2 and WS18), as well as in two 3rd order streams (Ball Creek and Shope Fork), and in two contrasting channel morphologies in the 5th order stream (Coweeta Creek) beyond the basin (16 transects total). Measurements will be conducted at two frequencies, monthly and during individual storms, and will include water levels and nutrient concentrations. Terrain and soil features would be analyzed using terrain analysis programs used previously (Yeakley et al. 1994). Nutrients measured will include those expected to vary either with elevation or during storms (i.e., NO_3 , SO_4 , HCO_3 , SiO_2 , Ca, K). Products from this work include quantification of near-stream saturated zone variation at Coweeta with respect to

gradients in topography, soils and stream power. Results would augment an ongoing effort to parameterize models of soil moisture dynamics across the Coweeta basin (Yeakley et al., in preparation). Further this work will provide information on how near-stream saturated zone nutrient delivery dynamics vary with precipitation frequency and duration, topographic, soils and stream size in the southern Appalachians.

We will also determine the fate of precipitation borne sulfate in samples collected from riparian zones located within and outside the Coweeta basin. The potential negative impact of excess sulfate loading on streams in the surrounding forests is believed to increase if this anion becomes mobile and thus, causes leaching of divalent cations. Although mechanisms for organic S formation and sulfate adsorption are well established for forest soils in the basin, until recently, little was known of these processes in near-stream soils, or active channel and stream sediments. Samples from three transects that bisect a first order stream in Watershed 55 will be collected for the six-year grant period on a quarterly basis, and these will be assayed for the capacity to form organic S and adsorb added sulfate. This work will be carried out in conjunction with assays for organic S content, total S, and C ([Table 5](#)).

II.D.2.b. The role of Rhododendron in riparian zone function

In both riparian zones and upper slope topographic positions, rhododendron forms dense thickets which intercept most incoming light (Clinton 1995), and inhibit regeneration of other species (Clinton et al. 1994, Clinton and Vose 1996), resulting in a thick litter layer. In the previous grant, we initiated research to test the role of *Rhododendron maximum* in riparian zone function. We hypothesized that riparian rhododendron thickets act as organic filters that impact riparian and stream ecosystems by: 1) reducing light transmission, 2) preventing terrestrial debris and soluble nutrients from reaching the stream, and 3) altering carbon and nutrient cycling processes in the forest floor. In the previous grant, we initiated a removal experiment to determine the role of rhododendron in riparian zone function (i.e. carbon, nutrient, and water cycling) and we propose continuation of most components of that experiment in this grant. After collecting two years of pre-treatment data ([Table 5](#)), rhododendron on the treatment hillslope (10 x 30 m section) was removed (cut and moved off-site) during August 1995. Shortly after the cutting, the control site experienced several treefalls due to Hurricane Opal. Upper slope lysimeters on the control hillslope were destroyed, but we retained operation of near-stream lysimeters and wells on the control hillslope, as well as lysimeters on the uncut portion of the treatment hillslope. Pre-treatment data include seasonal and annual dynamics of microbial C, N, and microbivorous nematodes (Maxwell and Coleman 1995), and we are now measuring microbial P as well. Litter mass loss, litter inputs, litter movement, in situ N mineralization (Knoepp and Swank 1995), sulfur dynamics, site hydrology, stream periphyton biomass, dissolved nutrient and organic carbon fluxes, root growth dynamics, and vegetation regrowth (treated site only) are also being measured on control and treated sites. We will continue observations on these hillslopes for three years, until the fall of 1998, to determine organic matter, nutrient and water flux responses on the treatment hillslope.

II.D.3. Forest ecosystems (Bolstad, Clark, Coleman, Crossley, Haines, Hendrick, Kloeppel, Knoepp, Meyer, Swank, Vose, Yeakley)

In the previous grant, we established a series of plots in undisturbed watersheds which span an environmental and species composition gradient. In these plots, we have been characterizing pools and fluxes of carbon, nutrients, and water and associated driving variables (Table 6 and Figure 3). Our objectives were to understand the role of environmental heterogeneity in regulating ecosystem function and the impacts of "natural disturbance" (e.g. drought, herbivory, etc.) and stress on biogeochemical cycling and ecosystem processes. A unique aspect of this research is that a suite of process and pool size measurements have been made at the same place and time, and a research infrastructure is in place to facilitate long-term measurements. Because pools and processes often respond slowly to all but dramatic variation in environmental conditions, the value of the data collected on these plots will increase tremendously over time. Equally important, these measurements and subsequent understanding provide the foundation for scaling measurements to the watershed, landscape, and region via modeling. Carbon is the primary focus of our regional studies because we have developed a moderate understanding of regulators of pools and fluxes in both terrestrial and aquatic systems, yet there are still major uncertainties in carbon, nutrient, and water cycling responses to environmental heterogeneity and disturbance. To remove some of these uncertainties, we propose to build and expand upon our previous studies by asking three specific questions: 1) How do pools and fluxes of carbon, water, and nutrients vary across a heterogeneous landscape? 2) What is the relative contribution of species composition vs. environmental gradients in regulating variation in pools and fluxes? and 3) How are pools and cycles affected by disturbance and stress? Question 3) is addressed specifically in our study of regional C pools and flux response to land use change (Section II.D.3.a.5) and is inherent in our long-term studies of ecosystem processes on gradient plots.

II.D.3.a. Variation in pools and fluxes of carbon

Many aspects of the carbon cycle remain poorly understood (Tans et al. 1990). Carbon pools and fluxes, as well as controlling mechanisms, require quantification to fully understand C cycling processes and potential impacts of disturbance and stress. Part of our uncertainty is due to substantial spatial and temporal variation in terrestrial C pools and fluxes. C amount and distribution vary among and within ecosystems, and we have not adequately sampled or modeled this range of environmental and biotic conditions. For example, small-scale variation in soil conditions from dry ridge to streamside may result in an order of magnitude increase in belowground C. These fine scale variations are juxtaposed on climatic variation, often due to macro- and meso-scale changes in elevation and latitude. We propose to remove a major share of this uncertainty by measuring and modeling the C cycle at multiple scales (e.g., plot to region). Our approach will be to measure key carbon inputs, internal pools, and outputs. Modeling will be used to integrate and extrapolate measurements spatially and temporally.

II.D.3.a.(1). Carbon inputs and outputs. Canopy access towers and walkways are located in three of the five gradient plots and in a low elevation, xeric oak community type in WS 2. These towers have been used to collect leaf-level physiological data, such as photosynthesis (Sullivan et al., in press) and respiration rate (Vose and Bolstad, in preparation) by species. In addition, we have used these towers to determine the vertical distribution of environmental driving variables (i.e. light, temperature, relative humidity, leaf area index, and amount and vertical distribution by species (Vose et al. 1995). We propose to expand the network of

canopy towers (i.e. towers located at all gradient plots) to increase spatial sampling and include more sites and species, and to continue measuring leaf photosynthesis and respiration at those sites.

