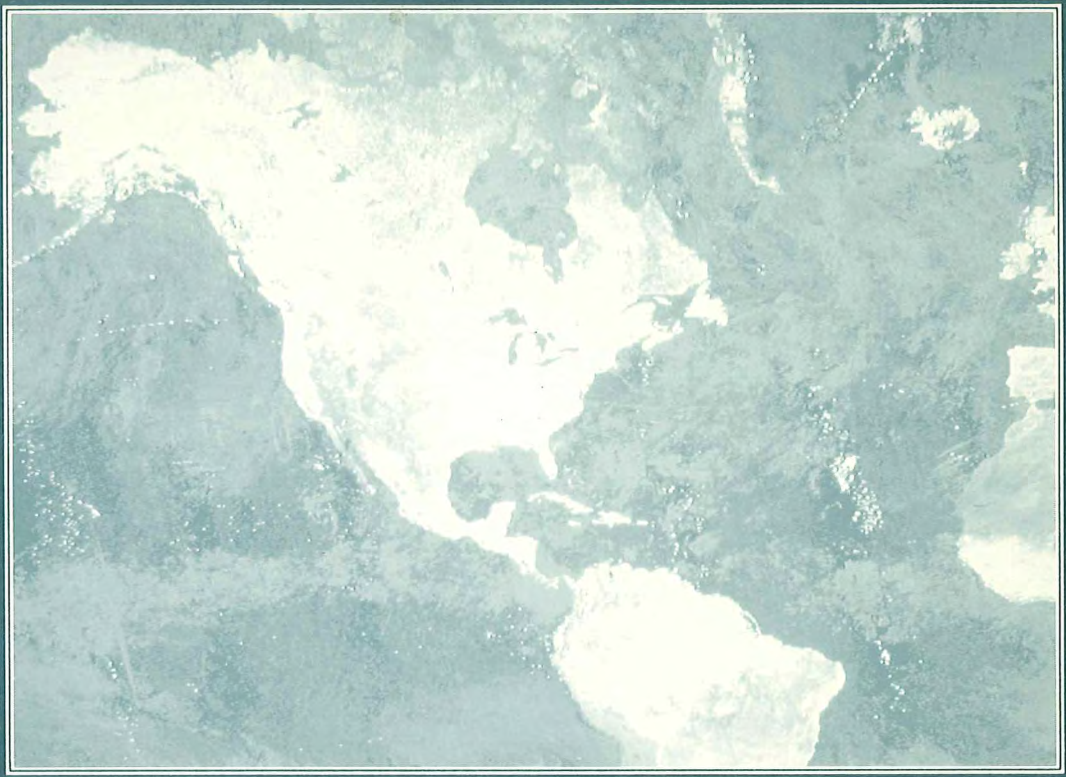

# LONG – TERM ECOLOGICAL RESEARCH IN THE UNITED STATES

## A Network of Research Sites 1991

*Sixth Edition Revised, LTER Publication No. 11*
*Long-Term Ecological Research Network Office, Seattle, Washington*

## Credits:

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# Long-Term Ecological Research In The United States

## A Network of Research Sites • 1991

(6th edition, revised)

**Edited by**

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and

Stephanie Martin

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NATIONAL SCIENCE FOUNDATION

*Directorate for Biological, Behavioral and Social Sciences*
*Division of Biotic Systems and Resources*

***Memorandum***

TO: Investigators Interested in Working at Existing LTER Sites

FR: Division Director, Biotic Systems and Resources, National Science Foundation

RE: Invitation for Extended Use of LTER Sites

The Division of Biotic Systems and Resources (BSR) at the National Science Foundation has undertaken the support of research to understand long-term ecological phenomena. One mechanism to assist in this important area of research was the establishment, in 1980, of a national network of sites, using the competitive review process, and termed the Long-Term Ecological Research (LTER) Network.

One stated objective in establishing these site-specific projects is to offer the braoder environmental biology research community the opportunity to use the sites for both long-term and short-term projects appropriate to individual sites, a group of sites, or the network as a whole. BSR promotes the extended use of LTER sites by collaborative and visiting scientists.

Some of the benefits of working at LTER sites include: (1) well-documented and assessible records of background and corroborative data; (2) field sites with ready access and long-term availability; (3) opportunity to interact with other scientists on subjects of mutual interest; (4) for some scientific problems, the opportunity to compare ecological patterns and processes across a range of sites.

Initial arrangements for collaborations must be made with personnel at the LTER site(s) under consideration. Proposals to NSF for such collaborative work should be submitted via normal means to the appropriate disciplinary program. Each proposal for work at an LTER site must include documented evidence of availability of required accommodation. It is advisable, also, to contact the program director of the appropriate disciplinary program, prior to preparing a proposal to NSF, to learn of any special, short-term additional funding opportunities that might arise from time to time.

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## *Development and Research Core Areas*

Long-Term Ecological Research (LTER) is a program supported by the National Science Foundation's (NSF) Division of Biotic Systems and Resources (BSR). The program was developed from 1976 to 1979 when the first open competition for support was announced. LTER acknowledges:

1. That there are ecological phenomena that occur on time scales of decades or centuries, periods of time not normally investigated with research support from NSF.

2. That many ecological experiments are performed without sufficient knowledge of the year-to-year variability in the system. Interpretation is, therefore, difficult. This is especially true when the system in which the experiment is performed is not at equilibrium.

3. That long-term trends in natural ecosystems formerly were not being systematically monitored. Unidirectional changes that were observed could not be distinguished from cyclic changes on long time scales.

4. That a coordinated network of sites was not available to facilitate comparative experiments. Furthermore, data management was not being coordinated between research sites. Therefore, comparative analyses could not be performed and theoretical constructs could not be conveniently tested.

5. That examples of natural ecosystems were being converted to uses incompatible with ecological research.

6. That as a result of advances in ecological research, phenomena at higher or lower levels of organization have been treated as insignificant or constant or have been oversimplified. This problem can be alleviated by performing intensive investigations at single sites, leading to an accumulation of overlapping information. Through time, site-specific research will generate increasingly valuable data sets, revealing pattern and control at several levels of ecosystem organization.

### *Five Core Areas*

Initial convergence of the LTER effort was encouraged by requiring that sites address research efforts in five core areas. These were:

- pattern and control of primary production;
- spatial and temporal distribution of populations selected to represent trophic structure;
- pattern and control of organic matter accumulation in surface layers and sediments;
- pattern of inorganic inputs and movements of nutrients through soils, groundwater, and surface waters; and
- pattern and frequency of disturbance to the research site.

The institutions serving in support of LTER sites are committed to encourage collaborative research by scientists at other institutions. LTER sites should be considered regional or national research facilities. Researchers interested in using these facilities should contact the appropriate site(s) identified in this book.


# H.J. Andrews Experimental Forest (AND)

## RESEARCH SETTING

The H.J. Andrews Experimental Forest research program has roots extending back more than 40 years. Long-term field studies and interdisciplinary studies of geomorphology-vegetation-stream systems have been the cornerstones of the research program, which is now evolving rather dramatically in response to new opportunities emerging from global change issues and from regional controversy concerning future management of Pacific Northwest forest and stream ecosystems.

The H.J. Andrews Experimental Forest was established by the USDA Forest Service in 1948. Research efforts focused on logging and regeneration in the 1950s, watershed research in the 1960s and, since the 1970s, ecosystem-level processes. Research use of the site expanded rapidly in the 1970s with National Science Foundation support of the Coniferous Forest Biome investigations as part of the International Biological Program. Since 1977, Oregon State University and the Forest Service have jointly administered the site to enhance research, education, and transfer of information into natural resource management. The Andrews site and the Ecosystem Research Group began participation in the Long-Term Ecological Research (LTER) Program in 1980. Approximately 50 scientists, 25 graduate students, and 15 undergraduate students utilize the site each year for research. Over 100 research projects are currently underway.

The Andrews is part of several networks of research sites in addition to LTER. Globally, the Andrews is a Biosphere Reserve in the UNESCO Man and the Biosphere program (MAB). Locally, six nearby Research Natural Areas (RNAs) of more than 400 hectares (ha) each provide additional examples of Cascade Mountain ecosystems. Three Wilderness Areas within 20 kilometers (km) offer opportunities for studies that do not require manipulations.

### Site Characteristics

The H.J. Andrews Experimental Forest is located in the rugged Cascade Range approximately 80 km east of Eugene, Oregon. It is 6,400 ha in size and ranges from about 412 to 1,630 meters (m) in elevation. The landscape has been deeply dissected by a variety of fluvial and mass erosion processes.

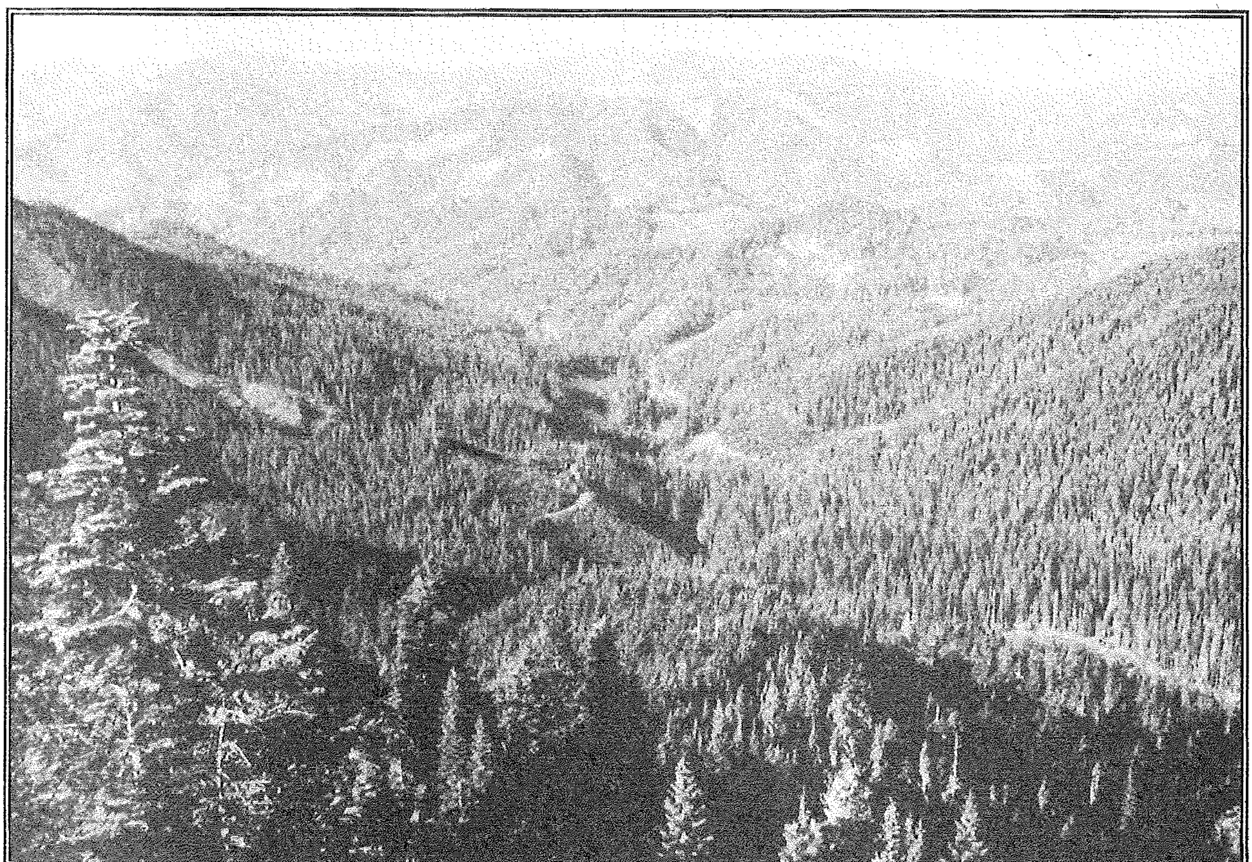
The maritime climate is mild with wet winters and cool, dry summers. Annual precipitation normally exceeds 2,540 millimeters (mm) and is concentrated in the winter, when deep snowpacks are common above 1,000 m elevation. Little rain falls during July and August.

When it was established in 1948, the Andrews was covered with virgin forest. Since then, approximately one-third of the Forest has been logged or manipulated for research and plantations of conifers have been established. Old-growth forest stands with dominant trees over 400 years old still cover about 40 percent of the total area. Mature stands (100 to 140 years old) originating from wildfire cover about 20 percent. Forest types at lower elevations are dominated by Douglas-fir, western hemlock, and western red cedar. Upper elevation stands consist of mixtures of true firs and mountain hemlock.

Low- and mid-elevation forests in this area are among the tallest and most productive in the world. Average heights are in excess of 75 m and a typical stand stores in excess of 600 megagrams of carbon per ha. These forests are also noteworthy for the large amounts of fine and coarse woody debris they contain. As elevation increases, Douglas-fir and western red cedar decline in importance and western hemlock is gradually replaced by Pacific silver fir. Non-forest habitats include wet and dry meadows, rock cliffs, and talus slopes.

Rapidly flowing mountain streams are the primary type of aquatic ecosystem in the Andrews Forest. Streamflow follows the precipitation pattern with winter maximum flows three orders of magnitude larger than summer minimum. First- and second-order streams under natural conditions are dominated by coarse woody debris and receive a large annual input of litter which provides the energy base for the aquatic organisms. Larger order streams have a higher proportion of the energy base provided by in-stream photosynthesis, but litter inputs and coarse debris remain important components of all stream ecosystems.

In terms of biological diversity, the Andrews Forest supports a rich flora and fauna for a north temperate ecosystem. More than 600 vascular plant species are known to occur on the Andrews Forest, and the nearby RNAs include more than 100 additional species. Typical 0.5-ha plots in the upland sites include 35 to 40 species of vascular plants and riparian sites twice that number. Over 3,400 arthropod species have been reported, which probably represent slightly more than half the estimated total. About 20 species of reptiles and amphibians, seven species of fish, and 50 species of mammals are found on the Andrews. Over 70 species of birds are known to nest here. Plant and animal species associated with old-growth forests of the Pacific Northwest, including the Vaux's swift and the northern spotted owl, are especially well represented.



*View westward down the Lookout Creek drainage. The H.J. Andrews Forest occupies the lower two-thirds of the photo.* F. SWANSON

The Andrews site resides within a matrix of land ownerships and land-use patterns. In addition to the preserves, such as Wilderness and RNAs, there are extensive, continuous tracts of industrial lands in young plantations and federal land with highly fragmented patterns of forest cutting. Potential establishment of Habitat Conservation Areas for conservation of the northern spotted owl (*Strix occidentalis*) would create yet another landscape scale treatment--no cutting in 20,000 to 40,000-ha areas where past cutting has created plantations over 20 to 40 percent of the landscape. These diverse land use patterns comprise a series of large-scale experimental treatments differing in grain size and timing and rate of cutting.

## RESEARCH PROGRAM STATUS

As the Andrews LTER program enters its second decade, we face the challenge of sustaining existing long-term studies while expanding synthesis studies and establishing new research on emerging regional- and global-scale issues. All of these activities fit with our overall goal of developing concepts, hypotheses, models, and other techniques to evaluate effects of disturbances, both natural and anthropogenic, on ecosystem structure, function, and species composition.

Field and modeling studies involve strong cooperation among LTER-related institutions and research projects. The Andrews LTER program and site provide a focal point for research by scientists at Oregon State University (OSU), the USDA Forest Service Pacific Northwest Research Station, Willamette National Forest, University of Washington, EPA/Corvallis Laboratory, US Geological Survey, and other institutions and agencies.

### *Long-Term Field Studies*

LTER research at H.J. Andrews has focused on seven areas of field studies and associated modeling.

**Disturbance regime:** Pristine Pacific Northwest landscapes were shaped by a variety of natural disturbances. Some aspects of the dendrochronologic record of natural disturbances extend back more than 800 years, the age of the oldest living trees in the area. Since World War II, logging, fire suppression, and other management activities have radically changed the disturbance regime of these high mountain landscapes. Major land-use change is underway in the region in the form of the conversion of natural forest to a mixture of plantations and areas reserved to meet wildlife and other non-timber objectives. In some ways this conversion is subtle; that is, it is not a conversion of vegetation type or dominant species. But some effects may be profound—for example, the great reduction in extent of old-growth forest habitat and the amount of carbon stored in the terrestrial ecosystem.

A period of rapid climatic change could markedly alter disturbance processes and patterns. The potential effects of changes in land use and climate present major challenges for predicting future ecosystem behavior under altered disturbance regimes.

Using aerial photography, dendrochronology, archival, and other techniques, we have characterized the pattern and frequency of disturbance, both natural (wildfire, flooding, landslides, windstorms) and human-induced (forest cutting, road construction, sheep grazing) for the Andrews and vicinity. Past research indicates that topography, geology, and soil characteristics exert substantial control over the spatial and temporal pattern of natural disturbance processes. Consequently, the disturbance regime of such mountain landscapes must be examined in a topographically specific fashion.

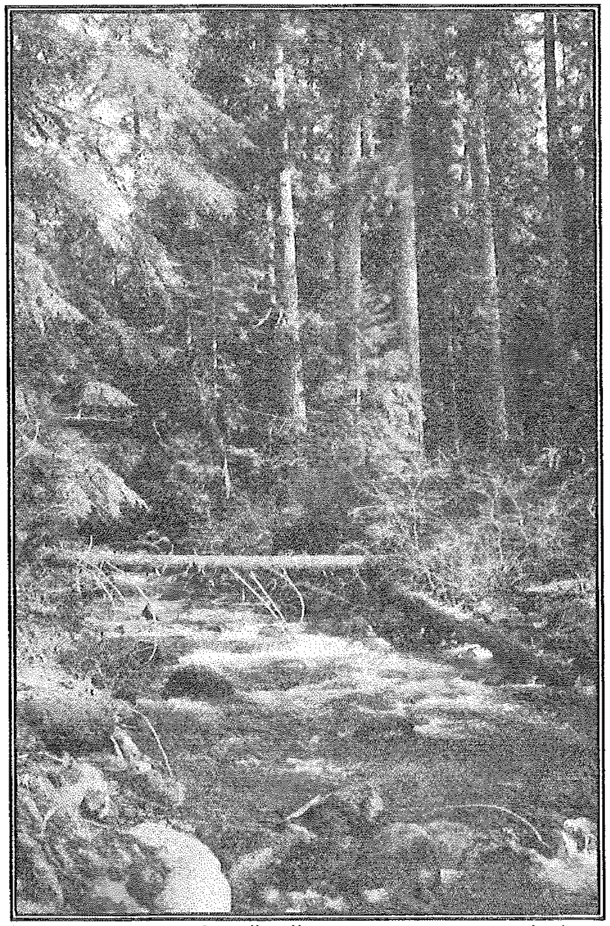
**Vegetation succession:** Several systems of permanent, terrestrial-vegetation plots are being used to characterize secondary succession, tree mortality, and associated processes and habitats. These plot systems cover both the Andrews Forest and coarser-scale, regional environmental gradients of forest types. A system of 1 ha reference stands includes representatives of the major plant associations in the central western Cascade Mountains. Plots up to several ha in size are located in stands originating after wildfire, logging, and volcanic disturbance (Mount St. Helens). Some plots represent a chronosequence beginning at the time of disturbance and extending to old growth. Plots established before disturbance and observed for more than 25 years after clearcutting and burning provide detailed information on patterns of early succession. Long-term mortality measurements of the regionally extensive array of reference stands offer insights into the rates and types of mortality in Pacific Northwest forests.

The permanent plot system has provided a data base with which we are examining local and regional effects of climate change on vegetation patterns and carbon dioxide ($CO_2$) fluxes. The latter study is especially intriguing in that it suggests that conversion of natural Pacific Northwest forests to intensively managed plantations has released substantial amounts of $CO_2$ to the atmosphere. Some global-scale studies argue, on the other hand, that these forests are a $CO_2$ sink rather than a source.

Under LTER and other funding, descriptive and experimental vegetation studies also address the scale of forest canopy gaps and stand edges, where discontinuities in stand structure affect microclimate, soil properties and processes, wildlife, and under-story plant populations. In these tall forests some aspects of the microclimatic effect of forest-clearcut edges may penetrate over 200 meters into the stand.

Arthropod ecology: Various studies, some based on sampling in the reference stand system of plots, has documented aspects of the arthropod fauna and its ecological roles in the Andrews Forest and vicinity. Sampling of soil, forest, and stream habitats of the Andrews has resulted in the identification of over 3,400 species of arthropods, comprising one of the best-known arthropod faunas of any research site in the world. Biological and ecological information is available for most species. Species diversity is remarkable; the soil in undisturbed forest, for example, contains 200 to 250 species of arthropods and 100,000 to 200,000 oribatid mites per square meter. Soil arthropod diversity increases through successional development of forest stands.

Canopy arthropod communities also differ among successional stages of vegetation. Old-growth forest canopies, for example, have a higher diversity of species and functional groups than young forests (10 years). The biomass of aphids is an order of magnitude higher in young stands and the abundance and diversity of predators, such as spiders, is greater in old-growth stands. Successional trends in terms of the functional group composition of canopy-arthropod communities in the Andrews are similar to those found in taxonomically dissimilar eastern deciduous forests of the Coweeta LTER site.



*Massive forests profoundly affect stream ecosystems in the Andrews Forest.* F. SWANSON

Young stand productivity: Much of the past research on nutrient cycling and stand dynamics in the region has focused on very young and very old stands. The point of canopy closure and associated self-thinning is a crucial, little-studied stage of stand development. Therefore, we installed a long-term experiment in 1981 to investigate the influence of forest structure and topo-edaphic factors on productivity and on self-thinning processes of 20- to 30-year-old Douglas-fir stands. Experimental treatments include thinning, pruning, and multi-nutrient fertilization replicated in four stands.