Plant respiration losses can account for as much as 50% of the gross carbon fixed in forest ecosystems. We have a limited amount of information for leaf and stem respiration, and those data indicate wide variation in respiration rates among species and measurement periods. We propose to expand these measurements (using portable cuvettes and an infrared gas analyzer) to include more species and sample periods to better understand this variation and associated driving variables. In years 1 and 2, litter decomposition will be measured using three species replicated three times per month at each of the five gradient plots. In year three, data will be synthesized. Soils contain a considerable proportion of ecosystem carbon; fluxes from the soil are a major component of the ecosystem carbon budget. To quantify the contribution of soils, we will measure diurnal soil CO₂ evolution from gradient plots in spring, summer, fall, and winter using an automated infrared gas analyzer measurement systems (Vose et al. 1995) in years 1 through 6. In the other months, we will use a static absorption technique which correlates well with the IRGA based system at the plot level. With both techniques, flux estimates will include the contribution from forest floor.

II.D.3.a.(2). Inter- and intra-annual variation in carbon pools. For inter-annual variation in wood production, trees on gradient plots will be re-measured to determine growth and mortality rates by species and diameter (converted to biomass with locally developed allometric equations). For intra-annual variation, dendrometer bands will continue to be measured on a sub-set of trees spanning variation in tree size and species. We will continue to estimate monthly leaf area index on gradient plots using light interception and locally developed extinction coefficients (Vose et al. 1995), and litterfall will continue to be measured monthly. Phenological development of overstory species, shrubs, and herbaceous vegetation will be quantified using weekly observations of phenological events (e.g. bud break, flowering, etc.). Forest floor mass (separated by L, F, and H layers) will be re-measured in years 1, 3, and 6 using destructive sampling from locations on the edges of the plots. In addition, as the forests at Coweeta age, we anticipate that coarse woody debris will increase in amount and importance in the overall carbon budget. Hence, coarse woody debris (by stage of decomposition) will be measured within the plots (volume measurements converted to mass using CWD density) in years 1 and 5 m.

We propose to expand our belowground sampling to better quantify fine root biomass, turnover, and linkages to aboveground phenological activity and environmental conditions. We will use existing root observation boxes to monitor long-term fine root growth phenology across all gradient plots. We will expand this work to include video images of each window prior to budbreak, immediately after 100% expansion, during midsummer, at the onset of leaf senescence and immediately after 100% leaf fall. These images will be digitized manually with the ROOTS (Hendrick and Pregitzer 1992) image analysis program, and the individual dimensions, development and fate of the roots will be determined. Fine root biomass will be determined from soil cores taken at the beginning and end of the growing season, and used in conjunction with the dynamics data to calculate belowground productivity. In addition to quantifying the relationship between above and below ground phenology across community types and environmental gradients, these data will help establish the magnitude of inter-annual variation in the timing and amount

of root growth and mortality. These measurements will be made during the entire 6 year funding period. Soil carbon (to a 15 cm depth) will continue to be measured on all gradient plots concurrent with in situ N mineralization and nitrification (see section II.D.3.b.2).

II.D.3.a.(3). Carbon modeling. A significant new component of the proposed research will be development, validation, and application of carbon cycling models within the Coweeta basin. Data collected to date, as well as data proposed to be collected in this grant, provide a unique opportunity for developing and testing models with complete and long-term data sets across a gradient of species and environmental driving variables. Modeling activities will include continuation of development and validation of micro- and meso-scale environmental models (i.e. soil temperature, air temperature, within and below-canopy micro-climate, soil moisture) which will be as drivers of C cycling rates. In addition, we will continue development of a physiologically-based basin scale model of net primary productivity and soil carbon cycling ([Figure 17](#)). Recent work has detected strong relationships between landscape position, vegetation type, and belowground carbon properties such as fine-root biomass and total soil carbon. We are currently modeling belowground processes and variables driven by landscape position, vegetation type, and soil temperature and moisture. The integration of sub-models, combined with additional sub-component carbon flux measurements and more detailed mapping of temporally static driving variables will be a major focus of our carbon modeling. The primary goal of these activities is to develop and validate a spatially-explicit carbon cycling model for the Coweeta basin.

II.D.3.a.(4). Regional carbon pools and fluxes. We propose to expand our study of carbon pools and fluxes within the Coweeta basin to the southern Appalachian region. In addition to quantifying carbon budgets across an expanded environmental gradient, a major objective of the regional study is to understand the effects of land-use change on carbon pools. We hypothesize substantial variation in C pool size, C distribution, and C-cycling rates among landcover classes. This research was initiated in 1995 as a result of the augmentation award to Coweeta. We propose to continue this research for all six years of the new grant period.

We propose two major activities to quantify the impacts of land-use change on C pools and fluxes in the southern Appalachians: 1) we will measure C pool and flux estimates from a network of field sites over a representative range of biotic and abiotic conditions; and 2) we will use recent historical and land-use/landcover characterization for the region and C cycling models to scale pool and flux measurements to the southern Appalachian region.

Our long-term goal is to replicate measures of fluxes and pools for a range of biotic conditions in each landcover class. We have one year of sampling for a subset of southern Appalachian ecosystems, and we propose to extend the sampling in years 1 through 5 both categorically (to include more landcover types) and spatially (to better sample within type variation) as a long-term activity. We will sample 10 landcover classes representing over 90% of the southern Appalachian land surface: old-growth, mature, and early successional forest types at each of ridge, slope, and cove positions, and pasture in low cove or valley conditions. Three replicates per each combination will be sampled, for a total of 30 sampling locations.

A suite of extensive measurements will be made to determine C pools at all sites ([Table 7](#)). Intensive measurements will be made at one replicate of each type (10 sites/year) to estimate fluxes and to more finely partition C pools. Beginning in 1995, these measurements are being made in the Little Tennessee and sites included old-growth forest in Joyce Kilmer/Slick Rock Wilderness, mature and early successional forests at Coweeta, and a pasture near Coweeta. In the next grant period, we propose to extend our sampling to southern Virginia and the French Broad region. We propose five permanent sites to facilitate inter-annual comparisons, one site in the ridge and cove mature and immature forest, and one in the pasture. The remaining five intensive sites will rotate among the remaining sites on a two-year interval, for a total of twenty sites over a five year period. Measurements at intensive sites will include direct soil CO₂ measurements using a recently developed system (Vose et al. 1995), comprised of surface cuvettes, connected through null-balance pumps to an infrared gas analyzer. Fine (2 mm) and coarse root (2-5 mm) biomass will be measured at the intensive sites coincident with each flux measurement, following locally developed (McGinty 1976) and regionally validated soil and root sampling protocols. These protocols involve sampling to 30 cm depth, washing over a 1-mm mesh to separate roots from soil, root classification by size and status (live or dead), and drying to a constant weight. Measurements at both intensive and extensive sites will include stem diameter and height, coupled with allometric equations to determine live vegetation C pools and recent (< 5 years) above-ground C accretion.

Stem respiration will be measured using easily-removed cuvettes and the same IRGA and solenoid sampling system (Vose et al. 1995) used for soil CO₂. Tree species and size were selected based on initial plot survey data by stratifying tree species density and size. Additional instantaneous tree respiration rates are measured to expand coverage of species and size classes. Sapwood temperature is measured with thermocouples concurrent with the stem respiration measurements. To understand effects of phenological and environmental variation, stem respiration is measured bi-monthly throughout the year to encompass periods of stem growth (summer), carbohydrate and water retranslocation (spring and fall), and dormancy (winter). Since phenology varies significantly between sites and species, six annual sampling periods allow sampling each species at least once during each primary phenological condition.