We have confirmed our hypothesis that available nitrogen (N) is the most important direct control over net primary production (NPP) in these forests. Other nutrients, however, appear to play an important role in the N cycle and in the ability of trees to take up N. For instance, N mineralization rates (anaerobic) correlate positively with concentrations of exchangeable base-metal cations (especially calcium, Ca) while foliar N concentrations correlate more closely with total soil phosphorus (P) and exchangeable Ca than with measures of soil N availability.

Self-thinning in these decade-old experimental plots has not begun, since competition is not yet severe enough to result in mortality. The experiment will continue at least through a major wave of mortality in the more heavily stocked stands.

Long-term site productivity: Soil N and organic matter (OM) stores are important to local long-term productivity of Pacific Northwest forests, and concerns have been voiced for more than 20 years that forest management practices in the region may remove excessive amounts of N and OM. The LTER group is teaming with a Forest Service research program investigating long-term productivity at a number of large experimental treatment sites in Oregon and Washington. The intent is to test various hypotheses concerning long-term effects of different manipulations of vegetation, severity of burning, and levels of logging slash and litter removal. The experimental site associated with the Andrews will be established in a nearby several-hundred-ha area of 80-year-old, post-wildfire forest.

This experiment will provide insights into mechanisms that help stabilize systems against natural disturbances, such as wildfire and insects, and against climate change. We believe that the spatial and temporal pattern of system recovery after catastrophic disturbance is determined by biological "legacies" from the pre-disturbance stand. Such legacies may be structural (e.g., decayed logs or soil aggregate structure created by the previous stand), biological (e.g., propagules of higher plants, mycorrhizal fungi, and other soil microflora and fauna), or chemical (e.g., local accumulations of carbon, N, or allelochemicals in the soil). The site productivity experiment, therefore, will selectively manipulate several of these legacy elements to determine the pattern and magnitude of their effect on primary production, nutrient cycling, and other ecosystem characteristics during secondary succession.

Decomposition processes: Andrews research on decomposition and release of nutrients from detritus focused primarily on coarse woody debris during the 1980s. A major task of LTER in the 1980s was installation of long-term decomposition studies of fine and coarse woody debris both on land and in streams. The thrust of these experiments is to determine effects of substrate size and quality and site environment on the pattern and rate of decomposition and nutrient release. In the largest and longest experiment, more than 500 logs (about 50 centimeters in diameter and 5.5 m in length) of four species were placed at six sites in old-growth forests. The present study design would accommodate 200 years of destructive sampling. Mass and N content have been sampled annually since installation of the study in 1985, revealing unexpectedly rapid decay rates for Pacific silver fir.

This experiment has offered an exceptional opportunity for detailed study of the decay process. In conjunction with another NSF grant rates of consumption by invertebrates, N fixation, water infiltration, leaching, fragmentation, respiration, and changes in carbon fractions (cellulose and lignin) were measured for two years. These studies revealed that during early stages of decomposition logs are net sources of N for the forest floor. The primary mechanism of export is the production and subsequent fragmentation of fungal fruiting bodies. Logs thus differ strikingly from fine litter, in which leaching controls N export and fungi primarily immobilize N.

Log and fine litter respiration are asynchronous at the Andrews; log respiration peaks at the end of summer drought when fine litter respiration is at a minimum. Such information on the role of water in decomposition processes is important in modeling effects of climate change on nutrient availability and $CO_2$ release.

In the 1990s we will continue the log decomposition work and increase emphasis on decomposition of smaller detrital components--fine litter, roots, and branch wood. The major effort on fine litter decomposition will be within the 10-year, 28-site, litter-exchange experiment initiated in 1990.

Forest-stream interactions: The Andrews group's broad-based analysis of forest-stream interactions has grown steadily in intensity and breadth since the mid-1970s. Research under LTER and related funding has involved experimentation in natural and artificial streams, computer simulation, and field observations. The major focus has been on influences of geomorphology and streamside vegetation on aquatic ecosystems, including distributions of aquatic organisms, rates of nutrient transport and processing through drainage networks, and basin-wide distribution of major vertebrate species (rainbow and cutthroat trout).

These studies of forest-stream interactions are set within a hierarchical framework of the structure of stream and valley floor ecosystems. Primary scales of interest are channel units (pools, riffles, boulder cascades) and reaches which are areas of valley floor hundreds of meters to kilometers in length that differ in the type and degree of geomorphic constraint on channel and valley floor width. A variety of geomorphic agents, such as landslide deposits and zones of hard bedrock, constrain some reaches. Unconstrained areas where the valley floor is wide have greater canopy opening over the stream, greater diversity of streamside vegetation, and more extensive and diverse aquatic habitat than neighboring constrained reaches. These unconstrained stream reaches have greater rates of nutrient and leaf litter retention, and higher standing crops of primary producers, and fish in response to higher light levels and greater foraging efficiency for fish than are observed in constrained reaches.

Another aspect of forest-stream interaction research is the long-term program of observations on small (9 to 100 ha), experimental watersheds and intermediate-sized (about 6,000 ha) watersheds in the Andrews and vicinity. Three sets of small, paired watersheds, consisting of eight total basins, include clearcut, partial cut, burn, and no-burn treatments as well as controls. Treatments were conducted in the 1960s and 1970s. Observations include revegetation and water, nutrient, and sediment budgets.

The intermediate-sized watersheds include the Lookout Creek drainage at the Andrews and the neighboring upper Blue River, which have had different histories of cutting and road construction. These watersheds, therefore, provide opportunities to examine the effects of forest cutting and regrowth on peak and low streamflows at a larger scale than traditional small watershed studies. Analysis of historical streamflow records and modeling of streamflow are now underway.

## FUTURE DIRECTIONS

Our commitment to long-term field experiments will continue through the 1990s. In addition, we will focus synthesis efforts on the question: How do natural disturbance (wildfire, geomorphic processes), land use (logging), and climate change (warming, drying), acting individually or jointly, affect key ecosystem variables at stand and landscape scales?

Emphasis on this question is timely for several reasons. Land-use practices, including extensive logging of old-growth forest, are altering the Pacific Northwest landscape at an unprecedented rate. Changes in global climate are likely to have dramatic and diverse impacts on the region's ecosystems. Studies in early stages on this question include land-use and climate change effects on carbon stores in terrestrial systems and on peak and low streamflow as a result of altered snow hydrology and hydrologic effects of vegetation.

Approaches to this question will include both conceptual and quantitative modeling designed to increase understanding of pattern and process across a hierarchy of temporal and spatial scales. We focus on stand/stream reach (ha), landscape (thousands of ha), subregion (thousands of $km^2$), and regional (10 thousands of $km^2$) scales. The time scales of interest must extend from decades to centuries, because these are the scales of land-use and climate changes, ecosystem responses to them, and the lifespans of dominant tree species. For example, centuries are required for some important ecosystem components to equilibrate after disturbance, as is true of levels of coarse woody debris after natural forest is converted to a plantation.

Models will necessarily play a major role in addressing such questions, particularly those involving long-term changes in productivity and landscape pattern. Specific modeling goals include the ability to forecast trends in: (1) primary production, biodiversity, water yield, and water quality (four variables that we hypothesize indicate overall ecosystem health); (2) fluxes of radiatively important trace gases (particularly $CO_2$), surface albedo, and evapotranspiration (variables that influence global climate); and (3) leaf chlorophyll content (a variable which, along with albedo, can be sensed remotely). Where appropriate, these studies will link closely with several NASA- and Forest Service-sponsored remote-sensing programs to verify model predictions at the landscape and regional scales. Modeling will continue to be conducted with a very high level of interinstitutional coordination for efficiency and comparative analysis among ecosystems and environments.

### *Applications to Land Management*

Results of Andrews research are applied to an impressive extent in management of soil and vegetation, landscapes, and stream and riparian networks. This has happened because of (1) the long-standing, close working relationships between managers and researchers, (2) the great debate in the region concerning the future of its natural resources setting the stage for ecosystem scientists to play a role in guiding change, and (3) the commitment of land managers involved in the Andrews group to test new ideas with on-the-ground practices. These new practices are being shared with other managers and the public through numerous field tours, media contacts, and other channels. Many of the new management approaches have been incorporated into planning documents and guidelines.

Results of our research on old-growth forests, spotted owls, stream ecosystems, biodiversity, and other topics have been pivotal in triggering the major changes underway in public expectations of management of Pacific Northwest ecosystems. Shifting public expectations of public forestlands create urgent needs for new information, and for greater incorporation of human factors in ecosystem management.

We believe that incorporation of ecosystem research results into socially acceptable, sustainable management systems is an important form of synthesis. This will be a major continuing activity for the Andrews group in the 1990s. ▪

*** AND Climate Record 1951 - 1980**

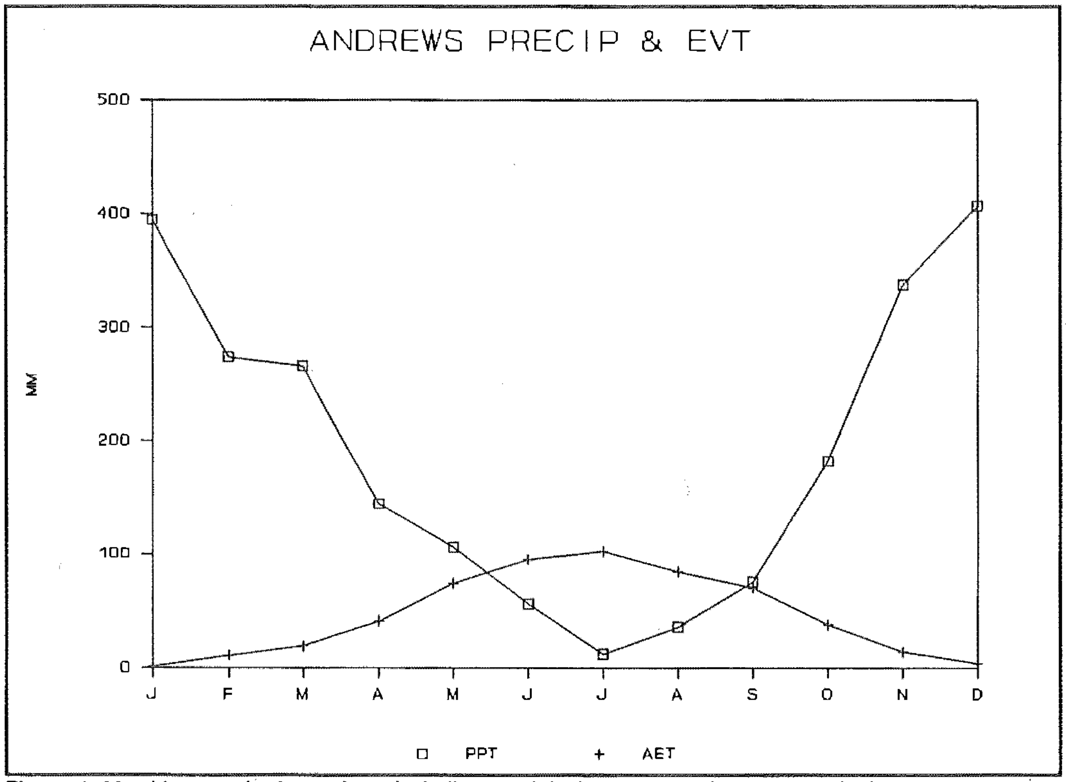



**Figure 1.** Monthly water budget values, including precipitation and actual evapotranspiration.

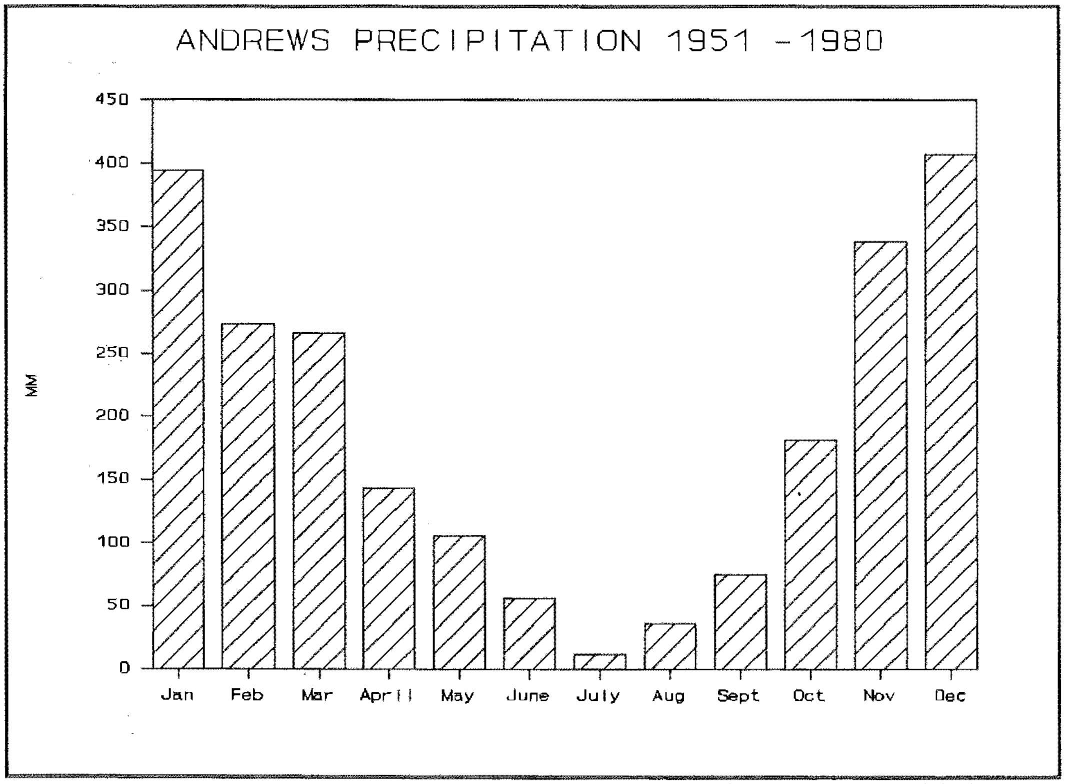



**Figure 2.** Average annual precipitation totals.

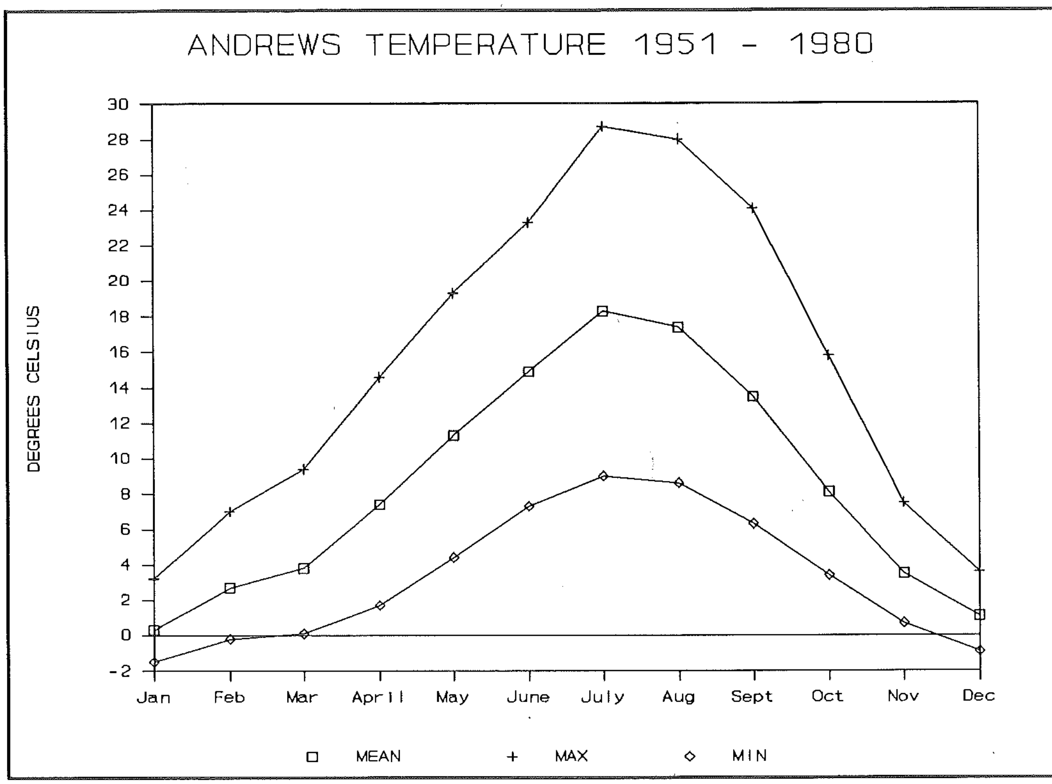
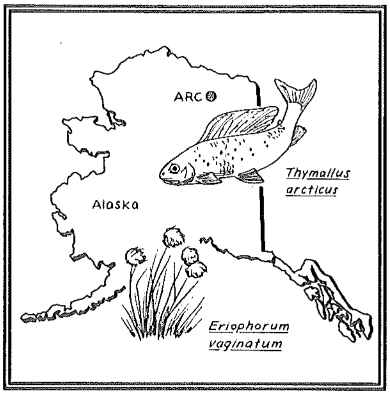


**Figure 3.** Average annual temperature values.

* Data from on-site or nearest weather station.




# Arctic Tundra (ARC)

## RESEARCH SETTING

The Toolik Lake research project in the foothills of the North Slope, Alaska, has collected data since 1975 with funding from the National Science Foundation's Division of Polar Programs and from the Long-Term Ecological Research Program and Ecosystems Research Program of the Division of Biotic Systems and Resources. The broad goal is to understand and predict how ecosystems of tundra, lakes, and streams function and respond to change, including climate change.

One specific goal is to understand the extent of control by resources (bottom-up control) or by grazing and predation (top-down control). The processes and relationships are analyzed in both natural ecosystems and in ecosystems that have undergone long-term experimental manipulations to simulate effects of climate and human-caused change. These manipulations include fertilizing lakes and streams, adding and removing lake trout from lakes, changing the abundance of arctic grayling in sections of rivers, excluding grazers from tundra, and shading, fertilizing, and heating the tussock tundra.

A second specific goal is to monitor year-to-year variability and to measure how rapidly long-term change occurs. The measurements include: for lakes, measurements of temperature, chlorophyll, primary productivity; for streams, nutrients, chlorophyll on riffle rocks, insect and fish abundance, and water flow; and for the tundra, amount of flowering, air temperature, solar radiation, and biomass.

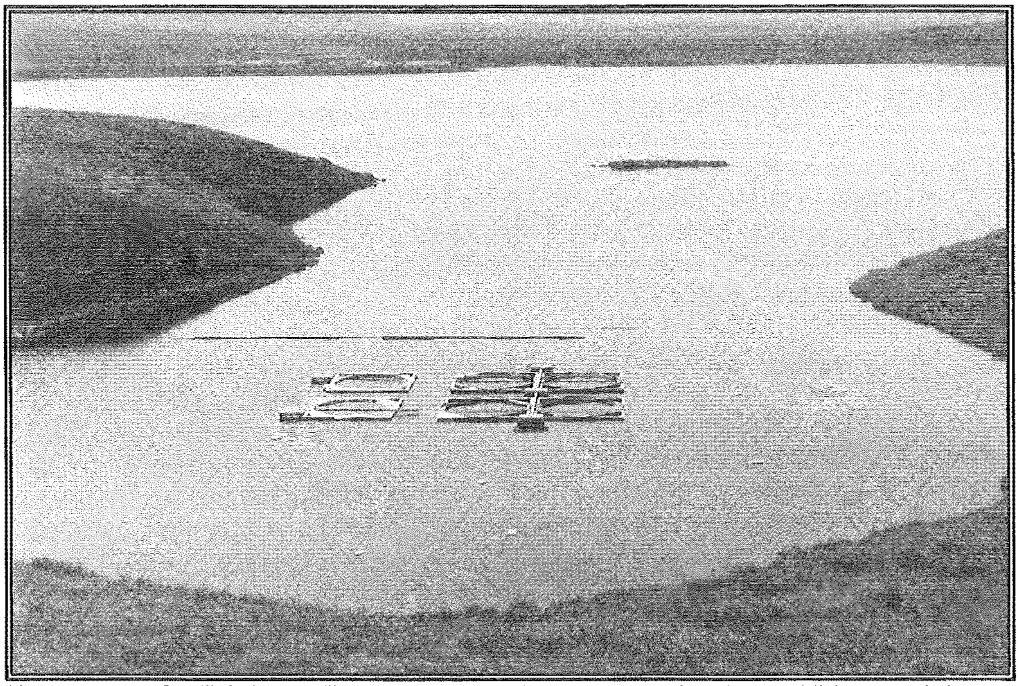
A third specific goal is to understand the exchange of nutrients between land and water. Measurements include the flow of water in rivers, the concentration of nitrogen and phosphorus in streams, lakes, and soil porewater, and the effect of vegetation on nutrient movement through the tundra soils. A dynamic model of nutrient fluxes in the entire upper Kuparuk River watershed is being constructed that will interact with geographically referenced databases. Eventually the model and process information will be extrapolated to the larger region; this will allow prediction of the export of nutrients from the whole of the North Slope of Alaska under future conditions of changed temperature and precipitation.

### Site Characteristics

Field research is based at Toolik Lake, Alaska, in the northern foothills of the Brooks Range (68°38'N, 149°43'W, 760 meters). The Toolik Lake Research Camp is operated by the University of Alaska, Fairbanks. Tussock tundra is the dominant vegetation type, but there are extensive areas of drier heath tundra on ridgetops and other well-drained sites, as well as areas of river-bottom willow communities.

The mean annual air temperature is -7°C and the total precipitation 250 to 350 mm. The tundra is snow-free from late May to mid-September while the sun is continuously above the horizon from mid-May until late July. Lakes are ice-free from mid- to late June until late September. The entire region is underlain by continuous permafrost which exerts a major influence on the distribution, structure, and function of both terrestrial and aquatic ecosystems.

Terrestrial research in the Toolik area began in 1976 with descriptive and baseline vegetation studies of many sites along the length of the Dalton Highway and at Toolik Lake. The next phase, research on the response of plants to disturbances of pipeline and road construction, led to studies of plant demography and population dynamics. From 1979 to 1982, plant growth and its controls were analyzed and a number of long-term experiments (fertilization, light, temperature) were set up. The present studies emphasize the soil-element cycling and have the goal of evaluating the lateral N and P fluxes in soil water moving downslope across the surface of the permafrost. Budgets of N and P for the various ecosystems through which the water flows have been developed and linked with a hydrologic model.



*Limnocorrals at Toolik Lake, Toolik Camp, for examining responses of nutrient and fish manipulation.*
JOHN E. HOBBIE

The primary focus of the streams research is the Kuparuk River, a fourth-order stream where it crosses the Dalton Highway. Intensive research on the Kuparuk River began in 1978, and its water chemistry, flow, and major species populations have been monitored for over 10 years. For much of this time, a section of the river has been fertilized by the continuous addition of phosphate. Recently, the abundance of the single type of fish in the river, the arctic grayling, was manipulated in various sections of the river to examine the effects of crowding and predation. In 1989, a monitoring program in Oksrukuyik Creek, a slightly smaller third-order stream about 15 km to the northeast, was begun with the intention of developing a long-term comparison and contrast with the Kuparuk River.

Toolik Lake has a surface area of 150 ha and a maximum depth of 25 m. Research began in 1975 with surveys of the biota, chemistry, and processes ranging from primary productivity to nutrient budgets. Dozens of other nearby lakes were also surveyed. In the 1980s research concentrated on the question of controls of populations, community structure, and processes. Large (60 $m^3$) plastic bags were set up for manipulations of nutrients and predators; entire lakes and divided lakes were fertilized and lake trout, the top predator, removed and added to various lakes. More recently the survey work has been extended to parts of the Arctic coastal plain and Brooks Range, as well as the northern foothills region.

To keep track of observations, the Toolik Lake project maintains a computerized database at the Marine Biological Laboratory at Woods Hole, Massachusetts, which contains a wide variety of long-term data sets for the Kuparuk River, Toolik Lake, and the Tundra sites.

## *Year-to-Year Variability & Long-Term Change*

Terrestrial Studies: Long-term monitoring and measurement of both climate and key ecosystem processes will help to determine if long-term changes in the arctic climate can be detected, and whether terrestrial ecosystems are changing in response. For example, growth and flowering of *Eriophorum vaginatum*, one of the most common and often dominant plant species throughout the arctic, has been monitored at 34 sites along the climatic gradient between Fairbanks and Prudhoe Bay since 1976.

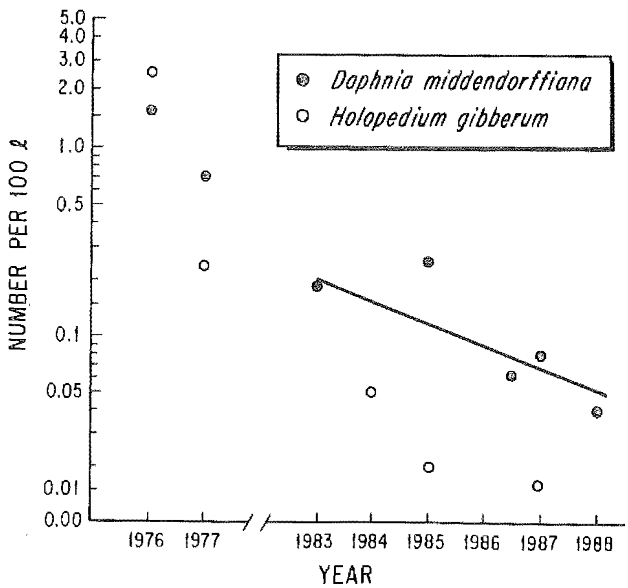



Figure 1. The numbers per 100 liters of two species of zooplankton in Toolik Lake, 1976-1988.

The combination of these approaches has allowed us to distinguish the effects of annual variation in weather from broad regional differences in climate at two time scales: In the long-term, we can show that genetically-based, ecotypic variation between populations accounts for much of the variation in plant size and growth rate that we observe in the field, and that this variation is correlated with long-term average growing-season temperatures. In the short-term, we can show that growth and especially flowering vary uniformly from year to year over most of Alaska, but these annual fluctuations are not clearly correlated with annual variation in any climatic variable. Short-term plant responses to climate must be strongly "buffered," or constrained, by other limiting factors such as nutrient availability; longer-term responses are constrained genetically. Detection and explanation of multi-year trends in plant growth in relation to climate, then, requires linking climatic changes to changes in soil nutrient cycling processes and nutrient availability.

Lake Studies: In the context of climatic change, the master variable for controlling productivity appears to be temperature. Temperature regulates weathering rates, decomposition, and the depth of thaw in terrestrial ecosystems, all of which alter the flux of nutrients through terrestrial landscapes and into lakes. Temperature also regulates the strength and extent of thermal stratification and thus the zone of highest productivity in the lake.

Under the present climatic regime, algal primary productivity is controlled by the amount of phosphorus entering the lake which in turn is controlled by the amount of streamflow. In Toolik Lake there was a positive correlation ($r^2 = 0.52$) between 14 years of summer primary productivity and the discharge of the nearby Kuparuk River.

Stream Studies: The flow of water through the landscape affects many key biogeochemical processes that will potentially change if the hydrologic cycle is significantly changed by either long-term trends or changing annual variability in discharge. For example, increased water flow will likely increase weathering rates of soils in the watershed and increase the export of dissolved cations, anions, nutrients and dissolved organic materials from land to rivers and lakes. Higher discharge will also lead to greater streambank erosion which captures peat. When discharge is low, the flux of materials from land to water is decreased and the balance between autotrophic and heterotrophic processes in streams and lakes is probably shifted in favor of autotrophy. If climatic change does alter either the amount of water flow through arctic watersheds or the timing of these flows, we expect large changes in nutrient fluxes and in biotic activity in rivers. Our monitoring program is designed to document these changes.

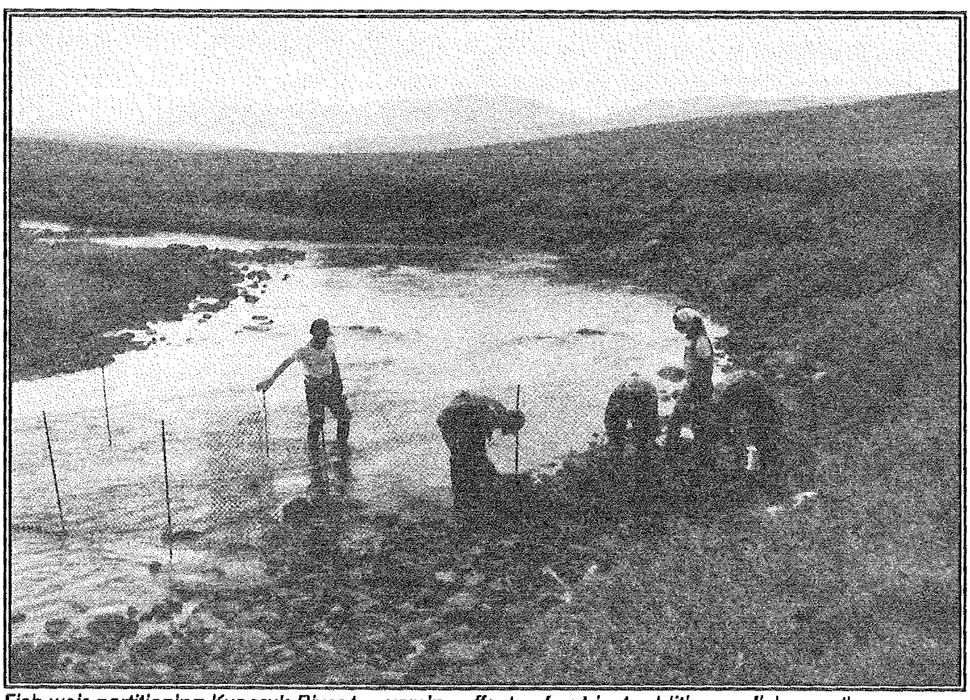
### *Control by Resources vs. Control by Grazing & Predation*

Terrestrial Studies: In a series of short- and long-term experiments begun in 1976, we have manipulated air temperature by building small greenhouses over the tundra, light intensity by shading, and nutrient availability by fertilization. Changes in nutrient availability have effects on productivity and composition of tundra vegetation that are far greater than changes in either air temperature or light. The main effect of increased air temperature is to speed up the changes due to fertilizer alone. Without fertilizer the effect of increased temperatures on the vegetation is slight even after nine years, and probably results from small increases in soil temperatures and increased nutrient mineralization. These results are consistent with results of our monitoring studies, and again lead to the prediction that effects of climate change on nutrient cycling processes are the key to understanding climate change in the Arctic.

Lake Studies: To isolate the effects of nutrient availability on productivity we initiated process-oriented studies on the effects of fertilization in 1983 using large limnocorrals. These have been expanded to whole systems with our current experiments in divided lakes. Nutrient additions enhance primary production almost immediately, but the transfer of carbon to higher trophic levels proceeds more slowly. Additions of tracer amounts of $^{15}N$ to a whole lake also indicated a time lag of at least one growing season in the incorporation of new phytoplankton production into the benthic food chain. Thus, in the scenario of increased nutrient supply due to rising temperature we would expect rapid changes in primary productivity and a delayed, more complex response from the higher trophic levels.

To investigate the higher trophic levels and their interactions with populations below them in the context of climate change, we have been both monitoring and experimentally manipulating a series of lakes. We have data on long-term variability in zooplankton and fish populations in several ponds and lakes. We also have data and models of fish feeding on zooplankton and how this might change in response to climate. In 1988 we began investigating the feedback of higher trophic levels on changes in primary and secondary productivity. These experiments consist of adding and removing top predators in lakes that lie along a productivity gradient. Such experiments will help separate the influence of nutrients from shifts in trophic structure as patterns of energy flow are modified by climatic change. Finally, when added to results of our regional surveys our monitoring will enable us to predict effects of increasing water temperatures on species and populations of both zooplankton and fish.

One interesting observation is the virtual extinction of the large-bodied zooplankton in Toolik Lake. In the late 1970s, many large lake trout were removed by angling. This released the



*Fish weir partitioning Kuparuk River to examine effects of nutrient addition on fish growth.*
*BRUCE PETERSON*

predation pressure on smaller fish and they expanded both in numbers and in feeding on zooplankton in the pelagic zone of the lake. This has caused a dramatic drop in the numbers of the two large-bodied zooplankton (Figure 1).

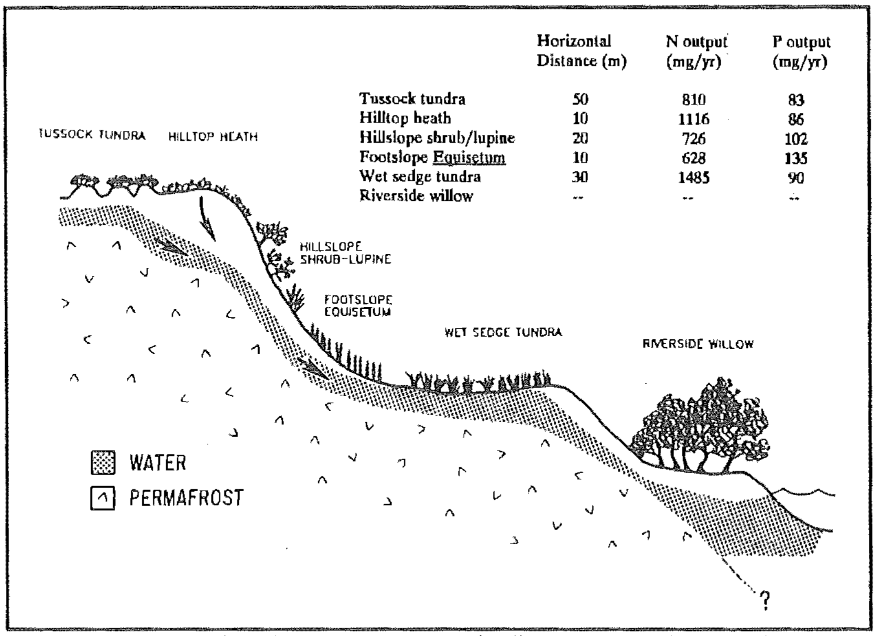
<u>Stream Studies:</u> The sequence of responses to phosphorus fertilization that we have measured over the past seven years is as follows: Dissolved phosphate added to river water stimulates the growth of epilithic algae. Increases in algal production lead to sloughing and export of algal biomass and increased excretion and mortality. Increased algal excretion and mortality stimulate bacterial activity which is also stimulated directly by phosphorus addition. Increased bacterial activity and biomass make possible an increase in the rate of decomposition of refractory compounds such as lignocellulose and many components of the decayed organic matter pool. The increases in algal and bacterial biomass provide increased high quality food for filtering and grazing insects. The insects respond with increased growth rate and, in the case of *Baetis* and *Brachycentrus*, with increases in density. However, *Prosimulium* density in the fertilized reach declines due to competitive interaction with *Brachycentrus*. The increases in insects other than *Prosimulium* increase the available food for grayling; both young-of-the-year and adult grayling grow faster and achieve better condition in the fertilized reach.

In the long-term, if the experimental nutrient addition were expanded to include the whole river, barring other overriding but unknown population controls, we hypothesize that the fish population would increase. If so, it is possible that predation by fish would exert increased top-down control over insects such as *Baetis* or *Brachycentrus* which are vulnerable to fish predation when drifting and emerging. Experimental evidence from bioassays using insecticides indicates that grazing insects control algal biomass. Finally, increases in epilithic algae and bacteria are responsible in part for uptake of added phosphorus and ammonium and for uptake of naturally abundant nitrate. Thus, the bottom-up effects of added nutrients are paralleled by several top-down effects of fish on insects, insects on insects, insects on epilithic algae, and epilithon on dissolved nutrient levels.

The entire biological system in the river is responsive to added P. Bottom-up effects propagate to all levels in the food web, and both top-down effects and competitive interactions are clearly important in the response of the ecosystem to fertilization.

## *Land-Water Interactions*

The question of what controls the fluxes of nutrients and water over the arctic landscape and into aquatic ecosystems is fundamental to our understanding of stream ecology and to predictions of climate change on arctic ecosystems. At the Toolik Lake site we already have many small plot measurements of nutrients in soil water and their interactions with plants. We also have large-scale data on the flux of nutrients out of entire watersheds. In the next few years we will construct a dynamic model of the movement of nutrients into streams and combine this with a geographic information system (GIS) to test our understanding of the system and to estimate the nutrient output from larger watersheds.




| | Horizontal Distance (m) | N output (mg/yr) | P output (mg/yr) |
|---|---|---|---|
| Tussock tundra | 50 | 810 | 83 |
| Hilltop heath | 10 | 1116 | 86 |
| Hillslope shrub/lupine | 20 | 726 | 102 |
| Footslope <u>Equisetum</u> | 10 | 628 | 135 |
| Wet sedge tundra | 30 | 1485 | 90 |
| Riverside willow | -- | -- | -- |

**Figure 2.** Ecosystem sites along a toposequence leading to an arctic river, and the amounts of N and P transported through each annually.

Terrestrial Studies: Our principal aim in terrestrial research is to evaluate the magnitude and relative importance of lateral N and P fluxes in soil water moving across the surface of the permafrost, between terrestrial ecosystem types and from terrestrial to aquatic systems. Our study site is a toposequence of six contrasting ecosystem types in a tundra river valley. To estimate N and P fluxes in soil water at this site we have had to develop and compare overall N and P budgets for all six ecosystems, and to link these budgets with a hydrologic model.

Our major conclusions are that the net uptake of N or P from moving soil water is small relative to internal fluxes such as annual plant uptake or N mineralization. However, each of the six ecosystem types has a major and very different effect on the total amounts of $NO_3$, $NH_4$ and $PO_4$ in soil water (Figure 2). This has important implications for the inputs of these nutrients to aquatic systems. Some ecosystem types, like tussock tundra and dry heath, are major sources of N to soil water. Other systems, particularly those occurring under or below late-thawing snowbanks, are important N sinks and P sources to soil water. Poorly drained wet sedge tundra is a P sink with a remarkably high N mineralization rate.

We have also learned a great deal about patterns and controls over N and P cycling processes along our toposequence. We have shown that nitrification is much more important along our toposequence than we suspected based on earlier research, and many plant species show high nitrate reductase activity. We also have strong evidence from stable isotope analyses that different plant species are using isotopically different N sources, and that these species differences are maintained across sites. The relative amounts of different forms of organic and inorganic P in soils also vary dramatically across sites.

Our work has shown that different terrestrial ecosystems differ strongly in their chemical interactions with the soil water, and thus have highly variable effects on the chemistry of water entering aquatic systems. This work is important in the context of global change, because if either the composition of the landscape mosaic changes, or the biogeochemistry of individual landscape units changes, the chemistry of inputs to aquatic systems will also change.

## FUTURE DIRECTIONS

To achieve one of our major long-term objectives of understanding controls of water and nutrient flux at the whole watershed and regional levels, we are focusing on four major questions:

- What is the role of various units of landscape in determining the amount and chemistry of water flowing from land to rivers and lakes?
- What is the specific role of the riparian zone in modifying the chemistry of water entering rivers and in determining the amount of allochthonous organic matter and light in rivers and lakes?
- What is the role of lakes in retaining and transforming organic matter and nutrients as this material moves downstream through a drainage?
- How do the communities of rivers and lakes change in response to changes in water quantity and quality caused by various units of landscape, riparian zones and upstream lakes?

From our history of experiments on fertilization of lakes and rivers, we know that both lake and stream biota are very responsive to short- and longer-term changes in phosphorus and nitrogen supply. Thus we have a large amount of information on question 4 and we know from current research on small plots that different terrestrial ecosystems will yield very different quality runoff water. In future research, we will focus on determining the relationships between larger landscape units (0.1 to 1 $km^2$) and water quality of runoff, the role of the riparian zone, and the role of lakes in determining river water quality.

The long-term plan is to make a model of nutrient processing and transfer which would follow nutrients from the interactions in the soil into a stream. This watershed model can be verified by the continuous measurements of nutrient flux from the watershed being made at the point where the Kuparuk River crosses the single road. Next, the watershed model would be calibrated to fit the different environments of northern Alaska. Finally, the model would be used to characterize the variability among Alaskan ecosystems so that statistical extrapolations could be made to the regional scale. The end result would be regional predictions of nutrient fluxes from land to rivers under various scenarios of climate change. The flux from an entire region to the Arctic Ocean could then be predicted.