We propose a two-step process for estimating regional C pools and fluxes. Our first approach involves delineating "homogeneous" geographic units (HGU's *sensu* Brand et al. 1991) and estimating state variables for each HGU such as landcover, soil properties, thermal and moisture regimes, and carbon stocks. HGU's will be developed via spatial overlay of relevant biotic and abiotic variables, some already developed (elevation, soils, temperature, precipitation), and some yet to be assembled (geology, landcover, current biomass). Once HGU's are identified, we will run point process models, CENTURY and the Coweeta C cycling model, with appropriate state variable estimates for each HGU. Pools and fluxes will be predicted at a range of grain sizes for the fine-grained spatial data (aggregating from tens to hundreds of meters), including 1930s/1950s (mapped counties) and 1970s/1990s landcover data developed for a 8000 km² region during the first two years of augmentation funding.

II.D.3.b. Variations in pools and fluxes of nutrients

Previous research at Coweeta has documented differences in nutrient cycling processes across the elevational gradient (Swank and Waide 1988) and results from the previous grant have shown that large differences exist in pool sizes and cycling rates of many nutrients among the gradient plots. We will continue to measure a subset of response variables to detect long-term changes to be used as drivers of other processes, such as carbon cycling. Other measurements, and measurement frequencies, will be phased-out or reduced, respectively, due to increased emphases in other areas, and due to budget limitations.

II.D.3.b.(1). Nutrient inputs and outputs. Hydrologic and nutrient budget studies continue to provide the framework for linking terrestrial and aquatic processes and responses to disturbance. We will continue to make long-term hydrologic and associated chemistry measurements for baseline and disturbed forested watersheds at Coweeta, including watersheds containing gradient plots. In addition, the long-term record of stream water chemistry at Coweeta includes measures of DOC concentrations in streams draining watersheds 7 (clear-cut in 1977) and 14 (low elevation undisturbed) since 1979 and watershed 27 (high elevation undisturbed). The data set documents recovery from clearcutting as well as differences in streams draining high and low elevation watersheds and will be continued. Throughfall chemistry has been measured on all gradient plots for a period of two years. We propose to continue these measurements for an additional 2 years to more completely analyze the data for spatial and temporal trends. Measurements beyond this period will be dependent upon findings.

II.D.3.b.(2). Inter- and intra-annual variation in nutrient pools and fluxes. Foliar chemistry was measured from border trees on all gradient plots in 1993. We propose to re-sample all previously measured trees in years 1 and 6. Nutrients in the forest floor (separated by L, F, and H layer) were measured in spring and fall of 1994. We propose to re-measure litter chemistry on samples used to determine forest floor mass in years 1,3, and 6. In addition, coarse woody debris will be measured for C, N, and total cations.

Exchangeable base cations (quarterly measurements) have been measured on the gradient plots for the past five years. We propose to re-measure base cation pools in years 3 and 6. Porous cup lysimeters are located at 15 cm and 60 cm depths and soil chemistry has been measured for the past two years. We propose to continue measurements for an additional two years and analyze the data for inter-annual temporal trends. Measurement will be suspended if these analyses indicate minimal inter-annual variation. By the end of 1996, we will have six years of N-mineralization and nitrification data at quarterly or monthly resolution. We propose to re-measure N-mineralization and nitrification in years 3 and 6.

II.D.3.b.(3). Nutrient modeling. Revised nitrogen and cation cycling models for undisturbed mixed hardwood forests will be completed and published. These revised models will synthesize a broad body of knowledge of cycling processes developed at Coweeta over the past years. The N cycling data will also be used to validate a N-saturation model (PnET-CN/CHESS) currently used by J. Aber, C. Driscoll, and M. Mitchell for northern hardwood forests.

II.D.3.c. Variations in pools and fluxes of water

Water is a major driver of ecosystem processes in the southern Appalachians. Abundant rainfall (between 1800 to 2300 mm per year) supports high terrestrial productivity, increases the importance of riparian zones, and results in numerous streams ranging from first to fourth order within the Coweeta basin. Despite the high average annual inputs, inter- and intra-annual variation is often large and ecosystems respond to this variation in subtle (e.g., growth reduction; Vose and Swank 1995) and obvious ways (e.g., tree mortality; Clinton et al. 1993, Smith 1991).

II.D.3.c.(1). Hydrologic inputs and outputs. The network of climatic stations and rain gage locations will continue to be used to estimate precipitation input for each gradient plot. Both watersheds containing gradient plots are gaged and will continue to be used for estimating streamflow and evapotranspiration (i.e. $ET = \text{precipitation} - \text{streamflow}$). In addition, models used for carbon cycling will also have an evapotranspiration component which will be used to predict ET across the gradient.

II.D.3.c.(2). Inter- and intra-annual variation in soil moisture. Gradient plots will continue to be measured weekly for soil moisture at 5 and 20 cm depth using Time Domain Reflectometry (TDR). Soil moisture measurements have also been expanded via extensive transects (225 - 350 m, 25 m interval plots, 2 depths x 4 replicates per plot) in other watersheds (WS2, WS36) and within watersheds containing gradient plots (WS18 and WS27). These additional watersheds expand the gradient of aspect, soils, elevation, and vegetation type ranges found within the Coweeta basin. Along with streamflow and climatic data, soil moisture data from these measurements (monthly beginning Oct 94) are being used to parameterize and calibrate a terrain-based hillslope hydrology model for watersheds spanning the Coweeta basin (Yeakley 1993; Yeakley et al. in prep). Model output of lateral and vertical soil moisture distributions at approximately 10 m x 10 m spatial scales, at temporal resolution as fine as hourly, will be developed. These data will be linked with models which require soil moisture as a driving variable (i.e., soil CO₂, NPP) and with studies assessing tree regeneration patterns in gradient plots.

II.D.3.c.(3). Hydrologic modeling. Long-term hydrologic studies at Coweeta will be utilized to further develop a hydrologic model (IHACRE) for predicting daily streamflow for ungaged forested catchments. This research will be a collaborative effort with Tony Jakeman and colleagues at the Australian National University and Wayne Swank at Coweeta. Application of the rainfall-runoff model to Coweeta catchments will provide insights into refinement of methods needed to quantitatively predict how differences in physical attributes of catchments affect their hydrologic response. In another collaborative effort, led by the H.J. Andrews LTER, we will continue to participate in an intersite synthesis of hydrologic data and modeling for baseline and disturbed forest ecosystems.

II.D.3.d. Linkages among carbon, nutrients, and water cycling

One of our primary objectives is to understand the linkages among the ecosystem attributes using long-term data sets being developed ([Table 6](#)). In addition to these analyses of long-term data, we propose to establish shorter-term studies to determine specific linkages.

II.D.3.d.(1). Functional role of coarse woody debris. Functional roles (i.e. as a water or nutrient source) of coarse woody debris will be determined by sampling highly

decomposed CWD to determine the quantity of roots occupying CWD on each site. At the time of collection, subsamples of roots will be placed in buffered solutions where uptake of Ca and K will be monitored over a 1.5 hour period. The uptake rates will be measured twice during the growing season, during a dry and wet period.

II.D.3.d.(2). Relationships between fine root phenology, canopy processes, and the soil environment. If fine root phenology is regulated by environmental factors to the extent that canopy development is, then the timing of root growth and mortality might be expected to change across climatic gradients, in an altered climate, or during extreme weather events. However, we are currently unable to detect these changes because of our inability to quantify the effects of the soil environment on fine root activity, or to discriminate between inter-annual variation and environmentally induced changes in fine root demography. Periods of high water demand might also be expected to be closely related to root production, especially relatively deep in the soil. Unfortunately, root dynamics at depth > 30 cm have received little attention.