*** ARC Climate Record 1951-1980**

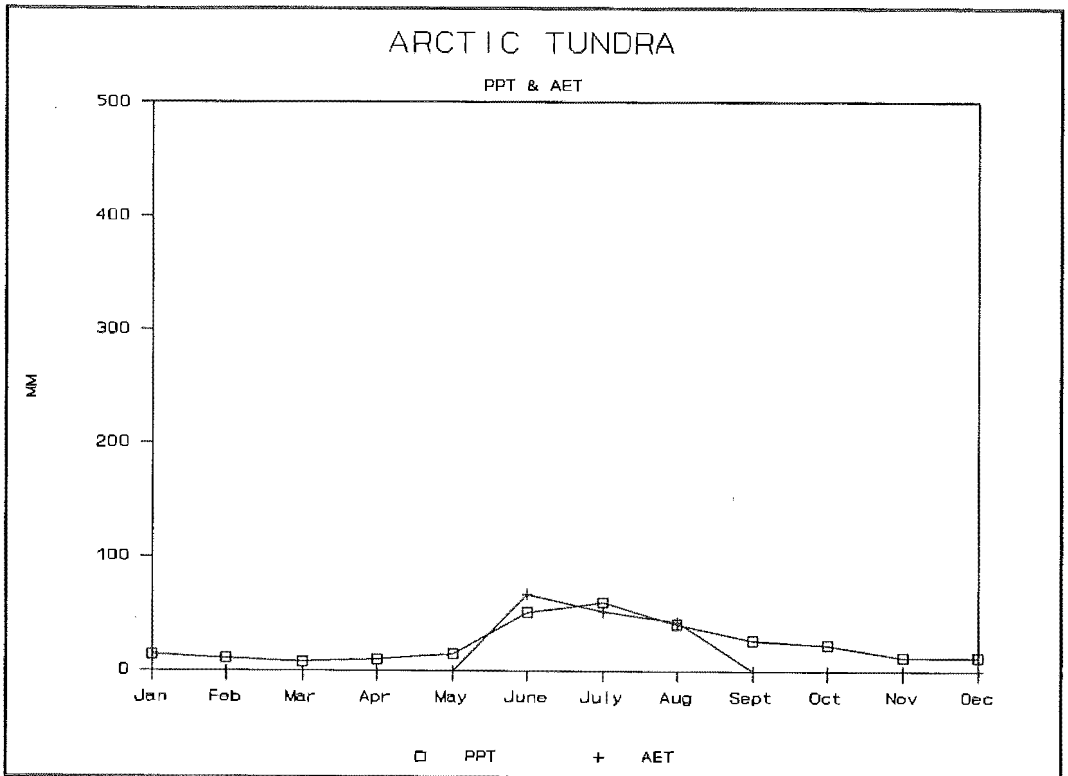



**Figure 3.** Monthly water budget values, including precipitation and actual evapotranspiration.

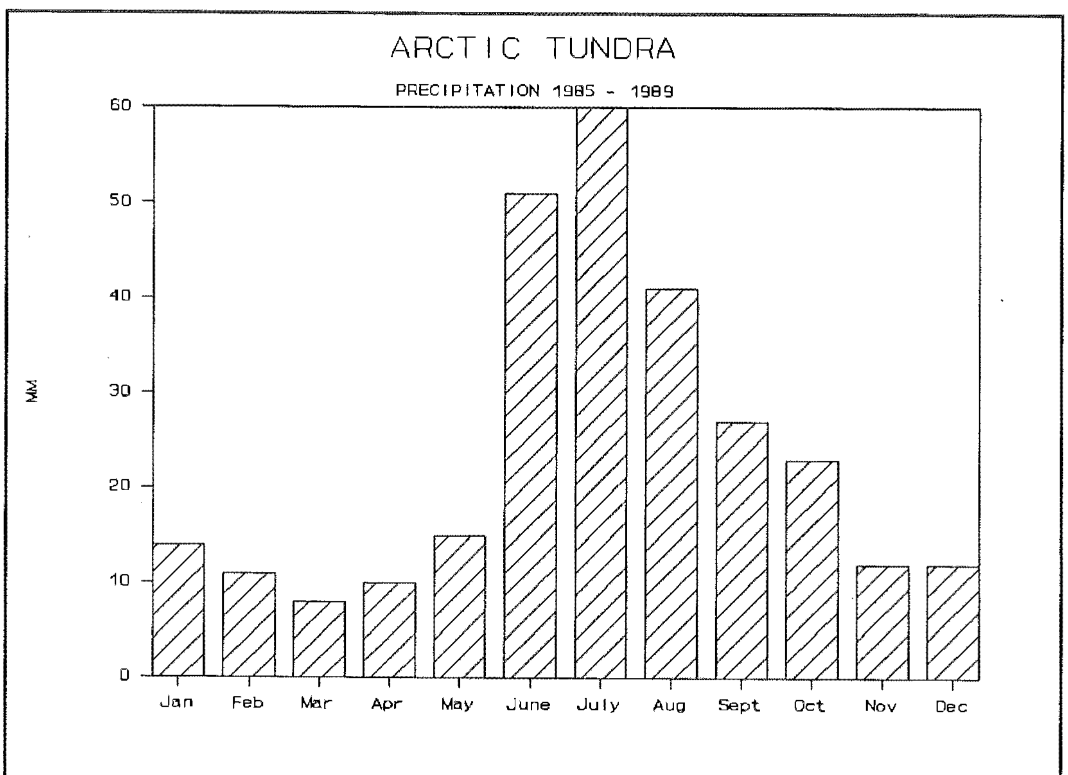



**Figure 4.** Average annual precipitation totals.

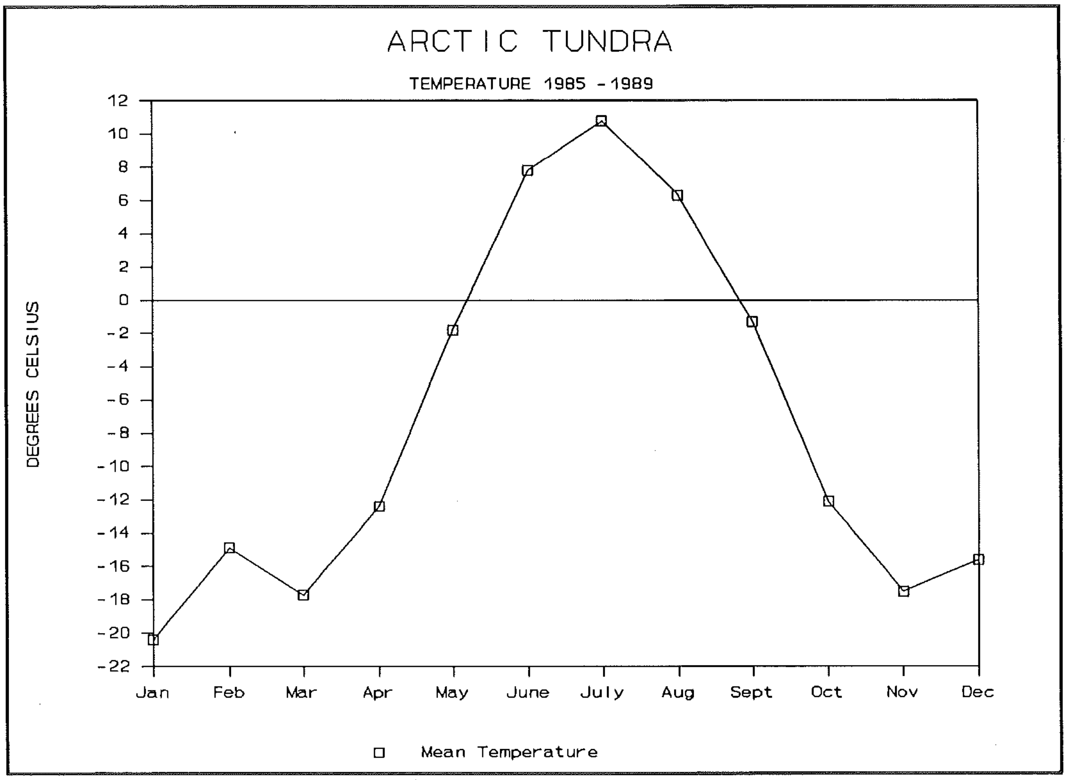
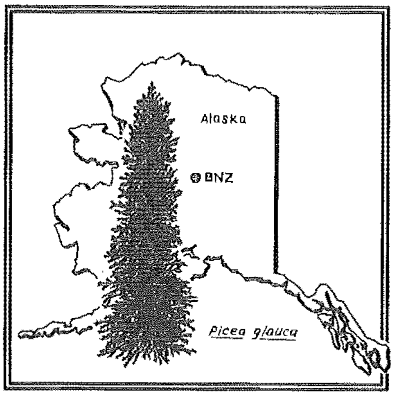


**Figure 5.** Average annual temperature values.

* Data from on-site or nearest weather station.




# Bonanza Creek Experimental Forest (BNZ)

## RESEARCH SETTING

Interior Alaskan forests are part of a circumpolar band of boreal forest. In interior Alaska these forests are unique for their association with an environment characterized by drastic seasonal fluctuation in day length (more than 21 hours on June 21 and less than 3 hours on December 21), temperature (extremes of -50° in January and over 33°C in July), a short growing season (100 days or less), consistently low soil temperatures, low precipitation (287 mm, 1/3 occurring as snow), and the occurrence of permafrost. Approximately 31 percent or 42,800,000 ha of the total 136,000,000 ha comprising interior Alaska is forested. Forest land which is considered of commercial value totals about 9,600,000 ha.

The Bonanza Creek Experimental Forest is located approximately 20 km southwest of Fairbanks along the Parks Highway. The Forest is within the Tanana Valley State Forest, a unit managed by the Division of Forestry, State of Alaska. The vegetation of BNZ is a mosaic of forest and non-forest types resulting from interactions of topography, soils, slope and aspect, elevation and fire history in the uplands, and on the floodplain, recent history of flooding and deposition. The vegetation in general corresponds to four broad topographical zones: upland hills and ridges, lowland toeslopes and valley bottoms, old Tanana River terraces, and the active Tanana River floodplain.

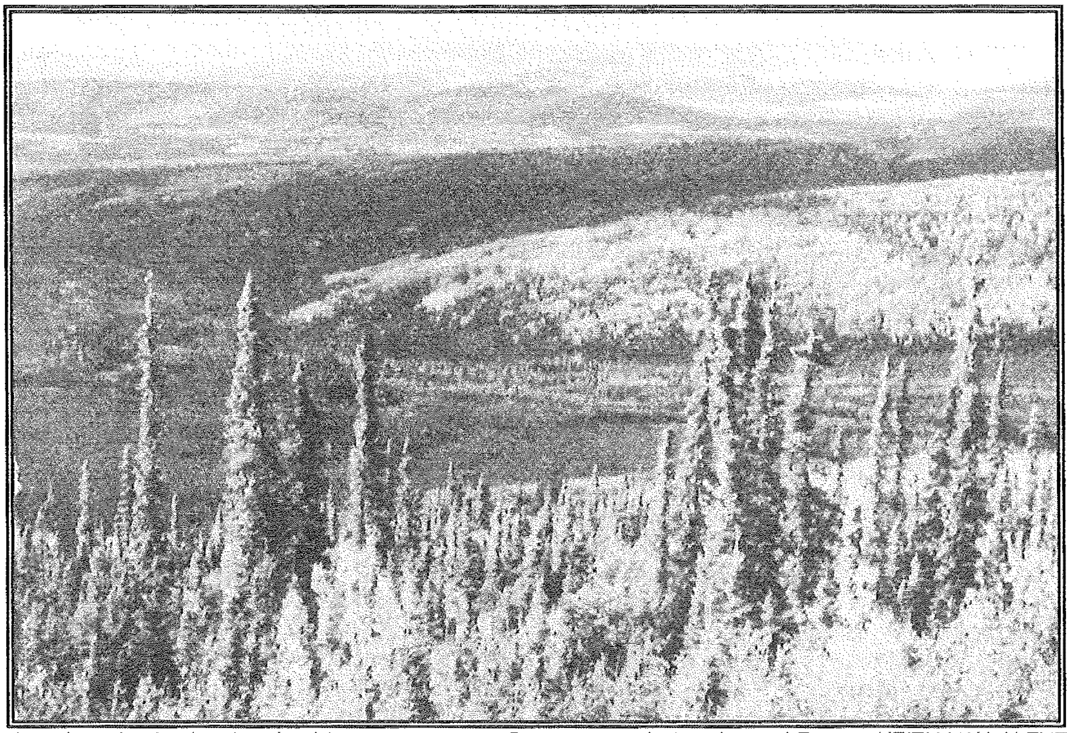
Representatives of each of the major forest types occurring in central Alaska are found in the Experimental Forest. The six principal tree species that occur on BNZ have ranges that extend across North America to more southerly latitudes in eastern Canada. The presence of black spruce (*Picea mariana*), larch (*Larix laricina*) and bogs generally indicates the presence of permafrost. Occurrence of quaking aspen (*Populus tremuloides*), and white spruce (*Picea glauca*) generally indicates permafrost-free conditions. Paper birch (*Betula papyrifera*) is common on both permafrost and permafrost-free sites. Balsam poplar (*Populus balsamifera*) develops in extensive stands on permafrost-free floodplain locations.

Under the influence of the cold-dominated environment at this latitude, soil development has been minimal. Morphological description and physical and chemical analysis shows little chemical alteration of the parent material. In the uplands, soils are classified as inceptisols while inceptisols and entisols are encountered on the floodplain. Floodplain soils are salt affected. They display high surface concentrations of calcium sulfate and calcium carbonate early in succession. Both salts arise through pedogenic processes and the carbonate also from parent material weathering in the Alaska Range.

### *Site Characteristics*

Interior Alaska is bounded on the south by the Alaska Range and on the north by the Brooks Range. The principal river system draining interior Alaska is the Yukon, and the river closely associated with our study area is the Tanana which flows into the Yukon about 200 km below BNZ.

The Alaska Range is glacially sculptured, and trends west and southwest 1,000 km from the Canadian border to the Aleutian Range. It contains numerous peaks over 3,000 m in elevation and culminates in Mt. McKinley at 6,195 m. This mountain wall is an effective barrier to coastal air masses, and is responsible for the continental climate experienced at BNZ.



*Overview of upland and lowland forest cover types, Bonanza Creek Experimental Forest. KEITH VAN CLEVE*

The southern portion of the Yukon-Tanana uplands and adjacent Tanana River valley to the south, is the location for our research activities at BNZ. The physiography and geology of this area include loess-mantled bedrock hills (the strongly weathered, Precambrian quartz-mica and quartzite schist of the Birch Creek formation), lower hill slopes and creek-valley bottoms, organic-rich lowlands at the base of hills, and the Tanana River floodplain. The Tanana River valley is a large structural basin, and much of its bedrock floor is below sea level. Fluvial and glaciofluvial sediments, largely from the rising Alaska Range, have accumulated in deposits 91 to 230 m thick. These deposits have pushed the Tanana River northward, near the Yukon-Tanana Upland, as it flows through BNZ.

Central Alaska has not been glaciated but small cirque glaciers occurred in local mountainous highlands. Glaciers from the Alaska Range approached to within 80 km of Fairbanks during extensive glacial expansions. In the general vicinity of BNZ silt blown from the floodplain of the Tanana River was deposited as loess, blanketing ridges of the southern Yukon-Tanana upland in deposits from a few cm thick on summits to more than 45 m on middle and lower slopes. Topography of the east trending upland consists of rounded ridges 600 to 900 m in elevation with higher peaks projecting to between 1,500 and 1,800 m. Current tree line is at about 900 m.

Permafrost is discontinuous in the interior of Alaska and its continuous north of the continental divide in the Brooks Range. Permafrost thickness is greater than 600 m in northern areas but is only one to several meters thick near its southern limits. In the vicinity of BNZ permafrost thickness ranges up to about 80 m on floodplains and 110 meters in poorly drained lowlands.

In interior Alaska, permafrost distribution and active layer thickness (portion of soil profile above permafrost that thaws and re-freezes annually) are closely related to the topographic conditions of slope, aspect, drainage; thermal properties of the parent material; and vegetation. In the BNZ uplands, north aspects, valley bottoms, and poorly drained lower slopes are generally underlain by permafrost. Well-drained south aspects, and sediments adjacent to and beneath active river channels are permafrost-free.

## *RESEARCH PROGRAM STATUS*

The principal objective of our research program is to conduct a long-term study of ecosystem structure and function through examination of controls over successional processes in taiga forests of interior Alaska. The research assumes added significance at the far north location of our study site (64°N) in light of the potential for substantial temperature change in northern latitudes as a consequence of global warming.

### *Central Hypothesis*

The pattern of succession is determined primarily by the initial soil physical and chemical environment of the site and by the life history traits of component species. The rate of successional change is determined by vegetation-caused changes in environment and ecosystem function. Our central hypothesis addresses the pattern and rate of succession and environmental controls of these phenomena. A combination of experiments and observations is used to document the changing nature of ecosystem controls during primary succession on river floodplains and during post-fire secondary succession in the uplands. The following aspects are emphasized: (1) vegetation change and demographic controls; (2) vegetation-caused changes in resources (moisture, temperature, light, nutrients) and standing crops of biomass and nutrients; (3) controls over nutrient supply; and (4) the role of herbivores as consumers and modifiers of succession. Previous research enables us to identify a number of points along the successional trajectory that are of particular significance in the development of subarctic forests. We term these "turning points" in order to emphasize the fact that in relatively short time intervals critical changes in ecosystem structure are accompanied by functional changes which have far-reaching effects on ecosystem development. For example, the development of a complete ground cover of feathermosses is associated with soil cooling, consequent reduced organic matter decomposition, and slow rates of nutrient cycling. These turning points undoubtedly represent important changes in controls over ecosystem function and have been our primary criteria for choosing successional stages for intensive study.

*The middle stage, upland forest succession sequence (paper birch with young white spruce).* *L.A. VIERECK*

Hypothesis I. Change in species composition through succession is a function of life history traits modified by facilitative and competitive interactions.

Hypothesis II. Vegetation-caused changes in resource (light, soil temperature, nutrients, and moisture) availability during succession control vegetation biomass, productivity, and organic matter and nutrient distribution.

Hypothesis III. The availability of carbon accumulating on the forest floor as an energy supply for decomposer activity declines through succession, resulting in reduced rates of organic matter mineralization and supply of elements for plant growth.

Hypothesis IV. Selective feeding by herbivores promotes replacement of palatable early successional species by unpalatable later successional species.

### Research Design

In addition to the basic research outlined in the four hypotheses below, there is also a long term monitoring program at BNZ of both climate and vegetation parameters.

Climate at BNZ is monitored at two primary weather stations: one in the upland and one on the floodplain. At these sites air and soil temperature, relative humidity, soil moisture, precipitation (rain and snow), wind speed and direction, total radiation and photosynthetically active radiation (PAR) and evaporation are logged on an hourly basis and summarized as monthly and annual reports.

Selected environmental parameters are monitored at one of each of the eight successional sites, three in the upland and five on the floodplain. At these sites air and soil temperatures are logged on an hourly basis during the entire year. Precipitation and depth of thaw of the soil are measured weekly in the summer.

Vegetation parameters are measured at three sites in each of the five successional stages on the floodplain and three in the upland for a total of 24 sites. At each site 20 vegetation plots are measured within a 50 m x 60 m reference stand. Each vegetation plot consists of a 1 $m^2$ plot for ground vegetation, and a 4 $m^2$ plot for shrubs. In addition all trees and shrubs having a breast height diameter of 2.5 cm or larger are tagged and mapped. Ten trees of each species within the reference stand are also equipped with band dendrometers for measuring annual diameter growth at breast height. In young successional stands the vegetation plots are monitored every two years; in mature types they are monitored every five years. In addition, litter trays have been placed in each reference stand and seed traps in one of each of the eight successional stages.

At four points around the perimeter of each reference stand the forest floor and mineral soil profile was described and sampled using standard procedures. Bulk samples of both materials were obtained for physical and chemical analysis. These assessments will be repeated at 10-year intervals.

Hypothesis I. Research to test this hypothesis has two principal thrusts: (1) life history and population studies, and (2) studies of facilitative and competitive interactions and physiological processes among the major plant species across successional stages.

In the former case (1) seed rain, buried seed stores, and controls over seedling establishment, growth rate, mortality, and longevity are being examined. An additional objective is to characterize the production and turnover of coarse and fine root biomass and assess the percentage of gross carbon fixation that is allocated to the growth and maintenance of coarse and fine roots. In the latter case, (2) artificial communities are being established to evaluate the long-term balance between facilitative and competitive interactions between alder and white spruce. During the initial 5 years of this research we can only examine seedling interactions. However, within 10 to 15 years we expect dense alder thickets to develop in which patterns of nitrogen accumulation and the impact of N accumulation upon spruce saplings can be examined.

Hypothesis II. Research to test successional control of resource availability has the following principal thrusts: (1) contrasting the type of initiating disturbance for the successional sequence, and (2) examining vegetation response to change in resource availability. To contrast the type of initiating disturbance, long-term documentation of successional change in resources on sites recently disturbed by fire and logging is being examined. Fertilization treatments applied to selected plots on floodplain clearcuts will be used to assess nutrient availability (N and P) to recently planted floodplain species (white spruce, balsam poplar, aspen and thinleaf alder).

Vegetation response to changing resource availability is being examined using a series of nutrient availability treatments and a moisture deficit treatment in one turning point in both the floodplain and upland successional sequence. The

Table 1. Highlights of Organization, Bonanza Creek LTER Program

| Activity | Hypothesis | Experimental Design |
|---|---|---|
| Long-Term Monitoring | I, II, III, IV | In floodplain and upland seres, permanent, replicated plots to monitor change in environmental controls over structure and function in successional forest ecosystems. |
| Species competition through succession | I | In setting described above, plant species occurrence and growth rates, invertebrate animal distribution in forest floor. Artificial plant communities. |
| Vegetation-caused changes in resources | II | In setting described above, examination of resource limitation of plant growth. Primarily manipulation of moisture and nutrient supply for plant use. |
| Carbon availability in forest floor | | Within framework of the replicated experimental areas in the two successional seres, assessment of primary and secondary forest floor carbon chemistry. Manipulation of carbon chemistry to test impact on plant inorganic element supply from forest floor. Influence of plant primary and secondary organic chemicals on N supply. |
| Selective feeding by herbivores | IV | Emphasizes replicated early successional sites in both seres. Use of exclosures to evaluate influence of large and small mammals on successional processes. |

nutrient availability treatments include the addition of sucrose, sawdust, and nitrogen fertilizer applied separately on all replicates of the selected turning points. The moisture deficit treatment is applied to the turning point that represents the change from a hardwood-dominated canopy to a softwood-dominated canopy. Measurements to assess impact of changing resource availability on plant growth include: yearly diameter growth, foliage quantity and quality, litterfall quantity and quality, and fine root biomass and production.

Hypothesis III. Research to examine successional control of forest floor carbon availability for microbial activity, and in turn element supply for plant use, includes the following directions: (1) Assessment of present organic structural and secondary chemical, and inorganic element composition of the forest floor in each of the respective upland and floodplain successional stages. This analysis will provide an indication of the change in decomposition and element loss for litter in the respective successional stages, and will establish the time course for change in litter chemistry as the detrital materials approach the chemical composition of established forest floors. The control over decay and element recycling processes exerted by organic chemical composition of the materials will be more clearly resolved by this experiment. (2) Manipulation of substrate chemistry across the successional stages. This experiment tests the hypothesis that with advancing succession detrital materials become increasingly recalcitrant to decomposition, with the resulting consequence that element supplies for plant use also become restricted. Readily metabolized and recalcitrant sources of carbon were separately applied to forest floors in all of the replicate successional stands. The consequence of these manipulations for decomposition and element supply is being assessed through estimation of plant growth, litterfall production and chemistry, and soil respiration. (3) Influence of plant secondary chemicals on soil nitrogen dynamics. Laboratory incubations are employed to examine the influence of methanol and ether extracts of balsam poplar forest floors on ammonification and nitrification in alder forest floor organic matter. Chemicals included in the ether extracts appear to be most effective in reducing nitrification. Dominance of balsam poplar over alder with advancing floodplain succession is associated with marked reductions in nitrification in the field. Physiological controls over nitrifier populations dynamics also are being examined. (4) Changes in microbial populations and their activity with succession. Several approaches are being employed to examine this question including: measurement of microbial biomass and activity, fungal/bacterial ratios, and the ability of microbial populations to utilize byproducts of decomposition such as cellobiose and simple phenolics (vanillic acid).