To quantify the relationships between fine root dynamics, soil moisture, and canopy physiology we will use the xeric oak and northern hardwood gradient plots, and establish two more plots at each forest type. These sites represent reasonable contrasts in overall soil moisture regimes, probabilities of growing season soil water deficits, and a balance between forest types in which root dynamics are relatively well (northern hardwoods) and poorly (xeric oak) understood. These sites also provide the opportunity to link this project with externally funded research on canopy water dynamics (Vose).

We will install five minirhizotrons (5 cm diameter x 2 m length) in each plot. Minirhizotron images will be collected monthly during the growing season on Hi-8 videotape (with a digital imaging camera) along a vertical transect in each minirhizotron inscribed with individually numbered image frames. Additional images will be produced during periods of drought or after significant rain events. The production and fate of each individual root appearing in the frame will be measured with ROOTS (Hendrick and Pregitzer 1992). Canopy water demand and balance will be determined from weekly measurements of leaf water potential and conductance using existing towers at the previously established gradient plots and less intensive measurements (shotgun sampling) at the new replicate plots. TDR will be used to measure soil moisture at all plots, and soil temperature will be installed at 0, 15, and 75 cm depths. Relationships between soil temperature, soil moisture, canopy transpiration, and root growth dynamics will be quantified.

II.D.3.e. The role of species vs. environmental heterogeneity in regulating ecosystem processes

Community types (i.e. species composition) vary considerably in response to the environmental heterogeneity which occurs across the gradient ([Figure 13](#)). Patterns of ecosystem processes such as nitrogen mineralization ([Figure 18](#)) and leaf decomposition ([Figure 19](#)) has generated questions about the relative importance of biotic vs. abiotic drivers of ecosystem processes. For example, the northern hardwood community soils and litter are coolest and, if temperature is a strong regulator of processes, we would expect process rates to be lowest in the northern hardwood community. However, this was not the case for many ecosystem processes. We will use transplant experiments to determine the relative importance

of species vs. environmental effects on organic matter decomposition and N-mineralization and nitrification. The soil transplant experiment is not a direct test of species effects per se, because of differences in soil type among the plots. However, large differences in soil carbon (ranges from 3.3 % on xeric oak/pine to 9.9 % on northern hardwood) and nitrogen (ranges from 0.1 % on xeric oak/pine to 0.7 % on northern hardwood) indicate that differences in species composition may be influencing soil characteristics.

II.D.3.e.(1). Decomposition. Nine species (*Pinus rigida*, *Acer rubrum*, *Acer saccharum*, *Liriodendron tulipifera*, *Betula lutea*, *Quercus coccinea*, *Quercus rubra*, *Quercus prinus*, and *Carya glabra*) representative of the dominant overstory composition among gradient plots will be studied. For wood decomposition, trees will be felled from areas outside the plots, and log segments 25-40 cm in diameter and 0.75 to 1 m in length will be cut. Eyebolts (30 cm long) will be placed in the ends of logs to facilitate weighing. Four randomly selected logs of each of the nine species will be placed at random locations (within reach of the walkways) in each gradient plot. Logs will be re-measured with a portable scale for weight loss (increment cores used to determine moisture for adjusting to dry weight) every year. Nitrogen and C content will be determined on wood from increment core samples, and logs will be visually scored for decay class. Small branch (< 1 cm) and leaf decomposition will be measured for the same species using litter bag techniques.

II.D.3.e.(2). Nitrogen Cycling. We will focus on three gradient plots: [northern hardwood (527), high elevation mesic oak (427), and xeric oak/pine (118)] representing extremes in environmental conditions and historical soil N cycling rates. We will use closed PVC cores to sample soil from ten random locations in each plot. Five of the cores will be removed (with the soil intact inside the cores) and transplanted in the following manner: northern hardwood to xeric oak/pine, northern hardwood to mesic oak, xeric oak/pine to northern hardwood, xeric oak/pine to mesic oak, mesic oak to xeric oak pine, and mesic oak to northern hardwood. The other five cores will remain on each site. Twenty-eight day *in situ* incubations will be carried out for 7 months during the growing season (April through October) for years 1 and 2.

II.E. Linkages to core areas of research

The network of LTER sites includes a broad array of research projects in diverse ecosystems. Throughout the life of the LTER program, one common thread at all sites has been research that addresses five core areas. The proposed research program at Coweeta continues this tradition of research in five core areas in both terrestrial and aquatic ecosystems of the southern Appalachians. 1) We are studying the pattern and control of primary productivity along environmental and disturbance gradients in hillslope forests, riparian zones, and streams. 2) Other research addresses the spatial and temporal distributions of populations representing different trophic levels and encompasses a diverse mix of taxa: algae, aquatic insects, stream fishes, understory and canopy plant species, birds, small mammals, amphibians, canopy insects, nematodes, and oribatid mites. 3) The pattern and control of organic matter accumulation in surface layers and sediments is being assessed in both forest soils and stream sediments along elevation, stream size, and disturbance gradients. 4) Our three-decade record of precipitation and streamwater chemistry, supplemented with focused studies of nutrient uptake and transformation in soils or streams, permits assessment and modeling of the dynamics of the input and

movement of nutrients in terrestrial and aquatic systems. Our riparian research is designed to quantify the movement of nutrients between these two ecosystems. 5) The pattern and frequency of both natural and anthropogenic disturbance in the southern Appalachians is a central focus of our proposed research.

II.F. Synthesis

Our proposed long-term studies build upon and expand our knowledge of populations, communities, and ecosystems in the southern Appalachians. Our research includes a diversity of studies at a range of spatial and temporal scales; however, they are integrated by a common focus on understanding the interaction and relative importance of disturbance and environmental heterogeneity on populations, communities, and processes. We include studies in both terrestrial and aquatic ecosystems at scales ranging from the plot, watershed, landscape, and southern Appalachian region. Our outward look beyond the Coweeta basin has required study of the interactions between humans, land use change, and ecological processes.

Our research approach melds long-term measurements, short- and long-term experiments, and modeling, to scale temporally and spatially and to synthesize diverse studies. Results from these studies will require between a few years (e.g. experimental forest canopy gaps) to decades (e.g. carbon cycling) to be fully completed. A longer-term goal, which we are just beginning in this proposal, is to link functional patterns and processes with the patterns of biodiversity which exist in the southern Appalachians. Currently, our research on oribatid mites and other soil invertebrates, shrews, and plant communities suggest that the southern Appalachians contain some of the most diverse communities in the temperate region. This work is most appropriately addressed by networks of investigators working within a long-term framework such as the LTER.

We will synthesize much of our present and anticipated future understanding with models of different temporal and spatial scales. For example, processes quantified at plot through regional scales will be linked through modeling ([Figure 14](#)); in fact, some of the models are already available while others remain to be developed during the course of the proposed research. Moreover, as described in the sections of proposed research, it will be necessary to couple sub-models to address broad environmental questions. For example, at a regional scale we will link C cycling and landscape land use changes to interpret the past and predict the future responses to disturbance and heterogeneity. Our past collaborative efforts of modeling processes and environmental responses to disturbance have been very fruitful for both understanding and assessment (SGM, PROSPER, NuCUM, PnetIIs) and we intend to continue this approach to synthesize findings.

III. LITERATURE CITED AND COWEETA LTER PUBLICATIONS

Please note that the literature cited in this proposal may occur in one of two places: A) in the Literature Cited below, or B) in the Coweeta LTER Publications (1991-1996). This format eliminated the duplication of numerous citations.

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II.B.4. Articles in review (total = 41)

Aber, J.D., A. Magill, S.G. McNulty, R. Boone, K.J. Nadelhoffer, M. Downs, and R. Hallett. 199_. Forest Biogeochemistry and Primary Production altered by Nitrogen Saturation. *Air Water & Soil Pollution* 00: 000-000.

Blood, E.R., K. Harlowe, W.T. Swank, and T.W. Williams. 199_. Hydrographic nutrient dynamics in a Coastal blackwater stream. *Water Resources Research* 00: 000-000.

Bolstad, P.V., and W.T. Swank. 199_. Cumulative effects of land use on water quality in a North Carolina watershed. *Water Resources Bulletin* 00: 000-000.

Clark, J.S. 199_. Environmental change and patch structure: can we distinguish changes in time with changes in age? *Conservation Biology* 00: 000-000.

Clark, J.S., E. Macklin, L. Wood, J. HilleRisLambers, and B. Cleveland. 199_. Spatial scales of recruitment limitation in southern Appalachian forests. _____ 00: 000-000.

Clark, J.S., B.J. Stocks, and P.J.H. Richard. 199_. Climate implications of biomass burning since the 19th century in eastern North America. _____ 00: 000-000.

Clark, J.S., L. Wood, P. Camill, and E. Macklin. 199_. Recruitment limitation in a southeastern Appalachian forest: evidence from seed production and dispersal in closed stands. *Ecology* 00: 000-000.

Clinton, B.D., K.J. Elliott, and W.T. Swank. 199_. Response of planted eastern white pine (*Pinus strobus* L.) to mechanical release, competition, and drought in the southern Appalachians. *Southern Journal of Applied Forestry* 00: 000-000.

Clinton, B.D., J.M. Vose, and W.T. Swank. 199_. Shifts in aboveground and forest floor carbon and nitrogen pools after felling and burning in the southern Appalachians. *Forest Science* 00: 000-000.

de Steiguer, J.E. and S.G. McNulty. 199_. An integrated assessment of climate change on timber markets of the southern United States. Pages 000-000 in *Southern Global Change*.

Elliott, K.J. and D. Hewitt. 199_. Forest species diversity in upper elevation hardwood forests in the southern Appalachian. *Castanea* 00: 000-000.

Gillespie, A.R., H.L. Allen, and J.M. Vose. 199_. Effects of canopy position and silvicultural treatment on the amount and vertical distribution of foliage in individual loblolly pine trees. *Trees: structure and function* 00: 000-000.

Hardt, R.A. and W.T. Swank. 199_. Structural and compositional characteristics distinguishing southern Appalachian old-growth from younger stands. *Natural Areas Journal* 00: 000-000.

Hendricks, J.J., J.D. Aber, and S.G. McNumty. 199_. Carbon and nitrogen chemistry of fine roots and foliage across a nitrogen deposition gradient in northeastern U.S. red spruce-balsam fir ecosystems. *Canadian Journal of Forest Research* 00: 000-000.

Johnson, D.W., R.B. Susfalk, and W.T. Swank. 199_. Simulated effects of atmospheric deposition and species change on nutrient cycling in loblolly pine and mixed deciduous forest. Pages 000-000 In *Southern Global Change*.

Knoepp, J.D. and W.T. Swank. 199_. Forest management effects on soil carbon and nitrogen. *Soil Science Society of America Journal* 00: 000-000.

Laerm, J., E. Brown, M.A. Menxel, and W.M. Ford. 199_. Distribution and status of *Cryptotus parva* in the southern Appalachians. *Georgia Journal of Science* 00: 000-000.

Laerm, J., W.M. Ford, B.R. Chapman. 199_. Records of *Zapus hudsonius* and *Napaeozapus insignis* (Rodentia: Zapodidae) in the southern Appalachians with comments on their conservation status. *Georgia Journal of Science* 00: 000-000.

Laerm, J., M.A. Menzel, and J.L. Boone. 199_. Mensural discrimination of *Sorex cinereus* Kerr and *Sorex longirostris* Bachman in the southeastern United States. *American Midland Naturalist* 00: 000-000.

Macklin, E. and J.S. Clark. 199_. Covariance of seed arrival and implications for tree competition: an example from southern Appalachian forests. *American Naturalist* 00: 000-000.

Mattson, K.G. and W.T. Swank. 199_. Nutrient fluxes from decaying hardwood woody debris. *American Midland Naturalist* 00: 000-000.

McNulty, S.G., P.L. Lorio, M.P. Ayers, M.P., and J.D. Reeve. 199_. Predictions of southern pine beetle populations under historic and projected climate using a forest ecosystem model. Pages 000-000 In *Southern Global Change*.

McNulty, S.G., J.M. Vose, and W.T. Swank. 199_. Predictions and projections of pine productivity and hydrology in response to climate change across the southern United States. Pages 000-000 In *Southern Global Change*.

McNulty, S.G., J.M. Vose, and W.T. Swank. 199_. Modeling loblolly pine hydrology and productivity across the southern United States. *Ecological Modeling* 00: 000-000.

McNulty, S.G., J.M. Vose, and W.T. Swank. 199_. Forest hydrology and productivity model development, testing, and validation at multi-spatial scales using a GIS. Pages 000-000 In *Scaling of remote sensing data for GIS*.

McNulty, S.G., J.D. Aber, and S.D. Newman. 199_. Nitrogen saturation in a high elevation spruce-fir stand. *Ecological Applications* 00: 000-000.

McNulty, S.G., J.M. Vose, and W.T. Swank. 199_. Potential climate change affects on loblolly pine productivity and hydrology on four sites in the southern United States. *Ambio* 00: 000-000.

- McNulty, S.G., J.M. Vose, and W.T. Swank. 199_. Predictions of net primary production, soil water deficit, evapotranspiration and drainage in southern U.S. loblolly pine stands. *Ecological Modelling* 00: 000-000.
- McNulty, S.G., J.M. Vose, and W.T. Swank. 199_. Prediction and validation of forest ecosystem processes at multi-spatial scales using a GIS. Pages 000-000 In D.A. Quattrochi and J.L. Star, editors, *Scaling of Remote Sensing Data for GIS*, Lewis Publishers, Chelsea, MI.
- Meyer, J.L. and W.T. Swank. 199_. Ecosystem management challenges ecologists. *Ecology* 00: 000-000.
- Ryan, D.F., J.D. Aber, J.S. Baron, B.T. Bormann, C.T. Driscoll, M.E. Fenn, D.W. Johnson, A.D. Lemly, S.G. McNulty, and R. Stottlemeyer. 199_. The changing role of nitrogen in forest ecosystems: Implications for policy and management. *Science Journal* 00: 000-000.
- Schaeffer, M.A., J.R. Webster, and E.F. Benfield. 199_. Microbial respiration on fine benthic organic matter in two Appalachian Mountain streams. _____ 00: 000-000.
- Sullivan, N.S., P.V. Bolstad, and J.M. Vose. 1995. Ecophysiology of twelve forest tree species in the southern Appalachian Mountains. *Tree Physiology* 00: 000-000.
- Sullivan, N.H., P.V. Bolstad, and J.M. Vose. 199_. Estimates of net photosynthesis parameters for twelve tree species in mature forests of the southern Appalachians. _____ 00: 000-000.
- Sullivan, N.H., J.M. Vose, J.M., P.V. Bolstad, B.D. Clinton, and W.T. Swank. 199_. Estimates of net photosynthesis parameters for a landscape level model of productivity for southern Appalachian hardwood forests. *Tree Physiology* 00: 000-000.
- Vose, J.M., K.J. Elliott, and D.W. Johnson. 199_. Soil respiration response to three years of elevated CO₂ and N fertilization in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). *Plant and Soil* 00: 000-000.
- Vose, J.M., and W.T. Swank, C.D. Geron, and A.E. Major. 199_. Emissions from forest burning in the southeastern US: application of a model determining spatial, temporal, and fire type variation. *Journal of Geophysical Research* 00: 000-000.
- Waterman, J.R., A.R. Gillespie, J.M. Vose, and W.T. Swank. 199_. The influence of mountain laurel on regeneration in pitch pine canopy gaps of the Coweeta Basin, North Carolina, USA. *Canadian Journal of Forest Research* 00: 000-000.
- Yeakley, J.A., B.L. Argo, D.C. Coleman, B.L. Haines, J.L. Meyer, and W.T. Swank. 199_. Hillslope nutrient flux during near-stream vegetation removal II. Pretreatment soilwater, groundwater, and streamwater dynamics. *Journal of Environmental Quality* 00: 000-000.