Hypothesis IV. Research to examine the influence of browsing by mammals on community and ecosystem processes has three major components. These are (1) measurement of the effects of browsing by snowshoe hare and moose on the early stages of plant succession in floodplain forests and upland forests; (2) measurement of the effects of browsing on litter quality; and (3) measurement of the effects of browsing on the biomass of roots and the turnover of fine roots.

Exclosure studies are being used to determine the effects of browsing on plant succession. On the floodplain of the Tanana River, seven exclosures span the willow alder interface, six include the vegetated silt stage of succession, and five include stands of sapling balsam poplar between the alder stage of succession and the spruce stage. On the uplands we have established two exclosures in the 1983 Bonanza Creek burn. Next year we will establish at least one more exclosure in the burn. These exclosures, with the exception of the exclosures in young poplar stands, enclose a minimum of 400 $m^2$. Within each of these exclosures and their paired control plot outside of the exclosure we are establishing at least five replicate 2 $m^2$ permanent quadrats. The poplar exclosures and their control plots are each 32 $m^2$ in area and contain one 2 $m^2$ quadrat. In these quadrats we are monitoring the effects of browsing on the establishment, growth, and survival of woody species, and their productivity. Additionally we are monitoring the growth and survival of 25 dominant individuals of important woody species inside and outside of each exclosure and in each successional stage included in the exclosures. The first data from these measurements indicates that browsing by snowshoe hare and moose on the Tanana River floodplain suppresses willow and balsam poplar growing in the tall willow stage of succession thereby facilitating the transition from willow to alder.

Our studies of the effects of browsing on litter quality have demonstrated that browsing alters the carbon/nutrient balance of woody plants resulting in an increase in leaf litter nitrogen and a decrease in leaf litter condensed tannin. Associated with these changes in leaf litter chemistry is an increase in the rate at which stream invertebrates process leaf litter. Preliminary results further indicate that browsing also increases the rate at which leaf litter decomposes in terrestrial ecosystems. In the future we will study the mechanism of this browsing induced change in the carbon/nutrient balance of individual woody plants and the effect it has on rates of litter decomposition in stream ecosystems and terrestrial ecosystems. We are also initiating long-term monitoring of changes in the species composition of leaf litter brought about by browsing and how these changes affect nutrient cycling inside and outside of exclosures.

In the 1990 field season we began placing minirhizotron tubes for monitoring effects of browsing on root biomass and turnover of fine roots. We expect that browsing of the intensity we have found on the Tanana River floodplain will affect root dynamics, because severe pruning results in increased root mortality.

### *Highlights of Current Progress*

A complete network of 24 replicated sites (three replicates of eight successional turning points) is established in floodplain and upland successional ecosystems. These sites are locations for ongoing experimental work designed to test the hypotheses dealing with controls of forest succession.

As part of this network of sites, and in conjunction with LTER network activities, two year-round weather stations are operational, one on the floodplain and one in the uplands. Data from these stations is incorporated into our local data base and contributed to the networkwide micro-met program. In addition to these "prime" stations smaller stations are located in one replicate of each of the eight turning points. This information is available to investigators interested in evaluating the impact of physical environmental controls of ecosystem processes.

In addition to installations for monitoring short- and long-term changes in the physical environment, permanent plots are in place for following vegetation dynamics in the successional framework. Both sources of information provide valuable baseline data for stand level process modeling activities.

Transplant gardens and artificial communities now established in early successional sites will provide tests of facilitative and competitive interactions among early and late successional plant species. Results of competition studies indicate that white spruce seedlings show the least competitive growth reduction in association with Equisetum spp. than when growing in association with blue joint grass or fireweed.

Experiments are in place to evaluate the effects of forest-floor carbon availability, moisture and nitrogen addition on plant element supply. Additions of sawdust, and sucrose (recalcitrant and readily metabolized sources of carbon) were applied at levels sufficient to raise the C:N ratio to approximately 40 in early and late successional litter layers. The consequences of these manipulations of element supply for plant growth are being assessed through: estimation of tree diameter growth, new foliage inorganic element and structural and plant secondary organic chemical composition, and litter fall biomass and chemistry. Field estimates show substantial increase in soil respiration in response to sucrose treatments and lesser, although still elevated, rates of $CO_2$ evolution in sawdust treatments. In general, the moisture reduction treatment lowered soil respiration.

Interaction between potential plant secondary chemicals produced by balsam poplar and alder forest floor nitrogen dynamics indicates up to a four- to fivefold reduction in nitrification in the presence of these materials. Work is continuing to refine ether extracts of poplar organic matter to more clearly establish the substances responsible for these effects. Tests also will be conducted to evaluate the possibility of $NH_4$ limitation to $NO_3$ production.

Forest-floor invertebrate animal distribution appears to be sensitive to successional stage. Rotifers and tardigrades are found in abundance in late successional white spruce forest floors where feather mosses are an important component of the plant community. This work is being extended to evaluate invertebrate colonization of detrital materials in our long-term litter decomposition study.

A total of 10 exclosures now are established on the floodplain and three in the uplands in early successional stages. These experiments are the focal point for evaluation of impacts of large and small mammal browsing on early stages of forest succession.

LINKAGES is now fully calibrated for the major tree species of interior Alaska. Climate change scenarios have been run to test the ecosystem response to various levels of increasing temperature and increasing precipitation. Results were presented at the International Conference on the Role of the Polar Regions in Global Change held in Fairbanks in June of 1990. The principal results of this work were: (1) the species combination of birch and white spruce was more productive than aspen and white spruce or pure white spruce; (2) without substantial increases in precipitation the interior Alaska taiga forests will suffer from increasing amounts of drought stress; and (3) after 50 years of gradual climate change the carbon balance of the Tanana Valley State Forest, in interior Alaska, is positive (the vegetation acts as a net sink for $CO_2$). This final result is based on simulations which do not account for periodic fires or include the black spruce vegetation type which represents 32 percent of the State Forest.

## *FUTURE DIRECTIONS*

Our immediate objectives deal with documenting results of experiments established to test controls of successional processes. Emphasis will be placed in the following areas: (1) controls of resource supply, (2) competition and facilitation, (3) impact of large and small mammal browsing on plant community development, (4) plant root growth dynamics, (5) role of invertebrate animals in forest floor decomposition, (6) trace gas production and consumption, (7) refinement of stand level process models to assess change in successional processes in context of global change and linking these models with GIS to broaden the scale of understanding of ecosystem processes.

Establishing a viable data management program is a high priority activity along with expanding our capability in geographic information systems. In both areas the State of Alaska and University of Alaska Fairbanks have provided substantial financial assistance.

We have received and cooperated in promoting a number of proposed activities with other LTER sites. Although funding for most of these activities has not materialized, we are eager to help launch newly funded, cross site research. Currently, we are cooperating with the cross-site litter decomposition comparison, climatological data summaries, and evaluation of variation in biological data.

New research initiatives undoubtedly will deal with climate change issues, and the use of GIS to integrate plot-based structural and functional knowledge at a landscape level. For example, experimental work may deal with plant community manipulations in the field to test plant species specific secondary chemical control of soil processes in a context of increased soil temperature. ■

**** BNZ Climate Record 1951 - 1980***

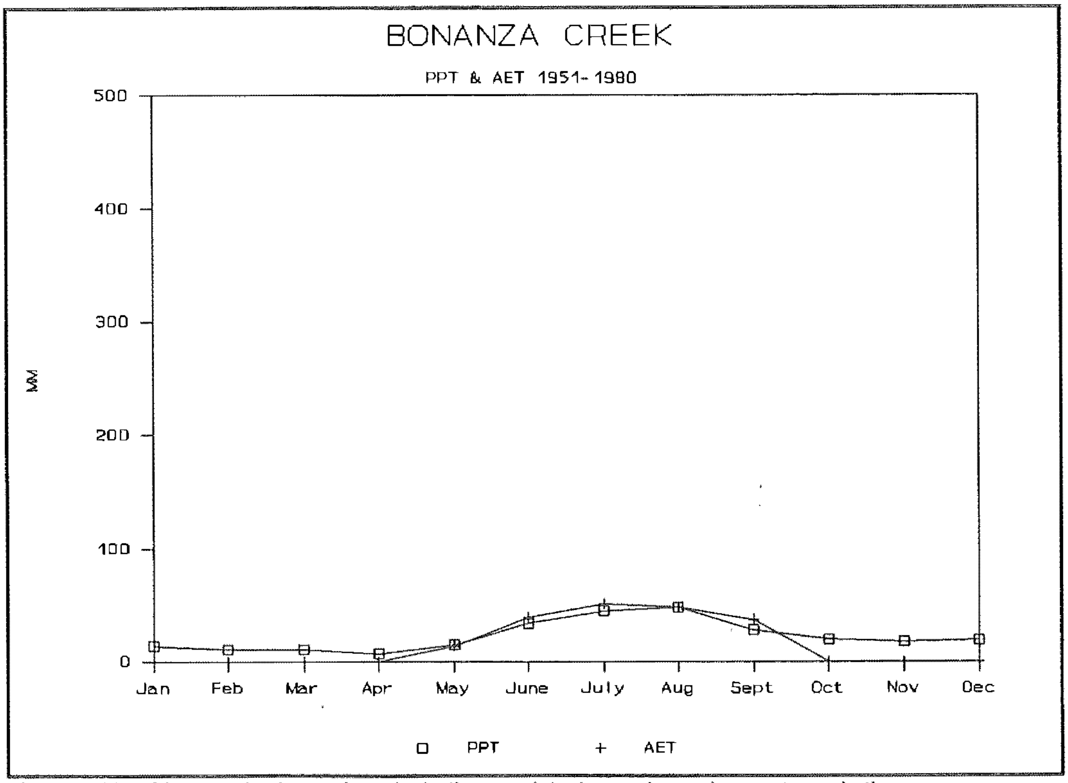



**Figure 1.** Monthly water budget values, including precipitation and actual evapotranspiration.

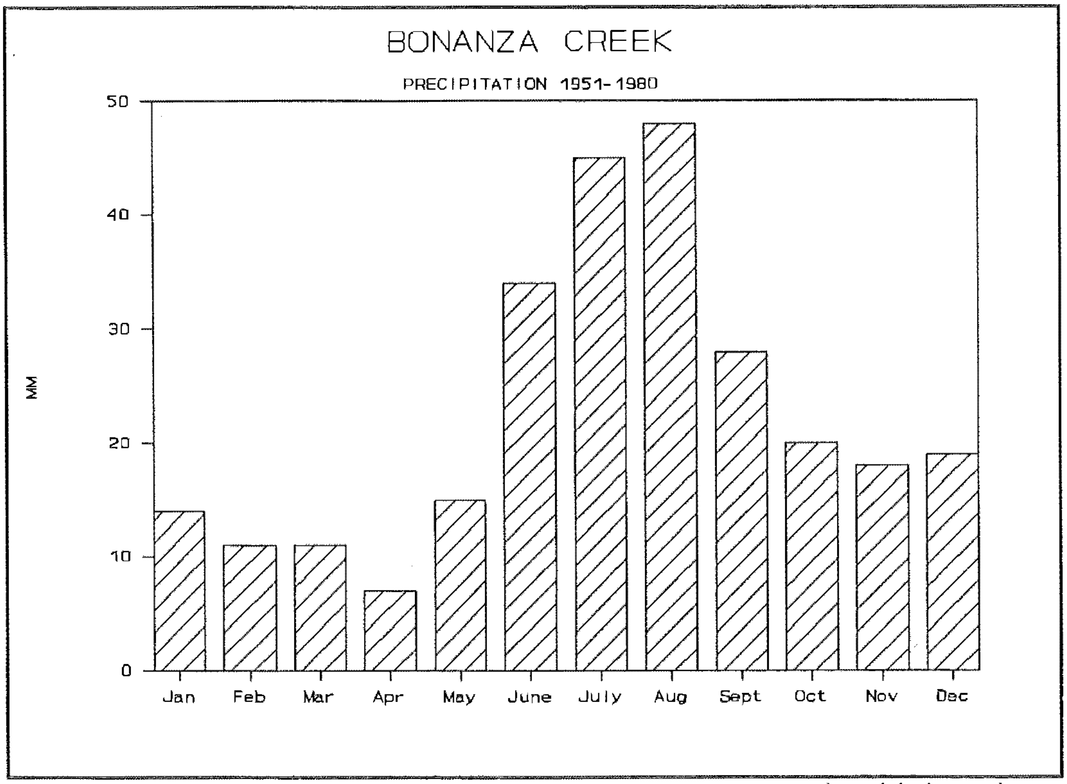



**Figure 2.** Average annual precipitation totals.

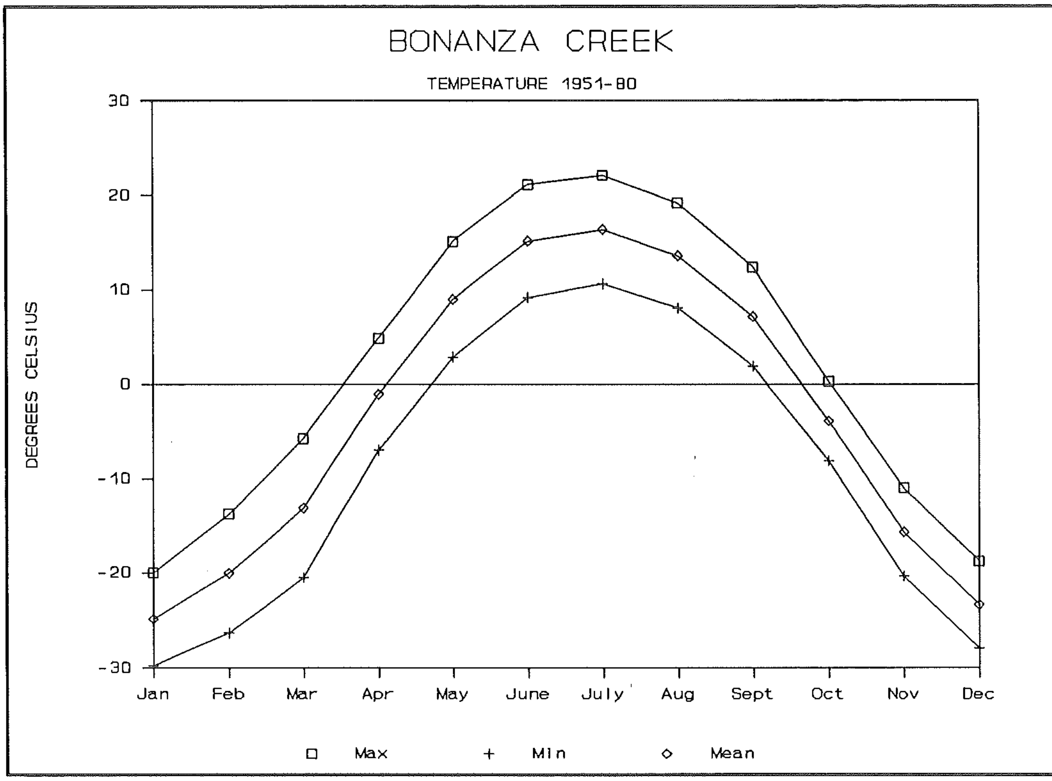
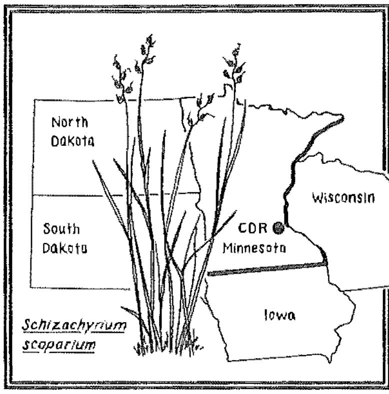


**Figure 3.** Average annual temperature values.

* Data from on-site or nearest weather station.




# Cedar Creek Natural History Area (CDR)

## RESEARCH SETTING

Cedar Creek Natural History Area (CDR) is a 2,200-ha experimental ecological reserve operated by the University of Minnesota in cooperation with the Minnesota Academy of Science. It is located in Anoka and Isanti Counties about 50 km north of Minneapolis and St. Paul, just east of Bethel, Minnesota. Cedar Creek lies at the biome transition between tallgrass prairie and oak woodland. As such, it is likely to be highly susceptible to climatic change.

### *Site Characteristics*

Cedar Creek is a mosaic of uplands dominated by oak savanna, prairie, hardwood forest, pine forest, and abandoned agricultural fields and lowlands comprised of ash and cedar swamps, acid bogs, marshes, and sedge meadows. Large tracts of the pre-agricultural ecosystems of the region are preserved within its boundaries as is a successional chronosequence of more than 80 old fields of known history. A program of prescribed burns, begun in 1964 in a large tract of native oak savanna, has 12 blocks with fire frequencies ranging from one per year, to one per seven years, to unburned controls. These have diverged dramatically in their vegetation and soils in response to fire frequency and some areas are now exhibiting characteristics not seen in this region since settlement in the 1800s.

The soils of Cedar Creek, derived from a glacial outwash sandplain, span five of the 10 soil orders. Upland soils are nitrogen poor; numerous nutrient addition experiments performed in both old fields and native savanna have shown that nitrogen is the major soil resource that limits plant growth. Cedar Creek has a continental climate with cold winters, hot summers, and precipitation (66 cm per year) spread fairly evenly throughout the year. The mean July temperature is 22.2°C, while the mean January temperature is -10°C.

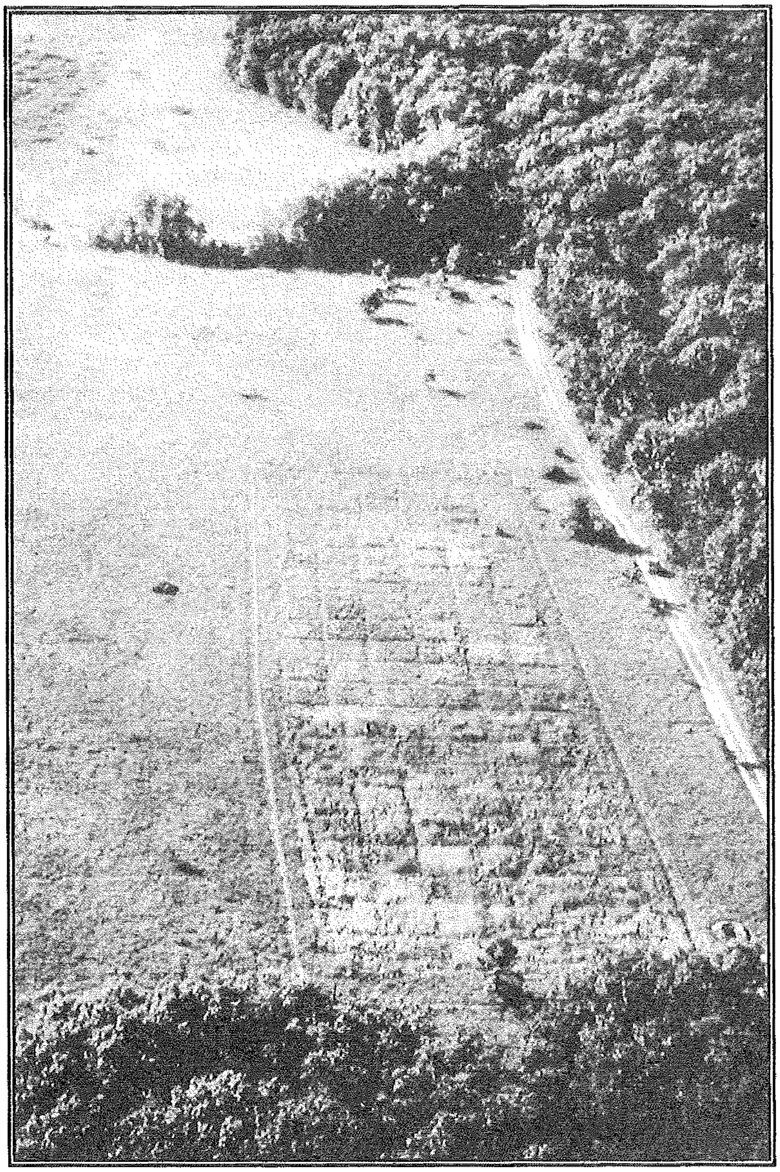
Cedar Creek has 11 permanent buildings, including a year-round laboratory, a shop building, a storage building and work area, a winterized animal holding facility, four year-round family homes, a duplex apartment building, and two summer cabins. There is a 12-person dormitory with a kitchen. The laboratory contains offices, two large work areas, an electronics laboratory, an analytical chemistry laboratory, an herbarium, an insect collection, and a mammal collection. Major items of equipment include IBM microcomputers, a Campbell meteorological station, $NH_4$ and $NO_3$ Autoanalyzers, a Carlo-Erba C-N-S analyzer, spectrophotometers, and analytical balances.

## RESEARCH PROGRAM STATUS

The central goal of our Long-Term Ecological Research (LTER) project is to understand the causes of the successional dynamics, spatial structure, and biodiversity of CDR ecosystems. Our approach synthesizes population, community and ecosystem perspectives. Cedar Creek is a mosaic of landscape elements that differ in productivity, herbivory, disturbance history, soil processes, and landscape position. Each of these factors interacts and co-varies with the other factors. To understand the cause of spatial and temporal dynamics, we uncouple these factors through experimentation, find how they are linked in nature through additional experiments and long-term observations, and synthesize these data through the development of ecosystem models and general ecological theory. Our work looks at the direct, indirect, and feedback effects of ecosystem elements on each other. Feedback effects, if positive, can cause ecosystem divergence and multiple stable equilibria. Even negative feedback effects can cause long-term oscillations that might influence successional dynamics and spatial structure.

Succession is slow at CPR. Sixty years after cessation of agriculture, fields have neither returned to pre-agricultural nitrogen levels nor re-attained their woody cover. Only long-term observations can describe adequately the slow secondary succession in these fields. And only long-term experimentation can unravel paths of causation, and distinguish spurious correlation from causation.