Yeakley, J.A., W.T. Swank, L.W. Swift, Jr., G.M. Hornberger, and H.H. Shugart. 199_. Soil moisture gradients and controls on a southern Appalachian hillslope from drought through recharge. *Journal of Hydrology* 00: 000-000.

III.B.5. Dissertations and theses (total = 29)

Baer, S.G. 1995. Colonization dynamics of benthic macroinvertebrates on artificial substrates in Appalachian headwater streams. M.S. Thesis. University of Georgia, Athens, GA.

Chung, K. 1992. Recovery of macroinvertebrate fauna from insecticide-induced disturbance in small headwater streams. Ph.D. Dissertation. University of Georgia, Athens, GA.

Davis, J.R. 1992. Nesting and brood ecology of the wild turkey in the mountains of western North Carolina. Ph.D. Dissertation. Clemson University, Clemson, SC. 76 p.

Dobbs, M.M. 1995. Spatial and temporal distribution of the evergreen understory in the Southern Appalachians. M.S. Thesis. University of Georgia, Athens, GA. 100 p.

Ehrman, T.P. 1994. Transport and retention of fine particulate organic matter. M.S. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, VA. 90 p.

Golden, K.S. 1991. Sulfur cycling along environmental gradients. Ph.D. Dissertation. University of Georgia, Athens, GA. 133 p.

Griffith, C., Jr. 1993. Relations between leaf nutrient concentrations and mineralization rates along an elevational gradient in the southeastern Appalachians, USA. M.S. Thesis. University of Georgia, Athens, GA. 89 p.

Grubaugh, J.W. 1994. Influence of elevation, stream size, and land use on structure, function, and production of benthic macroinvertebrate communities in two river ecosystems. Ph.D. Dissertation, University of Georgia, Athens, GA.

Houston, E.S. 1994. Macrofaunal community structure and production in depositional, riffle, and bedrock outcrop habitats along a second to fifth order stream gradient. M.S. Thesis. University of Georgia, Athens, GA.

Hutchens, J.J. 1994. The diet and growth of a leaf-shredding caddisfly, *Pycnopsyche*, in streams of contrasting disturbance histories. M.S. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, VA.

Lamoncha, K.L. 1994. Spatial and temporal variation in diversity of soil oribatida in Southeastern Appalachian Forests. M.S. Thesis, University of Georgia, Athens, GA.

Lugthart, G.J., III. 1991. Macrofaunal community structure and production in disturbed and undisturbed headwater streams. Ph.D. Dissertation, University of Georgia, Athens, GA. 165 p.

Marcilio, A. 1993. Macrofaunal community structure and production in a headwater stream: comparison of microhabitats, stream reaches, and years (1991-92 vs. 1983-84). M.S. Thesis. University of Georgia, Athens, GA.

Maxwell, R.A. 1993. The effect of *Rhododendron maximum* upon microbial populations in a southern Appalachian watershed. M.S. Thesis. University of Georgia, Athens, GA. 47 p.

McCaig, B.C. 1993. The clonal structure of black locust (*Robinia pseudoacacia*) in clearcut populations. M.S. Thesis. University of Georgia, Athens, GA. 62 p.

Paul, M.J. 1995. Fungal biomass in an Appalachian stream. M.S. Thesis, University of Georgia, Athens, GA. 94 p.

Rasmussen, C. 1994. The effect of the shape of seed dispersal curves on forest model predictions of community structure. M.S. Thesis, Duke University, Durham, NC, USA.

Rauch, S.D., III. 1991. Forest floor nitrogen mineralization and nitrous oxide emissions associated with fell-and-burn site preparation. M.S. Thesis. University of Georgia, Athens, GA. 125 p.

Reynolds, B.F. 1995. Elevation effects on forest canopy insect herbivory in southern Appalachian hardwood forests. M.S. Thesis. University of Georgia, Athens, GA. 74 p.

Sankovski, A. 1994. Diversity and structure of southern Appalachian and southwestern Caucasus forests with respect to historical events and present environment. Ph.D. Dissertation. University of Georgia, Athens, GA. 180 p.

Schaeffer, M.A. 1993. Effects of land use on oxygen uptake by microorganisms on fine benthic organic matter in two Appalachian Mountain streams. M.S. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, VA.

Smith, R.N. 1991. Species composition, stand structure, and woody detrital dynamics associated with pine mortality in the southern Appalachians. M.S. Thesis. University of Georgia, Athens, GA. 163 p.

Stone, M.K. 1995. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic macroinvertebrate community structure. M.S. Thesis, University of Georgia, Athens, GA.

Sun, L. 1993. Isolation, characterization, and bioavailability of dissolved organic matter in natural water. Ph.D. Dissertation. Georgia Institute of Technology, Atlanta, GA. 138 p.

Tank, J.L. 1992. Microbial respiration on decaying leaves and sticks along an elevational gradient of a southern Appalachian stream. M.S. Thesis. Virginia Polytechnic Institute and State University, Blacksburg, VA. 90 p.

Whiles, M.R. 1991. First-year benthic recovery of a southern Appalachian headwater stream following an insecticide induced disturbance. M.S. Thesis, University of Georgia, Athens, GA.

Whiles, M.R. 1995. Disturbance, recovery, and macroinvertebrate communities in southern Appalachian Mountain streams. Ph.D. Dissertation, University of Georgia, Athens, GA.

Wohl, D.L. 1994. Benthic macroinvertebrate community structure along a Southern Appalachian stream continuum: the influence of spatial scale. M.S. Thesis, University of Georgia, Athens, GA. 84 p.

Yeakley, J.A. 1993. Hillslope soil moisture gradients in an upland forested watershed. Ph.D. Dissertation, University of Virginia, Charlottesville, VA.

III.B.6. Presentations of the Coweeta LTER Project

From 01 July 1994 to 30 June 96, we had over 165 regional, national, and international presentations at various annual meetings and symposia. Complete bibliographic references of these presentations were located in the Coweeta LTER Annual Reports submitted in June of each year.