Our highest priority initially was to establish long-term experimental and observational plots in old fields. We now have over 1,100 permanent experimental plots, as well as 2,300 permanent observational plots distributed among 22 fields in a successional chronosequence. We are building a systematic, long-term data set that has already proven useful, but increasingly unique and powerful, with each additional year of data.



*Experiment on the effects of soil nutrient dynamics, herbivory and disturbance on composition and dynamics of grassland vegetation.* DAVID SMITH

## *Field Experiments*

Field experiments, each well-replicated within a given field and most repeated in four different successional fields, fall into five classes of studies:

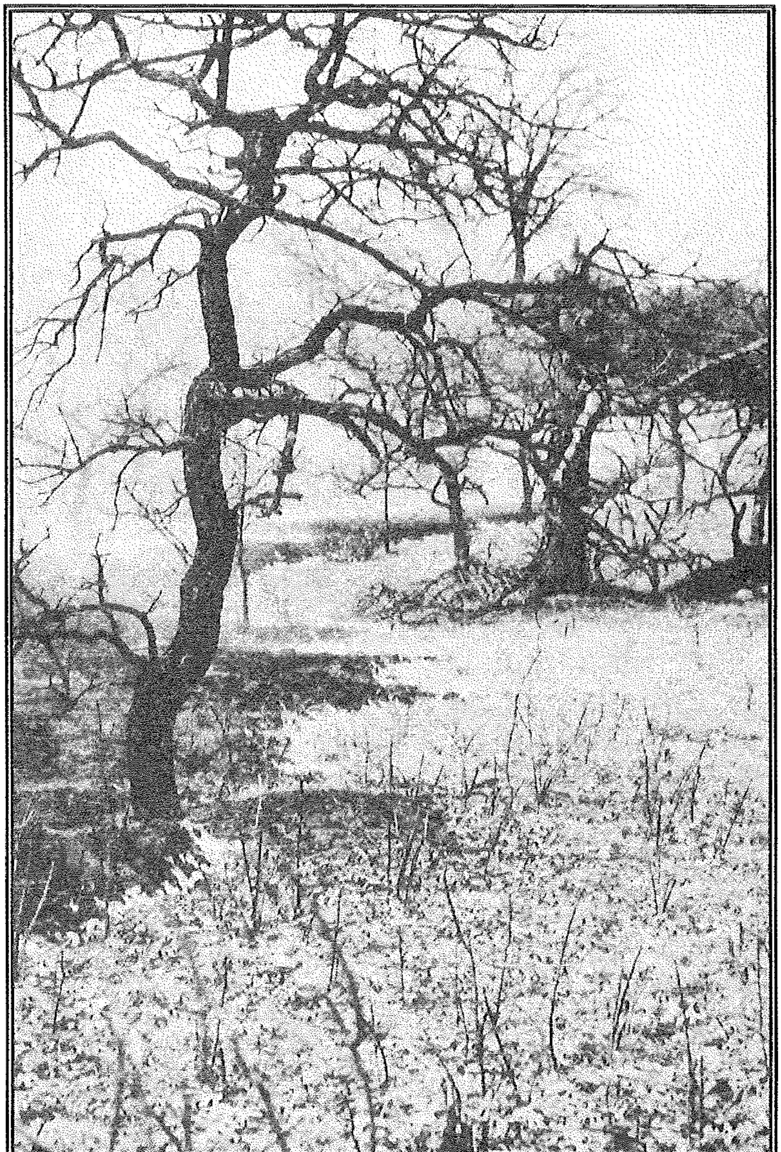
- soil carbon (C) and nitrogen (N) dynamics and controls,
- primary productivity,
- herbivory,
- disturbance regimes, and
- controls of biodiversity.

Studies of C and N Dynamics include (a) feedback effects of individual plant species on nitrogen mineralization; (b) effects of nitrogen addition on nitrification and leaching losses; (c) experimental studies of N fixation of soil algae, legumes, free-living soil bacteria, and associative N-fixers; (d) studies of denitrification; (e) studies of microbial biomass, dissolved organic C and N dynamics; and

(f) changes in the composition and structure of the microbial community.

Primary Productivity experiments include (a) addition of nutrients one at a time or in combination to determine which limit production; (b) experimental productivity gradients of natural vegetation within deer and gopher exclosures; and (c) similar experimental productivity gradients with all herbivores present.

Herbivore Experiments include (a) selective removal of herbivore guilds (foliage-feeding insects, xylem- and phloem-feeding insects; below-ground feeding insects; *Microtus pennsylvanicus*; *Geomys bursarius*; all herbivores); (b) deer exclosures at the margins of old fields to determine the role of deer herbivory in succession; and (c) comparisons of fenced and unfenced N gradients to determine effects of gophers and deer; (d) studies of grasshopper feeding preferences and competition.


*One of 16 burn compartments in an experiment to determine the effects of burning frequency on vegetation at the prairie/forest boundary. DAVID TILMAN*

Disturbance Experiments include (a) comparisons of disturbed vs. undisturbed plots that receive different N additions; (b) a 27-year running set of prescribed burns in large blocks of native oak savanna designed to test effects of fire frequency; (c) prescribed burns at various frequencies in a 25-year-old field; and (d) manipulations of water-table depth to mimic the potential impact of climate change. Most studies have been done in the same fields in a coordinated manner, so that results of one study are directly relevant to those of others.

Biodiversity Studies include (a) long-term observations on effects of climatic variation on biodiversity in permanent plots; (b) experimental studies of effects of different levels of soil heterogeneity and of herbivory on plant diversity; and (c) experimental studies of effects of local recruitment limitation and neighborhood competition on plant diversity in old fields and native prairie.

### *Permanent Observational Plots*

Permanent observational plots are located in a chronosequence formed by 22 old fields of different ages. Within each field we established 100 permanent quadrats (150 in two fields) for repeated, non-destructive sampling of vegetation to species, soils (total N, pH, organic matter, sand, silt, clay), and disturbance events. Other quadrats have been sampled for total plant biomass (above- and belowground, the former separated to leaves and stems), soil chemistry (total N; pH; dissolved organic C; total organic C; extractable $NH_4$ and $NO_3$), microbial biomass, microfungi, mycorrhizal fungi, small mammals (to species), and grasshoppers (to species). This chronosequence has provided a rich description of the changing importance of various processes during succession. By periodic resampling, we will determine the extent to which inferences based on a chronosequence are indicative of the actual pattern of dynamic change during succession.

Our observational studies suggest that N dynamics, light, colonization rates, disturbance history, and possibly herbivory are the major factors influencing successional dynamics and spatial patterning at CDR. Low levels of N in newly abandoned fields, and the 100-plus years required for soil N levels to return to that of undisturbed savanna, may partially explain the pattern and rate of succession, especially the slow revegetation by woody plants. However, this cannot explain the domination of early successional, N-poor fields by annuals and short-lived perennials. Might their dominance be the result of the transient dynamics of competitive displacement or of a tradeoff between the competitive ability of a plant species versus its dispersal ability?

Our experiments have shown that transient dynamics are a general response of ecosystems to perturbation. Are the results that we have observed after ten years of nutrient addition indicative of the eventual relations between ecosystem structure and productivity? Or are the species that dominate after ten years also transients to be displaced by other species? We do not yet know how long experiments such as our productivity gradients must proceed before it is possible to distinguish between transient dynamics and long-term effects. Our models predict that transient dynamics may last for 30 to 40 years in grasslands. If this is so, our experiments may need to proceed for another 25 to 35 years.

Slow increases in soil N and plant biomass during secondary succession at CDR suggest that the successional gradient is also a productivity gradient. However, contrary to our initial hypothesis, there are dramatic differences between the correlational patterns observed between ecosystem structure and productivity in successional fields and those observed in native, undisturbed ecosystems. We do not know what causes these differences. Why, for instance, do plants that dominate the poorest soils of secondary succession have root:shoot ratios almost five times lower than plants that dominate the least productive areas of non-successional ecosystems? Why is *Agropyron repens* dominant on N-poor soils during succession, but on the most N-rich soil in our experimental N gradients? Given the length of time that successional fields remain free of a woody overstory, why do woody plants of N-poor, undisturbed soils, such as *Corylus* and ericaceous species, not come to dominate the old fields? In other words, why is species composition along the successional productivity gradient so different from that along a non-successional productivity gradient, though both have similar physiognomic characteristics? We shall address these questions by continuing our existing research and by expanding it to include studies of productivity gradients in additional non-successional habitats.

Our work to date has demonstrated the power of combining experimental, observational and theoretical approaches, and the need for long-term observations and long-term experiments. It has led us to formulate a series of general theoretical predictions that we now wish to test not only at Cedar Creek, but also by performing comparisons across the North American productivity gradient represented by the LTER Network.

## FUTURE DIRECTIONS

Our research will continue to seek the underlying mechanisms that cause broad scale patterns in ecosystem composition, diversity, and productivity. We are currently interested in and greatly concerned about the potential impact of global climatic change on biotic diversity, and believe that our long-term experimental and observation studies will help address this issue.

Furthermore, we have just begun a new series of experiments designed to determine the roles of various processes (dispersal, competition, soil heterogeneity, disturbance) in allowing the local coexistence of numerous species.

*** CDR Climate Data 1951 - 1980**

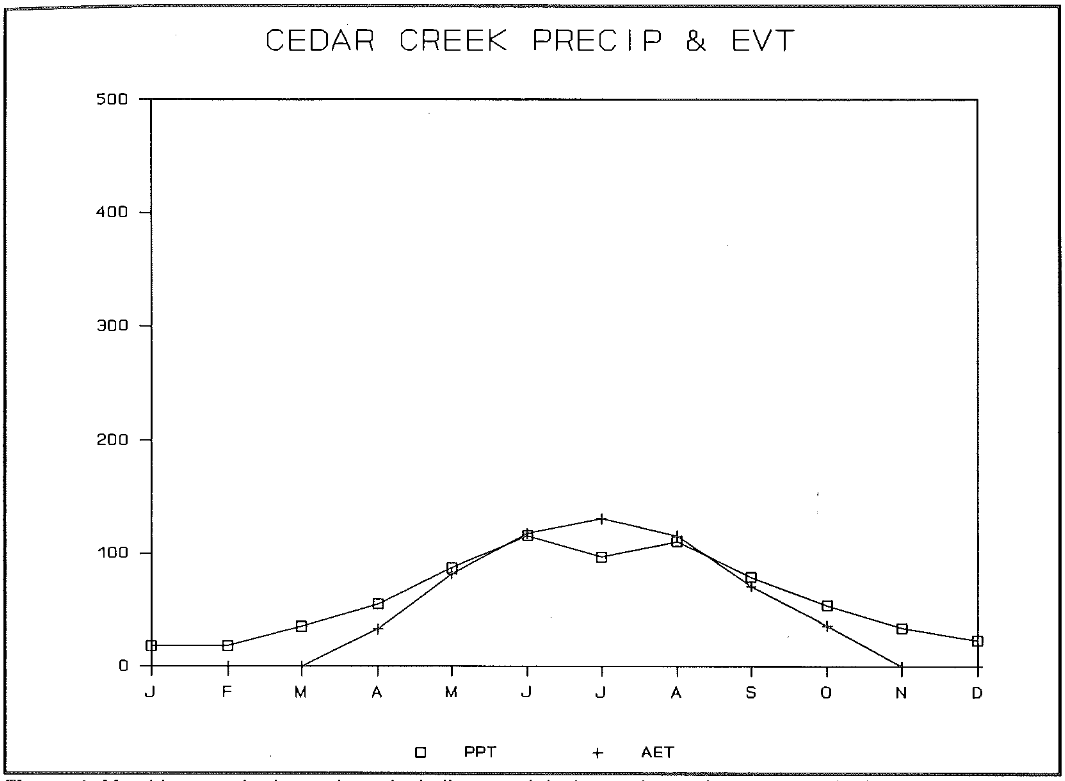



***Figure 1.*** *Monthly water budget values, including precipitation and actual evapotranspiration.*

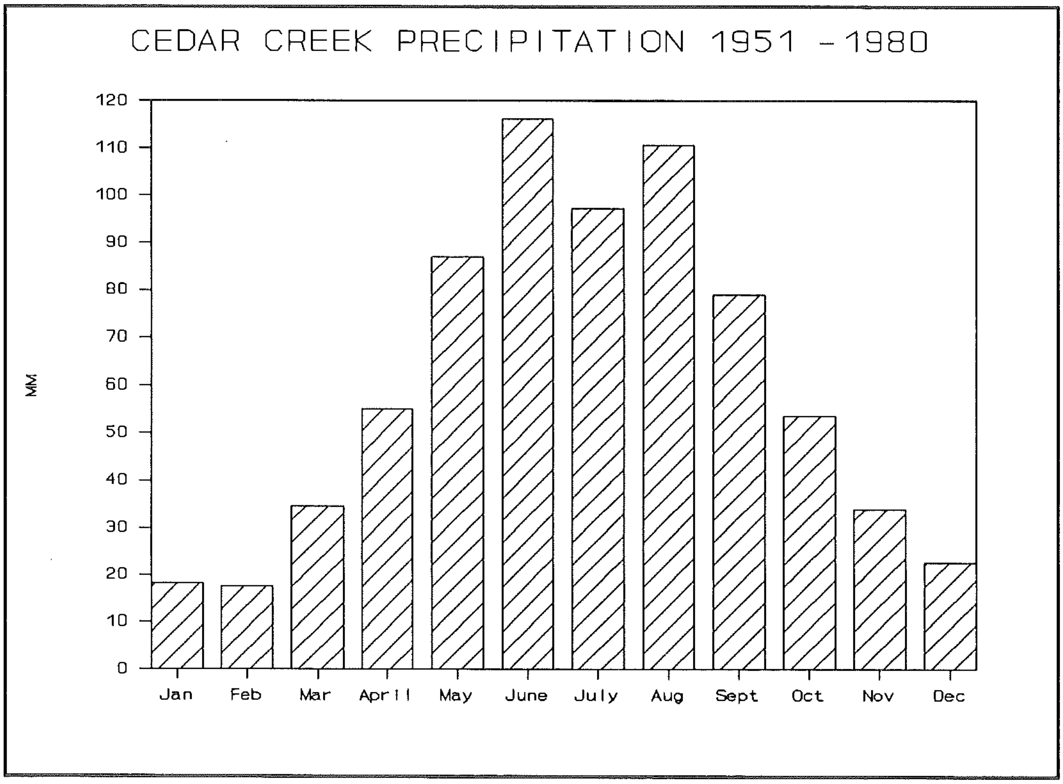



***Figure 2.*** *Average annual precipitation totals.*

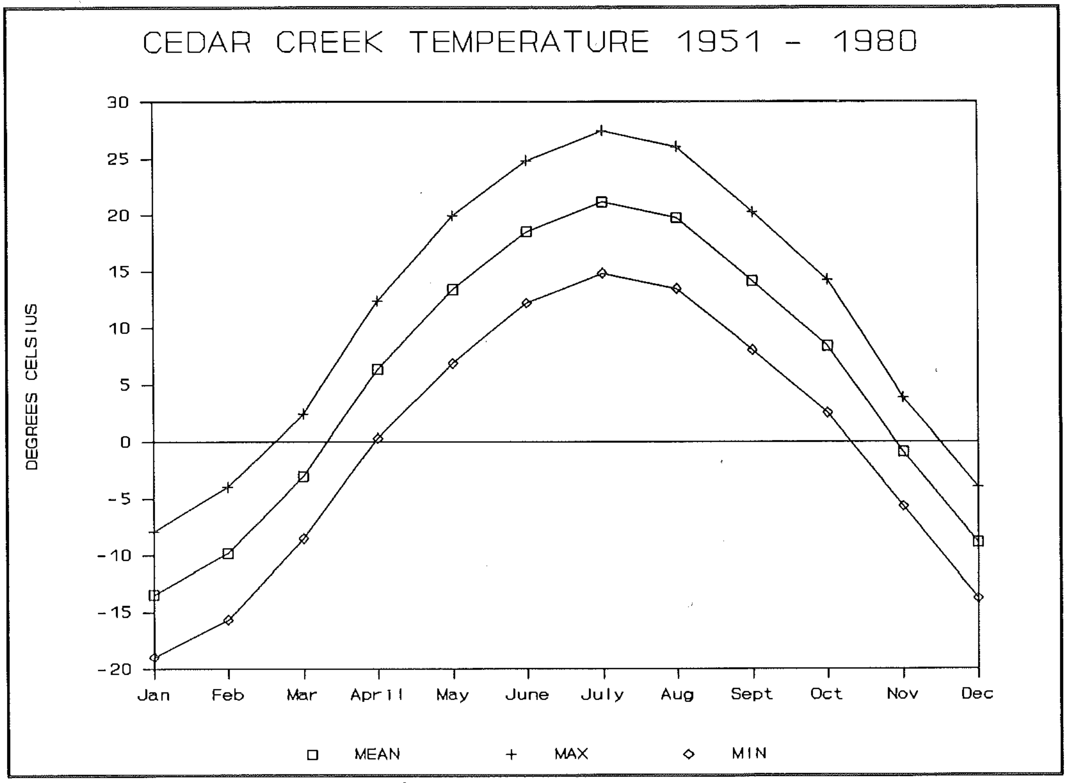



***Figure 3. Average annual temperature values.***

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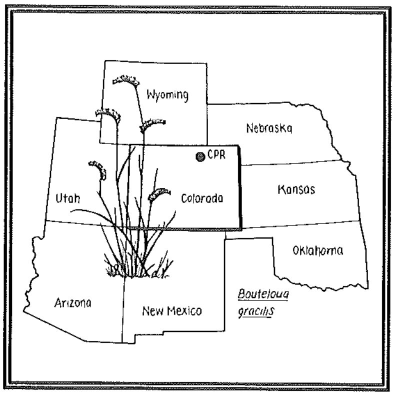
* Data from on-site or nearest weather station.




# Central Plains Experimental Range (CPR)

## RESEARCH SETTING

The semiarid Great Plains of North America comprise a mosaic of native grassland and cropland adjacent to the eastern face of the Rocky Mountain chain. Motivation for careful evaluation and monitoring of this region at the end of the 20th century comes from two sources. First, the Great Plains contains the major wheat producing areas for the entire continent, in addition to important grazing lands for livestock. Second, current models of atmospheric circulation indicate that climatic change, as a result of increased greenhouse gases, will be relatively larger here than in most other parts of temperate North America. The combination of socioeconomic importance and vulnerability of the region to both climatic fluctuations and climate change make it essential that we expand our understanding of long-term ecological relationships, particularly climate-landuse-ecosystem interactions.

The Central Plains Experimental Range (CPR) has an excellent location in the central Great Plains to represent the important long-term ecological issues of consequence for much of the region. The CPR Long-Term Ecological Research (LTER) project benefits not only from the location of the site, but also from the presence of long-term field facilities and experiments, and from the availability of historical data.

The CPR LTER project represents the continuing development of a research tradition that began with the U.S. International Biosphere Program (IBP) Grassland Biome project in the late 1960s, the time at which ecosystem science was formally recognized as a sub-discipline in ecology. Research at CPR over the past 20 years has had an important interactive relationship with the development of ecosystem science. The Grassland Biome project focused on the issue of productivity of natural ecosystems. Grasslands were conceptualized as homogeneous entities, appropriately described by an average square meter. The transition from the IBP project to the LTER project in the early 1980s involved a change in thinking about the importance of spatial variability. Our involvement in the LTER program (LTER I 1982-1986) began with spatially explicit ideas and questions about the importance of landscape structure, particularly the classic soil catena model, in the long-term development and maintenance of shortgrass steppe ecosystems. In the second phase of the project (LTER II 1987-1990) we expanded our concept of long-term processes to include the origin and persistence of spatial patterns at a range of spatial scales (Figure 1). This work included substantial questioning of the generality of the catena model at CPR and in the shortgrass steppe region. Work in the third phase builds upon the first and second and expands the depth of our investigations into interactions between spatial and temporal patterns in ecosystem structure and function.

### Climate, Geomorphology & Landuse Interactions

Climate is a major driving force for biological processes in semiarid regions, constraining the kinds and numbers of organisms that can survive, compete, and reproduce; determining overall ecosystem structure and potential productivity; and altering the dynamics of ecosystem processes. Climate exerts major control at the regional level, accounting for most of the observed spatial variation in many ecosystem attributes. Interactions of climate with landform and topographic position cause spatial patterns in microclimate at landscape scales. In the shortgrass steppe, interannual variability in precipitation is a key control over annual net primary production (NPP). Within a growing season, pulse precipitation events create important short-term spatial variation in biological activity.

Long-term geomorphic processes are responsible for the structure and stability of the landform and soil as a template for ecosystem development and sustainability. Over geologic time, the interaction of the geologic template with climate—wind, precipitation, temperature—drives weathering and fluvial and eolian redistribution of sediments across landscapes and regions. At the scale of decades to centuries, erosional and depositional processes at the toposequence and physiographic unit spatial scale may be important in shaping landforms via redistribution of material (Figure 1). The shortgrass steppe is particularly vulnerable to erosion during droughts, especially when subjected to intensive management such as cropping, as was apparent in the Dust Bowl of the 1930s.

Landuse in the shortgrass steppe has an important impact on system status. Climatic zones establish regional patterns in landuse, with greatest cropping intensity in highest rainfall areas. Geomorphologic processes determine spatial patterns in landuse, with the most productive lands —generally those on loamy soils—all under cropping, and grazing on less productive sites. Weather variability among years, commodity prices, and current status of land determine the temporal variation in landuse.