III.B.7. Graduate students involved with Coweeta LTER Project

We presently have 31 graduate and 44 undergraduate students supported by the LTER project.

IV. PROJECT MANAGEMENT, DATA MANAGEMENT, AND INTERSITE ACTIVITIES

IV.A. Project management

As Principal Investigators (PIs), Coleman and Vose will be responsible for overall direction and management of the project; Meyer and Swank had this responsibility during the previous granting period. Significant decisions involving operational changes, significant costs, or personnel are referred to an Executive Committee composed of Coleman, Meyer, Swank, Vose, and Kloeppe - LTER Site Manager and Researcher. This group communicates regularly by telephone and email. In the event that "conflicts of interest" on site use, disturbance experiments, or other agency/cooperator decisions cannot be resolved by the PIs or Executive Committee, the ultimate decision resides with the Director of the Southern Experiment Station, as provided in the basic cooperative agreement. It is important to note that this administrative tool has never been needed despite numerous cooperative studies conducted at Coweeta for the past 30 years.

Scientific decisions are reached by group consensus. This process has worked well for the three decades we have been doing interdisciplinary research at Coweeta. For

example, the transition in leadership was accomplished smoothly and by group consensus. A leadership transition at this time was planned in our 1990 renewal because we anticipated that Meyer and Swank would want to devote more time to their personal research interests. We believe that periodic changes in project leadership are consistent with the long-term nature of LTER projects. CoPI budgets are mutually agreed upon with the knowledge of the whole group.

Our project has expanded in scope and personnel over the past six years. We had 16 Co-PIs at 4 institutions in our 1990 LTER renewal proposal, whereas the current proposal has 30 Co-PIs at 8 institutions; 13 of these Co-PIs were a part of the 1990 proposal, 14 have been added during the course of the last 6 years, and 3 new Co-PIs were added for the renewal. As young scientists with needed expertise came to the Institute of Ecology and to the Forest Service at Coweeta, we sought to integrate them into the LTER project because we believe this to be an important mechanism for ensuring continuity in a long-term project like Coweeta.

Co-PIs and other staff at UGA meet monthly with the site manager and others for informal discussion and planning sessions over lunch. Notes from these meetings are circulated to all Coweeta researchers via email. One-day winter meetings of all Co-PIs provide an opportunity for intensive project planning and coordination, while two-day summer meetings for all Coweeta researchers, students, and technicians enable all to learn about the diversity of on-going research and to explore opportunities for joint research. Historically, we have utilized an external advisory committee to review the progress and direction of our LTER research. Comprised of 4 to 5 scientists who represent a range of disciplines, the group has convened at appropriate stages in our program. The advisory committee input has been an important, substantive tool for enhancing our science and it is our intent to continue the committee in the ensuing grant period.

On-site operations are handled by Kloeppel, our Site Manager and Researcher, who is assisted by a Field Technician, Analytical Lab Supervisor, and Analytical Lab Assistant. These people live near Coweeta and meet at least weekly to coordinate field activities and oversight of dorm facilities, field equipment, and field vehicles.

IV.B. Data Management System

IV.B.1. Introduction and philosophy

The Coweeta LTER Information Management System (IMS) began its efforts in 1989, with the establishment of the Coweeta Data Management (DM) and Geographic Information System (GIS) Laboratory. Using funds from NSF, a newly renovated computer facility was created at the Institute of Ecology, University of Georgia, and two full-time staff were hired to administer its development.

Recognizing the need to protect the legacy of the Coweeta data sets, our research team has made data archival and documentation an integral part of long-term research. Hence, the impetus for Coweeta IMS is to link quality-controlled data sets and metadata with their respective supporting publications and Principal Investigator (PI) information. This model does not separate data from metadata, and it assures all descriptive information about a particular research study is treated as one dynamic information entity.

IV.B.2. System description

The Coweeta IMS is comprised of a network of Sun SPARC workstations, and operated under the Unix environment. Its GIS is built around ESRI's ARC/INFO and ARC/VIEW software, and uses a digitizing tablet, color scanner, color printer, and pen plotter as its main input and output devices. In addition, the ERDAS package is used for the analysis of digital satellite images and multi- spectral aircraft data. Hence, the Coweeta GIS supports tools for both vector and raster analysis.

The Coweeta DM system uses the SAS data warehousing engine for most of the Coweeta data management tasks. By using the SAS/ASSIST module, one can easily create/update data sets, generate QA/QC procedures, and interactively summarize, graph, and analyze any of the archived data sets. This interactive view of the data has greatly improved the turn-around time for data archival. More importantly, it has given the data management personnel the necessary time to develop a front-end to the Coweeta database which is independent of both computer architecture and operating system. By combining the process strength of our SPARC server with the intuitive feel of WWW's hypermedia environment, Coweeta LTER data sets and other site information are now at the fingertips of all Coweeta PI's; and to a lesser extent to the rest of the web world. This has been possible by developing gateway interfaces between our databases and the webserver, and by writing numerous lines of HTML code. We are currently expanding these information distribution system services.

IV.B.3. Data gathering and information dissemination

Since its introduction, the Coweeta Data Management and GIS Laboratory has more than doubled its size and every piece of hardware and software used in the lab has been upgraded. In the last six years, our IMS evolved from a collection of ascii files residing on a 9mm Magnetic tape, to an interactive,online information system, with full support for GIS and data analysis. Several new products have sprung from this continuous growth. We welcome both LTER and non-LTER communities to access these services via our web server (site access at <http://oikos.ecology.uga.edu>). You will find the following information:

IV.B.3.a. Coweeta LTER site

An introduction to over 60 years of information about the history of the Coweeta Hydrologic Laboratory, and more recent details about the Coweeta LTER project and its mission.

IV.B.3.b. Research team

Information about the Coweeta Research Team. This page is under construction, and is currently testing the CNIDR Isearch index engine. This search routine allows for the full index and interpretation of HTML pages. (Compare it with the waisindex engine currently used with the Coweeta bibliographic database).

IV.B.3.c. Bibliographic references

There are over 50 years of Bibliographic References (> 800 **in total**), comprising both Coweeta non-LTER and LTER publications. These references are currently indexed with the waisindex engine under our Gopher server.

IV.B.3.d. Description of ongoing research

A full description of all ongoing LTER research studies, including our recent southern Appalachian Landscape study.

IV.B.3.e. Coweeta data sets

This is the heart of the Coweeta Information System. We have linked raw data and metadata with their respective supporting publications and PI's information. We currently have 63 core data sets on line. Notice that the ongoing research area is restricted to Coweeta LTER PI's only. You can check this area by logging in as "reviewer" and using the password "nsf-guest". Each PI can interactively document his/her own data set. If you have any problem accessing this area please contact Gil Calabria at (706) 542-5691 or gil@sparc.ecology.uga.edu.

IV.B.3.f. Coweeta GIS atlas

Displays Coweeta and Southern Appalachian Study GIS layers. The Coweeta Basin map is linked to physical description and treatment summaries for all watersheds.

IV.B.3.g. Coweeta photo album

Currently under construction, we plan to include historical photos of watershed treatment (site instrumentation, landscape characteristics, etc.) in this new section.

IV.B.4. Future direction = interactivity

The incredibly fast developments on the World Wide Web (WWW) have promoted the dissemination of information and interactions between end-user and networks. This includes taking advantage of Object-Oriented technology to increase the interactivity between the Coweeta IMS and Coweeta researchers. We are closely following the advances on the JAVA programming environment, and plan to use this powerful language to create real-time models of Coweeta data sets. This high level approach will promote communication among the Coweeta LTER researchers, and also facilitate intersite comparisons and further intersite research.