The relative importance and impacts of climate, geomorphologic processes, and landuse on patterns in ecosystem properties change across scales. This is an important reason why conducting research across spatial scales can significantly improve our understanding of controls over system behavior. Our understanding at a particular scale is limited to the range of conditions we have observed; the realm of inference is thus limited to the same range of conditions. For example, a study

*The CPR and the shortgrass steppe region are characterized by broad valleys separated by low hills.* *STEVE TORBIT*

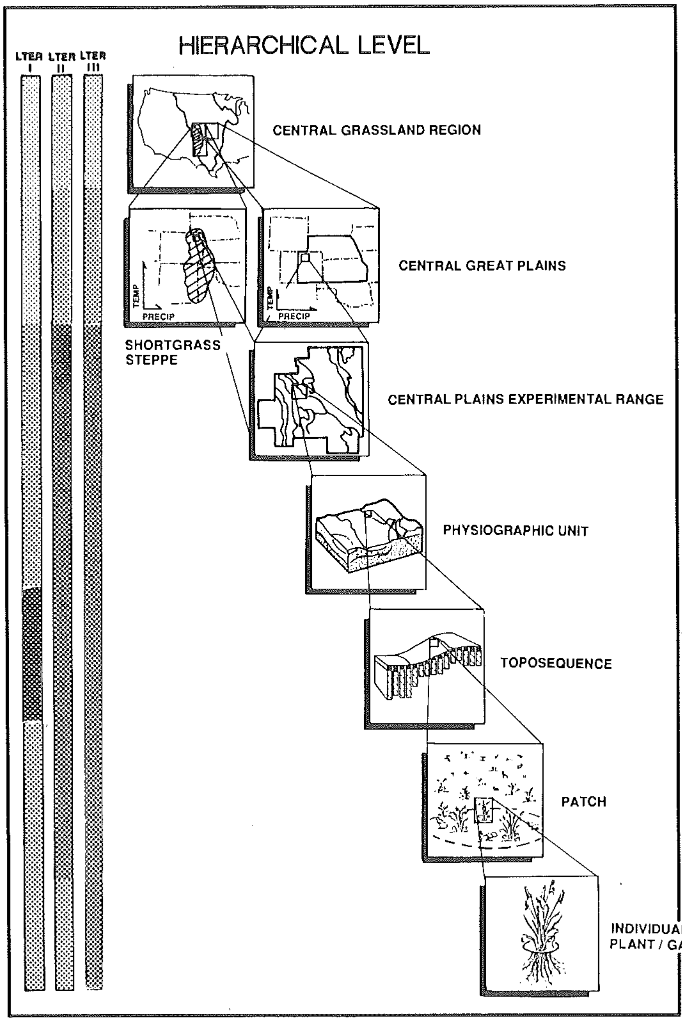



Figure 1.

of soil organic matter (SOM) on a particular toposequence at CPR suggests that slope position is an important control over carbon accumulation. Expansion to the scale of physiographic units (multiple toposequences [Figure 1]) suggests that spatial pattern in SOM is controlled by soil texture, parent material, and grazing history, as well as slope position. Finally, spatial pattern in SOM at a regional scale is most closely related to mean annual temperature and precipitation, modified by soil texture and landuse history. What are the rules for generalizing spatial pattern among scales? Can we use rules based on spatial variation to make predictions about temporal variation?

### Site Description

The Central Plains Experimental Range is a 6,280-ha tract of shortgrass rangeland located in the piedmont of northcentral Colorado approximately 61 km northeast of Fort Collins and the campus of Colorado State University (latitude 40°49'N; longitude 104°46'W; elevation 1,650 m). The CPR is administered by the USDA Agricultural Research Service (ARS).

The climate of CPR is typical of mid-continental semiarid regions in the temperate zone except for the strong influence of the Rocky Mountains approximately 60 km to the west. Mean monthly temperatures range from -4 to 22°C seasonally and have a daily average maximum-minimum range of 17°C. Annual precipitation averaged 322 mm over the past 51 years, ranging between 107 and 588 mm. Approximately 70 percent of the mean annual precipitation occurs during the April-to-September growing season.

The vegetation of plant communities on CPR is dominated by shortgrasses (64 percent), forbs (7 percent), succulents (21 percent), and half-shrubs (8 percent). The key species of these groups are *Bouteloua gracilis* and *Buchloe dactyloides*; *Sphaeralcea coccinea; Opuntia polyacantha*; and *Chrysothamnus nauseosus, Gutierrezia sarothrae*, and *Eriogonum effusum*, respectively. Average aboveground net primary production is 125 $g/m^2$ and ranges from 60 to 180 $g/m^2$, depending on available soil water. Major differences in vegetation structure occur in saltgrass meadows dominated by *Distichlis stricta* and *Sporobolus asper*, and on floodplains where the shrub *Atriplex canescens* is an important component.

Past and current research provides an important base and source of information for accomplishing our LTER goals. Our core research emphasizes: relations between the hydrologic cycle and primary production, evaluation of key microbial responses, studies of plant succession, plant and animal population dynamics, processes associated with aggradation or degradation of soil organic matter, response of plant community and soil processes to long-term cattle grazing, the nature of the erosion cycle and its influence on redistribution of matter, nutrients, and pedogenic processes, and the influence of atmospheric gases, aerosols, and particulates on primary production and nutrient cycles.

The main LTER headquarters building (214 $m^2$) has offices, laboratories, a dining/meeting room, and a kitchen. Adjacent to the headquarters is a storage/sample processing building (134 $m^2$) with facilities for washing and drying samples. The dormitory has six rooms; five capable of double occupancy and one with four beds. In addition there are large-animal handling and holding pens and a residence for the site manager.

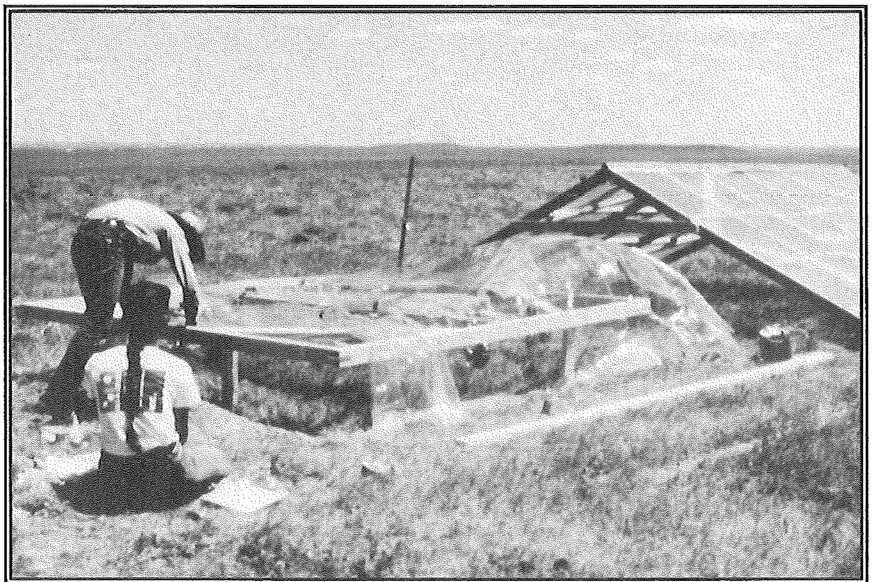
## RESEARCH PROGRAM STATUS

Our overall objective is to understand the long-term processes responsible for the origin and sustainability of shortgrass steppe ecosystems. To achieve this objective, we will evaluate the climatic, geomorphic, and human-induced controls over ecosystem structure and function across a range of temporal and spatial scales, extending from intraseasonal variation to geologic periods, and from individual plants to the central grassland region (Figure 1).

Our research focuses on how climate, geomorphologic processes, and landuse impact spatial and temporal patterning of ecosystem properties and processes. Each has important spatial and temporal heterogeneity across a range of scales, and exerts its influence at a particular combination of levels (Figure 1). How do these controls interact to influence spatial variation in system structure and function at any particular scale? How does interaction affect prediction at the next higher scale? The next lower? The scope of such an undertaking dictates that multiple research approaches be used; we are studying these interactions using long- and short-term experiments, simulation models, and regional analysis. Experiments allow us to test and improve our understanding at a limited set of spatial and temporal scales, confined by feasibility to single or multiple locations and from weeks to decades. Simulation models are important tools that allow us to test and improve our understanding across a range of temporal scales. Modeling is especially important in the study of climate change, allowing us to extend beyond the bounds of observed conditions. Finally, regional analyses allow us to extend our spatial domain beyond the bounds of our experiments and observations.

## FUTURE DIRECTIONS

One of the most exciting future directions for the CPR LTER project is associated with a collection of new experiments to evaluate the development of patterns and processes in grazed and protected ecosystems. We are establishing new experiments in areas that have been heavily grazed or protected from cattle grazing for the past 51 years. We are constructing new exclosures in pastures that have been grazed as well as beginning to graze areas that have been



*Root production plots labeled with $^{14}C$ are providing important new insights into belowground processes.* *D.G. MILCHUNAS* protected. This work will allow us to evaluate the temporal development of responses to protection and grazing, and will provide us with the opportunity to gain a process-level understanding of these responses.

Another new direction for the project is the production of a synthesis volume on Great Plains grasslands. After six intensive years of investigation during the IBP project and nine years of LTER research, as well as 52 years of work by the ARS, we think the time has come to put together an overview product that capitalizes on all of the research at the CPR and other sites in the region.

## * CPR Climate Record 1951 - 1980

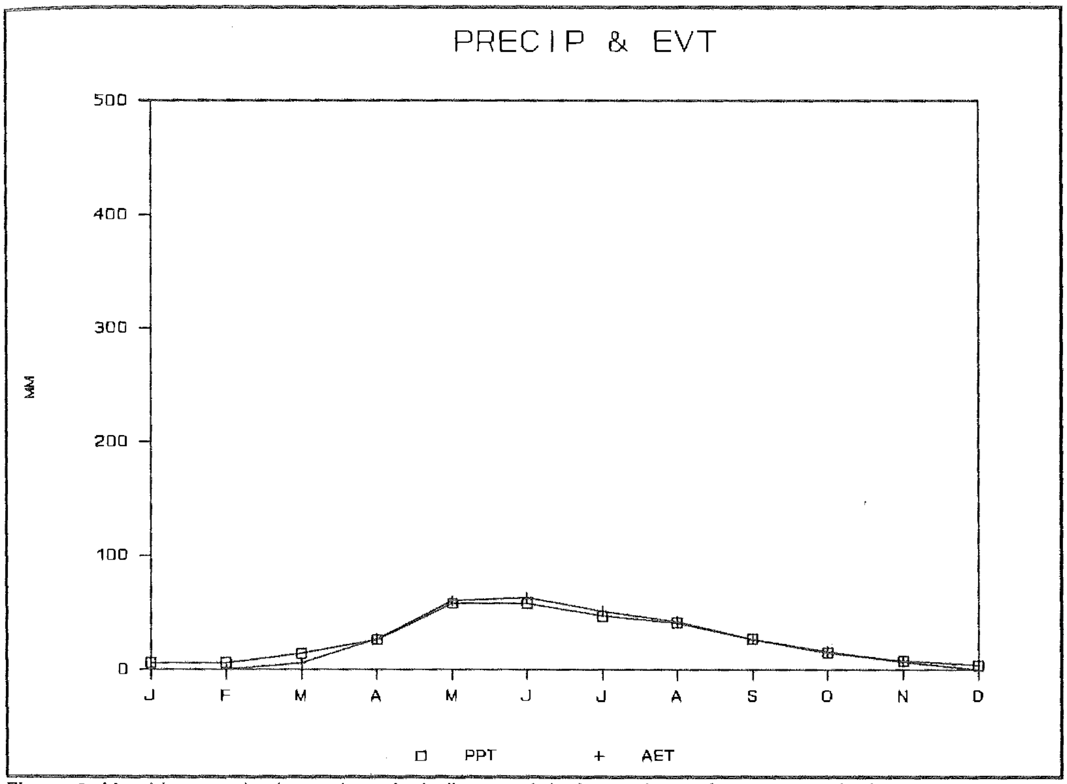



**Figure 2.** Monthly water budget values, including precipitation and actual evapotranspiration.

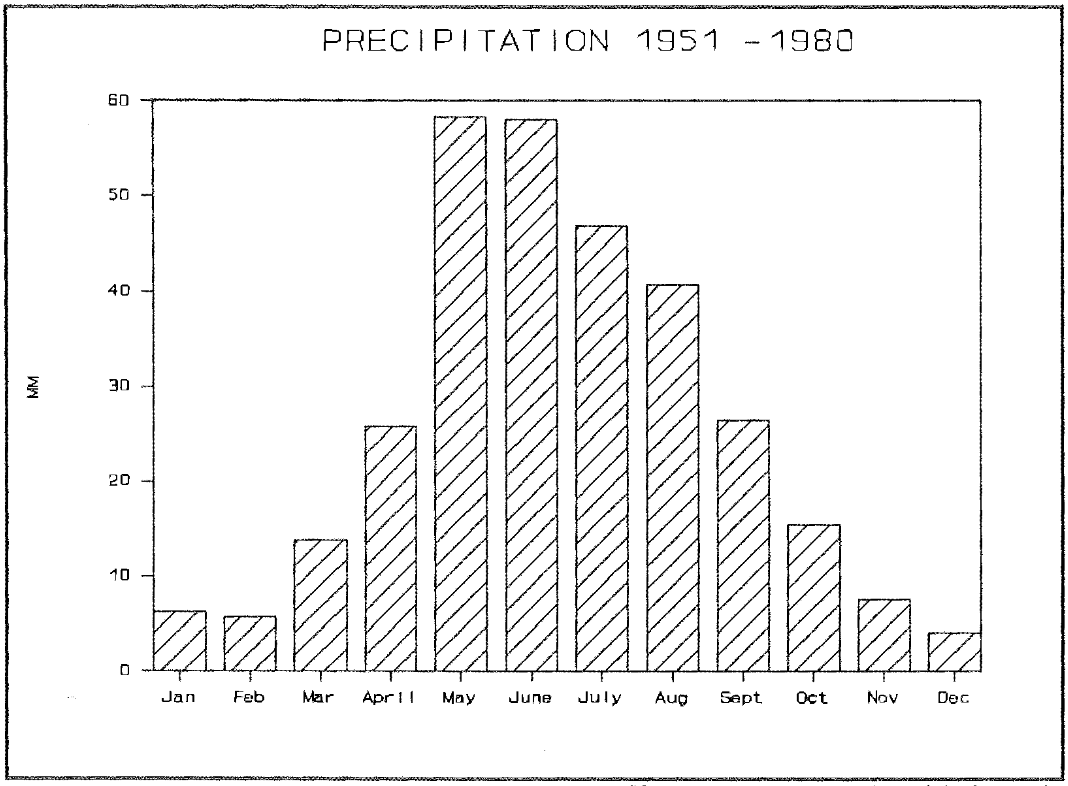



**Figure 3.** Average annual precipitation totals.

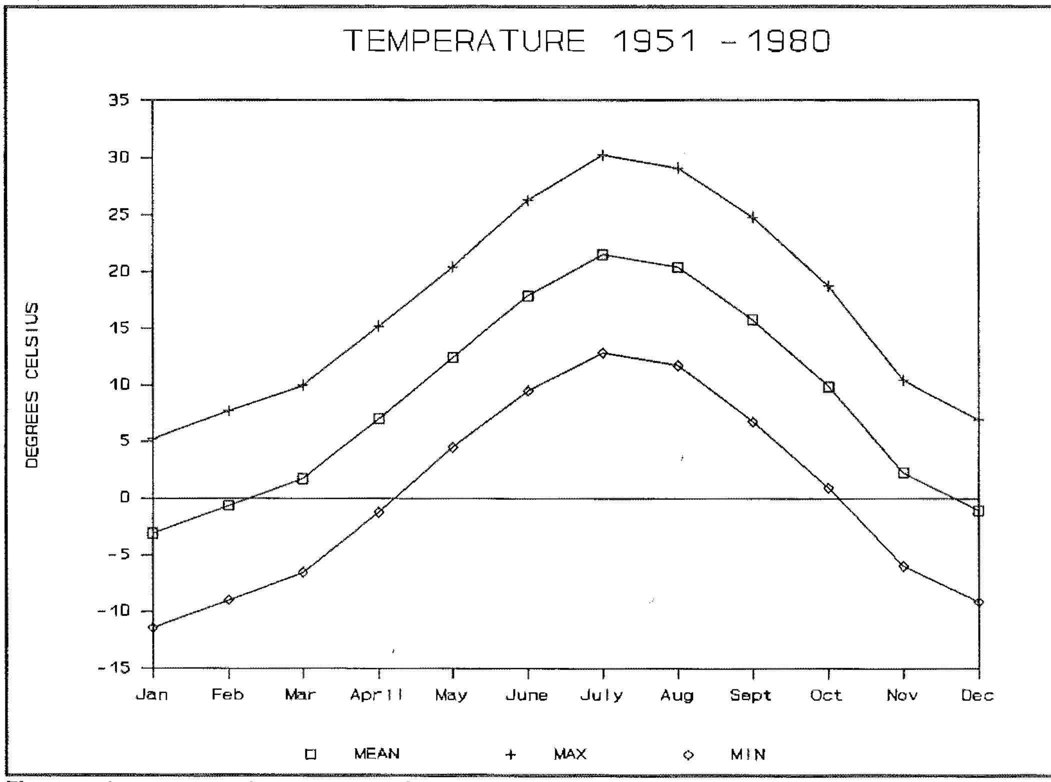
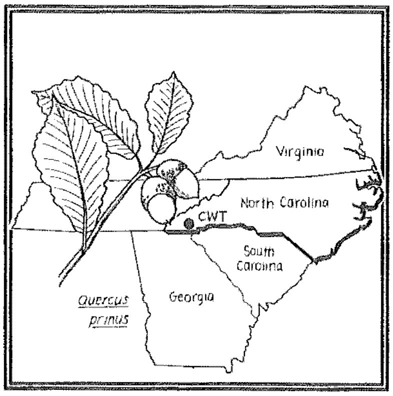



**Figure 4.** Average annual temperature values.

* Data from on-site or nearest weather station.




# Coweeta Hydrologic Laboratory (CWT)

## RESEARCH SETTING

The Coweeta Hydrologic Laboratory Long-Term Ecological Research (LTER) site is located in the southern Appalachian Mountains and contains stands of eastern deciduous forest of varying ages, white pine plantations, and numerous first- through fourth-order streams.

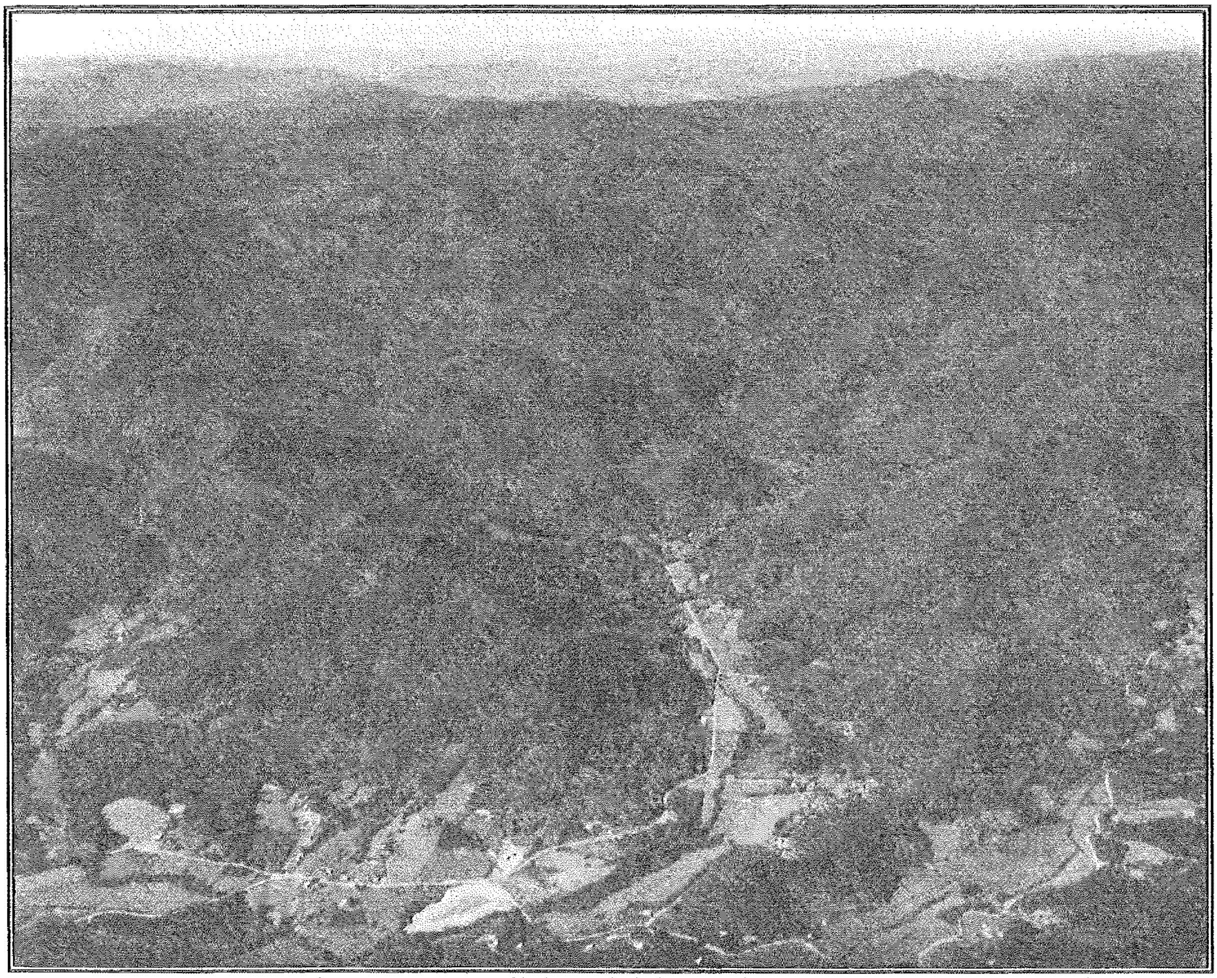
LTER research at Coweeta Hydrologic Laboratory has four primary goals: (1) to describe and explain functions and processes of forest and stream ecosystems; (2) to examine the response and recovery of forest and stream ecosystems to disturbance; (3) to assess the changing nature and effects of atmospheric inputs on the structure and function of southern Appalachian terrestrial and aquatic ecosystems; and (4) to apply this understanding to develop ecologically sound and effective forest management practices. We have used natural disturbances (insect outbreak and regional drought), anthropogenic disturbances (chestnut blight), and experimental disturbance (clear-cutting) as tools for studying ecosystem response to and recovery from disturbance. This is the core of our LTER program, which serves as a catalyst to attract additional support and science. Currently, more than 25 active cooperative agreements have been developed between the Forest Service and other agencies and institutions. Studies range from single investigator efforts to national projects involving numerous investigators and multiple sites.