IV.C. Intersite Research and Activities

During the past 6 years we have led or participated in more than 30 LTER intersite research projects. Currently, we are involved in a total of eleven Intersite or International activities, which includes virtually all of the LTER sites, and a joint USA/Russia bilateral project (Table 8). Other projects are in the development stage, including the Soils Standardization volume, organized by Phil Robertson, of the KBS LTER (Coleman as site representative). In fact, several of the intersite activities are funded by supplemental funds, enabling us to obtain leverage in that fashion.

V. RELATED RESEARCH

A principal source of additional funding is provided by the United States Forest Service funding the Coweeta Hydrologic Laboratory, which provides in kind support exceeding \$500,000 per year. We provide, in turn, support for travel and some maintenance items which might not otherwise be available. There are additional sources of funds for several projects at Coweeta via NOAA, the EPA, and other agencies which further broadens our funding base. Additional funding of several more intensive field studies, several funded by the NSF, gives us a greater extent of research activity, as well. These projects include the NSF-funded multiple-year study of litter exclusion effects on stream ecosystem function, on Watershed 55, with J. Bruce Wallace as P.I.

A total of 72 cooperative studies have been carried out or are ongoing, over the past five years at Coweeta ([Table 9](#)). These projects, many of which are conducted under formal cooperative agreements between the Forest Service and other agencies and institutions as noted. Studies range from single investigator efforts to projects involving numerous investigators and multiple sites. It is clear that LTER objectives and research activities provide a catalyst to attract additional research and this body of extramural research results in mutual leveraging of science and resources with the LTER program.

VI. TECHNOLOGY TRANSFER

Basic information and understanding derived from the Coweeta LTER research program is used extensively by resource planners, regulators, and policy makers at local, regional and national levels. These users encompass a wide array of federal (USFS, EPA, etc.) and state (Division of Environmental Management) agencies, private industry, and the general public. Only several specific examples of many possible cases are cited.

In one case, the ecological Principals derived from Coweeta LTER research have been incorporated into a large Ecosystem Management project on National Forest land in Western North Carolina. The desired future conditions on Wine Spring Creek watershed are partially founded on these Principals which are being tested in a management context. This interdisciplinary effort involves more than 50 investigators, with participants from the National Forest System, 6 Forest Service Research Work Units, 6 Universities, state agencies, conservation and environmental groups, EPA, and the general public. Resource prescriptions of prescribed burning, regeneration harvests, stream woody debris to maintain or enhance flora and fauna diversity, terrestrial and aquatic productivity, mixed hardwood old-growth, recreation opportunities, and economic returns. These applications provide not only dividends in improved resource management but also an opportunity to test and revise Principals in an operational context.

A second example is the incorporation of forest biogeochemical cycling knowledge, from a productivity perspective, in to the framework of a Decision Support System for the effects of management practices on National Forest lands. The effort synthesizes the long-term research on nutrient cycling responses to disturbance at Coweeta in to a user friendly management tool that will be used for planning purposes.

A primary, recurring mechanism for transferring science to user groups is through on-site tours to a wide array of groups. Highly tailored lectures and watershed tours are provided to more than 1400 visitors annually.

VII. FACILITIES AND EQUIPMENT

USFS facilities at Coweeta include two office buildings, three office and laboratory trailers, a laboratory building with a complete analytical laboratory and a 40-seat conference room, chemical storage building, visitor information center, record vault, storage building, maintenance and instrument repair shop, flammable storage building, a three-bedroom residence used for senior scientists on sabbatical leave and/or investigators from abroad, and a recently renovated dormitory. The research environment for visiting investigators at Coweeta was greatly improved during the late 1980's by completion of renovations to the dormitory, which was accomplished with funds from NSF Biological Research Resources Program. The facility fills a major need for overnight housing for Coweeta CoPIs and students and provides accommodations for investigators from other sites. The building accommodates up to thirty researchers with sleeping, cooking, bath and laundry facilities. It is operated by the Institute of Ecology at UGA under a cooperative agreement with the U.S. Forest Service.

Access to research sites at Coweeta is facilitated by three main gravelled roads, which are open most of the year and by service roads which require four-wheel drive vehicles and are closed to the public. Coweeta-LTER has 3 four-wheel drive vehicles, which are kept at Coweeta for use by CoPIs in the field and 3 vans which are used for transportation between UGA and Coweeta.

Major field installations include 6 climatic stations, 9 precipitation stations, and 17 active weirs. Elemental analysis is performed on stream samples from 16 of these watersheds, and stream temperature is measured on 3 watersheds. Air temperature, humidity, wind speed and direction, and rainfall are monitored at all climatic stations, while soil temperature is monitored at all but one station. Pan evaporation, dry deposition, trace metal concentrations, and solar radiation are monitored at the main climatic station. Standard and recording rain gages are located at 2 of the climatic stations and at 7 other locations within the basin. Precipitation samples for chemical analyses are collected at 8 locations. Ozone analyzers are installed at 10m at the main climatic station a higher elevation ozone analyzer was installed above the canopy at the ridgeline in a white pine watershed (WS 17).

The analytical laboratory at Coweeta contains standard laboratory equipment as well as a carbon analyzer, Technicon AutoAnalyzer, atomic absorption spectrophotometer with graphite furnace and a gas chromatograph. With this on-site analytical lab, investigators have access to a limited amount of bench space, chemicals, glassware, and other supplies and equipment, including balances, ovens, refrigerators and freezers, environmental chambers and modern analytical instruments.

Data processing facilities at Coweeta continue to be improved by the USFS. The processing center contains a Data 100 Series 70 terminal, which is used as a remote job entry station connected by dialup line to UGA. Microcomputers and modems are also used to access mainframe and microcomputers at UGA and other cooperators. A Numonics digitizer for digitizing strip charts and a Mitron paper tape reader are interfaced with microcomputers and used for reduction of the data collected by field

instruments at weirs and precipitation gages. IMB-PC's are interfaced with analytical equipment in the laboratory. The GIS system was described previously (Section IV.B.). We have also "hard-wired" full electronics communications between the Dormitory (for downloading data), laboratory, and office areas at Coweeta, facilitating communications with the UGA investigators, and all subcontract co-PI's.

LTER research at UGA is done primarily in the laboratories of the CoPIs. New data management and GIS facilities at UGA were described in Section IV.A. Analytical capabilities for LTER researchers at UGA were recently improved with the purchase of a new atomic absorption spectrophotometer with a graphite furnace and were further upgraded with funds from NSF's Division of Instrumentation and Resources. Equipment on hand includes a Tracermass stable isotope ratio mass spectrometer and Roboprep CN Dumas, a 5- sample preparation train, a VG Micromass upgrade and a Finnigan MAT Delta E isotope ratio mass spectrometer upgrade (for instruments at Stable Isotope Lab at UGA), an AlpKem flow-injection analyzer with digestion block, a Carlo Erba C-N analyzer, a Leco Sulfur Analyzer, a Shimadzu Ion Chromatograph, a gas chromatograph, and an image analysis system for use with minirhizotrons and hemispherical photography.

At the Virginia Tech laboratory, we have standard laboratory equipment plus DOC analyzer, ion chromatograph, spectrophotometer, HPLC, and fluorometer.