### *Site Characteristics*

The site is a 2,185-ha experimental facility in North Carolina, and is administered by the USDA Forest Service. It has been dedicated to forest hydrology research since its establishment in 1933. The area lies within the Blue Ridge geologic province; elevations range from 679 to 1,592 m. More than 50 km of streams drain the area. The regional climate is classified as marine with cool summers, mild winters, and adequate rainfall during all seasons. Mean annual temperature is 13° C. Annual precipitation is high and variable over the area, with an average of 178 cm at lower elevations to over 250 cm on upper slopes. Snow typically contributes less than 2 percent to total precipitation. Coweeta is the first major mountain range contacted by air masses moving over the industrialized Piedmont region to the south. Analyses of precipitation chemistry have shown the influence of both local and regional activities on nutrient inputs to forest ecosystems.

The annual pattern of streamflow is similar to precipitation, and perennial flow occurs for watersheds as small as 6 ha. Streams are high-gradient with dense rhododendron cover, and woody debris is an important structural feature. We have recognized four major patch types in streams: cobble riffles, rock outcrops, pools, and debris dams. Structural and functional attributes of these patches differ.

Geologically, this region has undergone great uplift, repeated and complex folding and erosion. The soils at Coweeta are classified as either



*Aerial view of Coweeta Hyddrologic Laboratory in the Coweeta Creek basin.* *USFS PHOTO*

immature Inceptisols or older developed Ultisols. Soil physical and chemical properties vary substantially over the basin. Soils are relatively high in organic matter and moderately acid with both low cation exchange capacity and percent base saturation, characteristics which are typical for highly weathered Ultisols.

Deciduous oak species are the dominant canopy species in Coweeta forests with an abundant evergreen understory component comprised of *Rhododendron maximum* and mountain laurel (*Kalmia latifolia*). Four major forest types are recognized: (1) northern hardwoods, (2) cove hardwoods, (3) oak (-chestnut), and (4) oak-pine.

Since Coweeta was established, 32 weirs have been installed on streams; 17 are currently operational. Stream gauging was initiated on most watersheds between 1934 and 1938, and stream chemistry measurements date back to 1968.

Research has been conducted on eight mixed hardwood control areas and 13 catchments where forest management prescriptions have been applied. Past treatments include varying intensities of cutting, ranging from light selection through clearcutting; conversion of hardwoods to white pine; conversion of hardwoods to grass and subsequent succession to hardwoods; multiple-use management; mountain farming; and the application of herbicides and fertilizers.

## RESEARCH PROGRAM STATUS

The LTER research project is continuing long-term studies of recovery from disturbance, concentrating on those that are of major consequence in the southern Appalachians, such as drought and altered atmospheric deposition. Understanding and predicting responses to current and emerging environmental problems such as global change, water quality, and cumulative effects requires research on an expanded scale organized along environmental gradients with a continued emphasis on use of experimental manipulation to examine ecosystem response to disturbance. This is the core of our LTER program.

We view the Coweeta landscape as three interconnected ecosystems: forested slopes, riparian zone, and stream. All are influenced by external physical (temperature, precipitation), chemical (atmospheric deposition), and biological (anthropogenic disturbance) driving variables. The nature of the driving variables and the responses of the three component ecosystems will vary across the elevational gradient. We have therefore chosen to focus our research on gradients and exchanges between landscape components. It is this aspect of the landscape that will be most susceptible to disturbance-induced alteration.

The elevational gradient represents a gradient in driving variables such as solar radiation, temperature, precipitation, atmospheric deposition, concentrations of atmospheric pollutants, soil characteristics, and stream size. Response to changes in driving variables (environmental disturbance) also varies along the gradient. An example of these changes can be seen in patterns of streamwater chemistry in response to acid deposition, discussed below. With this landscape perspective, the long-term ecological research on ecosystem response to disturbance along environmental gradients at Coweeta consists of projects designed around hypotheses formulated for the three component ecosystems. The ideas structuring our research in these areas are outlined in the following sections, and the measurements being taken are summarized in Table 1.

Forests: In the southern Appalachian landscape, the severity of disturbance caused by environmental disturbances such as global change and its impact on forest ecosystem structure and function is strongly influenced by the complex environmental gradient resulting from elevational changes in temperature, precipitation and soil types. To quantify the environmental regulation of key ecosystem processes (net primary production, nutrient dynamics, canopy consumption, soil organic matter/carbon dynamics), we are measuring these variables across gradients of temperature, moisture, and soil type. Forest structure and processes in the southern Appalachians are currently changing as a result of both historic chestnut mortality, recent drought-induced oak decline, and pitch-pine and dogwood mortality. We are examining experimentally and by remeasurement of long-term permanent plots, the impacts of overstory mortality and subsequent gap formation of ecosystem processes and long-term forest succession.

| Forests | Streams | Riparian Zone |
|---|---|---|
| Nutrient export in streams | Periphyton chlorophyll | Decomposition & litter mass |
| Soil mineralization & N, P, S immobilization | Periphyton production | Labile microbial nutrients |
| Decomposition & litter mass | Benthic organic matter (coarse and fine) | Forest floor biota |
| Forest floor biota | Benthic respiration (coarse and fine) | Litter fall and movement |
| Litterfall | Leaf litter processing rate | Soil solution chemistry |
| Climatology (air, soil temp., soil moisture, ppt., PAR) | Macroinvertebrate abundance & biomass | Climatology (air, soil temp., soil moisture, ppt., PAR) |
| Net primary production (above- & belowground) | Macroinvertebrate functional group analysis | Net primary production (above- & belowground) |
| Leaf area | Fish abundance, assemblage stability & production | Periphyton chlorophyll |
| Foliar elements | Substrate mapping | Stream invertebrate abundance |
| Canopy consumption | Retention characteristics | Fish abundance |
| Resurvey permanent plots | Streamwater chemistry | |
| Gap experiment | Hydrology | |

Table 1. Summary of measurements being made along environmental gradients in the three component ecosystems in the Coweeta landscape.

Streams: Differences in structural and functional characteristics of stream ecosystems along elevational and longitudinal gradients are a consequence of changes in the relative abundance of geomorphic patch types along the stream. In order to predict and measure impacts of global change on stream ecosystems, we must understand the effects of longitudinal and elevational gradients on stream processes. In addition to continuing long-term experiments examining recovery of streams from clearcutting and changes in ecosystem structure and function associated with debris dam formation, we are expanding our stream research to include the range of stream sizes found in the basin; previous LTER research had focussed on smaller streams. This new work includes studies of nutrient uptake, periphyton primary production, standing stock and respiration of benthic organic matter, litter decomposition, macroinvertebrate and fish assemblages.

Riparian Zone: This ecosystem component is a key regulator of exchanges between terrestrial and aquatic ecosystems in the southern Appalachian landscape. The presence of the dominant riparian species, *Rhododendron maximum*, alters rates of soluble and particulate element export from the forest and reduces primary productivity in streams. We are testing this hypothesis with a long-term experimental manipulation in which we selectively remove rhododendron from the riparian zone.

### *Impact of a Severe Drought*

The single, major event during the past five years at Coweeta was a prolonged drought. Rainfall deficits in late 1985 escalated into major precipitation shortfalls by 1986. The drought did not end until June 1989 when record precipitation occurred. Analysis of drought patterns during the 55-year record at Coweeta revealed that this drought was the most severe with a recurrence interval ranging from 90 to 250 years, depending on the data set. This analysis was accomplished with a new technique, which simultaneously considers both magnitude and duration of extreme events. Analysis of a longer-term precipitation record from adjacent sites indicates the period from the late 1960s to the mid-1970s was relatively moist and essentially free from droughts of even modest severity. This is significant because it was during this period that numerous baseline ecological studies were performed at Coweeta.

Characterization of canopy gaps, including those created during the most severe part of the drought, has been a recent focus of vegetation research. Severe mortality occurred for oaks and pines (*Pinus rigida*) in the Coweeta Basin, with the consequent creation of snags and deadfalls in gaps generated by one to 10 or more tree deaths. A consequence of this woody input to the forest floor has been an increase in termite populations, which were previously rare. An extensive study of canopy gaps concentrated on hardwood tree species, including historical and recent records. The distribution of gap age showed a significant increase in gap formation beginning in the drought year of 1986. The most common gaps were those created by single and multiple standing dead trees. The most frequent gap-forming species were oaks, especially *Quercus coccinea*. Sixty-five percent of the gaps sampled were formed within two years of the 1986 drought and resulted from the root pathogen *Armillaria* killing drought-stressed oaks. This episodic event will likely have long-term effects upon the structure and processes of hardwood forests at Coweeta.

Historical patterns of canopy arthropod load indicate responses to drought in 1978, 1981 and 1985, when arthropod mass and numbers decreased on south-facing, more xeric, slopes but increased on a north-facing watershed. Relationships of arthropod numbers or feeding to drought depended upon timing of precipitation. The best predictor for decreased canopy arthropod abundance was low dormant-season rainfall; droughts which occurred in summer months had little impact on canopy insects. This finding differs somewhat from predictions offered by current theories of climatic release of insect outbreaks. However, the drought years did produce mortality of native pine species in which the complex of bark-boring insects evidently played a major role.

Data from a separately funded project on the role of invertebrates in stream ecosystem processes combined with LTER data have allowed us to compare the effect of drought on organic matter processing in streams with the effect of macroinvertebrate removal. Leaf litter processing rates, seston concentration, and fine particulate organic matter (FPOM) export were significantly reduced by macroinvertebrate removal. The five-year period of this study encompassed the driest and the wettest years during the 55 years of record. During this period FPOM export in reference streams varied about three-and-a-half-fold, whereas variation in streams where macroinvertebrates were removed was sevenfold. In other words, variation in FPOM export as a consequence of biotic manipulation was greater than variation produced by a range in discharges encompassing the extremes for a 55-year period.

The impact of the drought on fish populations was examined as part of ongoing research on the relationship between environmental variability and assemblage dynamics. Recruitment and year-class strength for the four dominant species werestrongly affected by the drought. In some cases, the drought had a negative impact on species abundances; however, for many species, recruitment and year-class strength increased during the drought. This does not appear to be a consequence of positive effects occurring during low water periods, but to the cessation of winter flooding during the drought. The drought may also have contributed to the upstream invasion of sites by two species, Tennessee shiner and river chub. Consequently, the event appears to have played a strong role in the dynamics of Coweeta fish assemblages.

*Stream researchers sampling benthic organic matter at a site on Ball Creek. Note the dense rhododendron canopy over the stream.* JUDY L. MEYER

### Atmospheric Pollutants, Atmospheric Deposition & Sulfur Dynamics

High ozone levels during the 1984 growing season at Coweeta caused extensive damage to the white pine plantation. Ozone stress included premature senescence and loss of foliage, stimulation of pine seedling germination, reduced basal area increment, and small-but-measurable increases in $NO_3$-N and K concentrations in stream water. There were no observable effects of $O_3$ damage on nutrient concentrations of stemwood and foliage, but net nutrient accumulation was reduced because of lower stemwood production. Ozone injury did not predispose trees to root pathogens or bark beetle infestations.

Although there is no long-term trend of change in precipitation chemistry in the Coweeta Basin, streams appear to be in the initial stages of acidification with increased sulfate concentration and anion deficit and decreased concentrations of bicarbonate and calcium. Although all streams show these trends, high elevation streams have lower pH levels (annual average and during storms), reduced bicarbonate concentrations, and elevated sulfate concentrations. Watersheds at higher elevation receive greater precipitation and sulfate deposition, and exhibit higher streamflow. Soils are shallower, quickflow volumes are higher, and the potential for sulfate adsorption is reduced. Lower temperatures at high elevations result in reduced rates of microbial sulfate incorporation into organic matter and reduced C flow through the forests. Thus, compared to low-elevation catchments, high-elevation watersheds are characterized by an increased sulfate flux and reduced bicarbonate flux. These differences imply that high elevation forests and streams are more susceptible to acidic precipitation.

Soils research at Coweeta has emphasized microbial and faunal processes controlling mobility of elements in the forest floor, and biotic controls over decomposition and mineralization. Because of our interest in atmospheric deposition, particular attention has been given to sulfate absorption and incorporation of S into organic matter. Experiments are clarifying mechanisms by which Coweeta forests accumulate sulfate from precipitation, a phenomenon we have documented with our long-term record of precipitation and streamwater chemistry. We have also completed considerable intersite research on S dynamics, including work on S gas emissions from soil, litter and living plants at three sites to determine if discrepancies in the mass balance of S could be a consequence of failure to measure these emissions. Results to date indicate that gaseous emissions cannot account for the discrepancies in the mass balance. Comparative studies of S processing in soils and litter have examined the dynamics of S in soils at several sites. These studies have examined formation of organic S from precipitation sulfate as well as its mineralization in litter and upper soil layers. Differences in S dynamics between sites were related to both geologic and biotic processes.

### *Long-Term Recovery from Disturbance*

Long-term research on hydrologic and stream chemistry recovery on a clearcut and cable-logged watershed has been ongoing for 13 years. By the seventh year after cutting, annual streamflow returned to baseline levels. Hydrologic recovery is attributed to rapid regrowth and the reestablishment of leaf area indices close to values for the original hardwood forest. Concentrations of most dissolved inorganic nutrients have also returned close to baseline levels except for $NO_3$-N, which is still clearly above pretreatment levels. Elevated exports represent the combined influence of increased discharge and alteration of biological processes which regulate nutrient recycling.

Soil and detrital carbon dynamics have also been examined following clearcutting. Carbon dioxide $CO_2$ effluxes were 33 percent lower than in the reference forest and were associated with higher soil temperatures, smaller live-root masses, and larger forest floor masses. No long-term changes in soil C pools were apparent following cutting. After distinguishing between nitrification and denitrification as sources of gaseous nitrogen production in soil, we determined the relative importance of $O_2$, $NO_3$, organic C, and acidity on denitrification rates in soils of disturbed and reference watersheds. Carbon limitation is unimportant for denitrification in surface horizons at Coweeta, but C limitation does occur with increasing soil depth. Measures of *in situ* $N_2O$ diffusion demonstrated that gaseous losses from Coweeta soil are minor relative to other N transformations.

An evaluation of long-term changes in decomposition rates following disturbance showed that leaf litter decomposition rates continue to be reduced eight years following clearcutting. Decomposition of *Cornus, Acer* and *Quercus* litter was slower in the eight-year-old clearcut, as were absolute increases of N (net mobilization). Decay constants for woody debris during the first seven years after cutting were 0.083 and 0.185 $year^{-1}$ for coarse and fine debris, respectively. Carbon dioxide efflux accounted for two-thirds of the total mass loss.

We have also examined the effect of watershed disturbances on nutrient retention and organic matter processing in streams. Despite major differences in retentive characteristics and dissolved nutrient concentrations, we found no significant differences in phosphate and nitrate uptake in reference and disturbed streams; howeve r, mechanisms of nutrient uptake and retention in the streams may be quite different. Organic matter processes studied include allochthonous inputs, standing crops of fine, coarse, and woody particula te materials, export of organic particles, and wood and leaf breakdown rates. In general, forest disturbance decreases allochthonous inputs, accelerates transport losses, and greatly increases t urnover of material in the stream. As a result, there is a long-term degradation of material from the streambed.

Rates of invertebrate recovery from disturbances vary with the nature of the disturbance. Disturbances which produce long-term changes in the physical environment, such as logging, appear to require many decades. Our studies show no evidence for functional or taxonomic recovery of macroinvertebrate fauna five years after logging. In contrast, recovery from insecticide treatments is relatively rapid with functional group recovery occurring within two years and taxonomic recovery within five.

Streambed geomorphology can be altered by disturbance, and our studies have indicated a strong control of local geomorphology on structural and functional characteristics of stream ecosystems. Studies have examined the effect of local geomorphology on retention of nutrients and on abundances and functional group composition of macroinvertebrates at Coweeta.

### *Intersite Research Projects*

Questions in stream ecology have also been the focus of several intersite research projects. We compared solute retention using low-level releases of nutrients into the same substrate types in similar-sized streams at H.J. Andrews (AND) and Coweeta. The AND catchment is of volcanic origin, whereas Coweeta streams flow over granitic bedrock. At Coweeta strong biotic control of P uptake coupled with high P demand results in relatively short P uptake lengths and a strong impact of P spiraling on ecosystem dynamics. At AND strong biotic control of N uptake combined with strong N demand results in short N uptake lengths. These differences are predictable based on the N:P ratio in stream water, which is a reflection of the geology of the region.

In a recently initiated project, we are comparing wood breakdown and movement in headwater streams at Coweeta and the Luquillo Experimental Forest (LUQ). The streams are similar in geomorphology but differ in the amount of rainfall received. Incorporation of marked wood into debris dams will allow us to determine the dynamics of debris dam formation and the residence time of wood as it slowly moves downstream or decays.

## FUTURE DIRECTIONS

Past research at Coweeta has used both plot- and watershed-level experimentation. In future research, we intend to retain our extensive database on watershed-level processes while expanding our perspective to the landscape level. This expansion is possible with advances in technology such as the development of powerful geographic information systems (GIS). We have already made progress in coupling GIS with the extensive data base on water chemistry at Coweeta. Data layers of topographic features, bedrock geology, and soil maps were used to scale up stream chemistry data from past studies on first-order streams to a fourth-order stream. Concentrations of $NO_3$-N and $SO_4$ predicted were within 10 percent of measured values; similar results were obtained for cation predictions. Future efforts will further utilize GIS capabilities to scale-up stream chemistry to the entire Coweeta basin and, in combination with remote sensing, to develop methods appropriate for unified land uses on larger landscape units such as the Little Tennessee River Basin.

An instrumentation proposal recently funded by NSF is providing new analytical equipment for research on biological control of soil processes. Mass spectrometry is included, so that studies using stable isotopes at Coweeta are receiving new attention.

Additional plans for future research have been discussed in a previous section on central concepts. The work on experimental gaps, the riparian zone, and expansion of our stream studies to larger streams will begin in 1991. In the past, intersite research has complemented our studies at the Coweeta site, and we anticipate an extension of this in the future. ■

## * *CWT Climate Record 1951-1980*

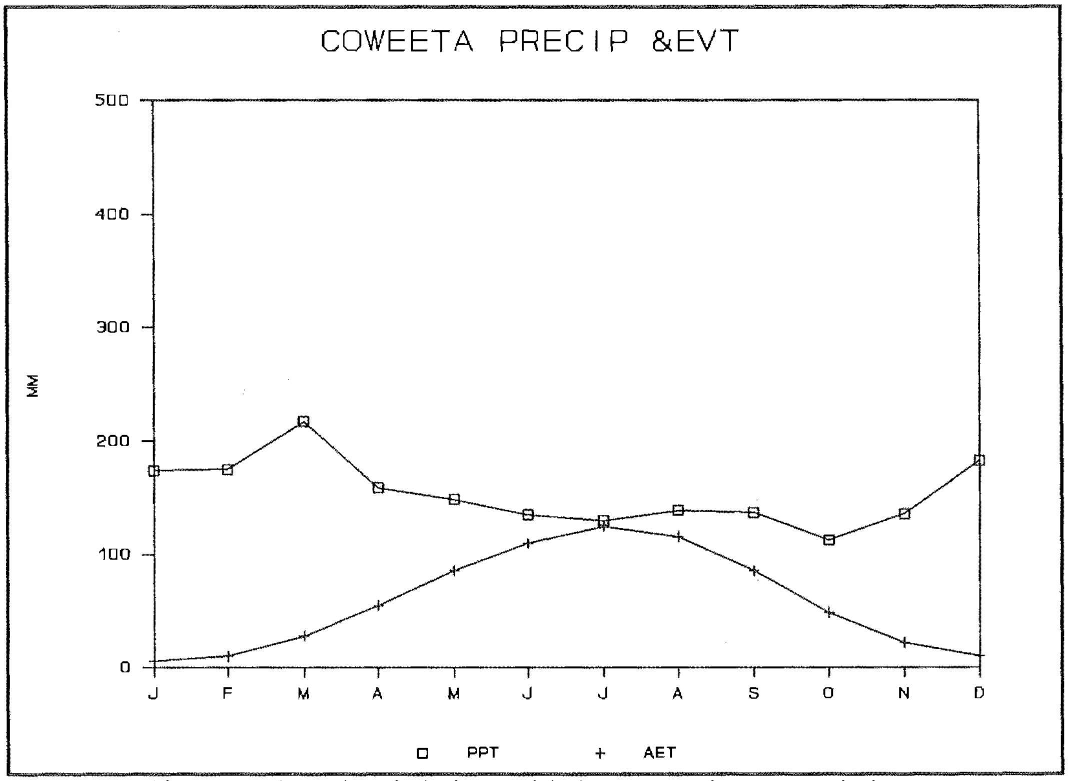



**Figure 1.** Monthly water budget values, including precipitation and actual evapotranspiration.

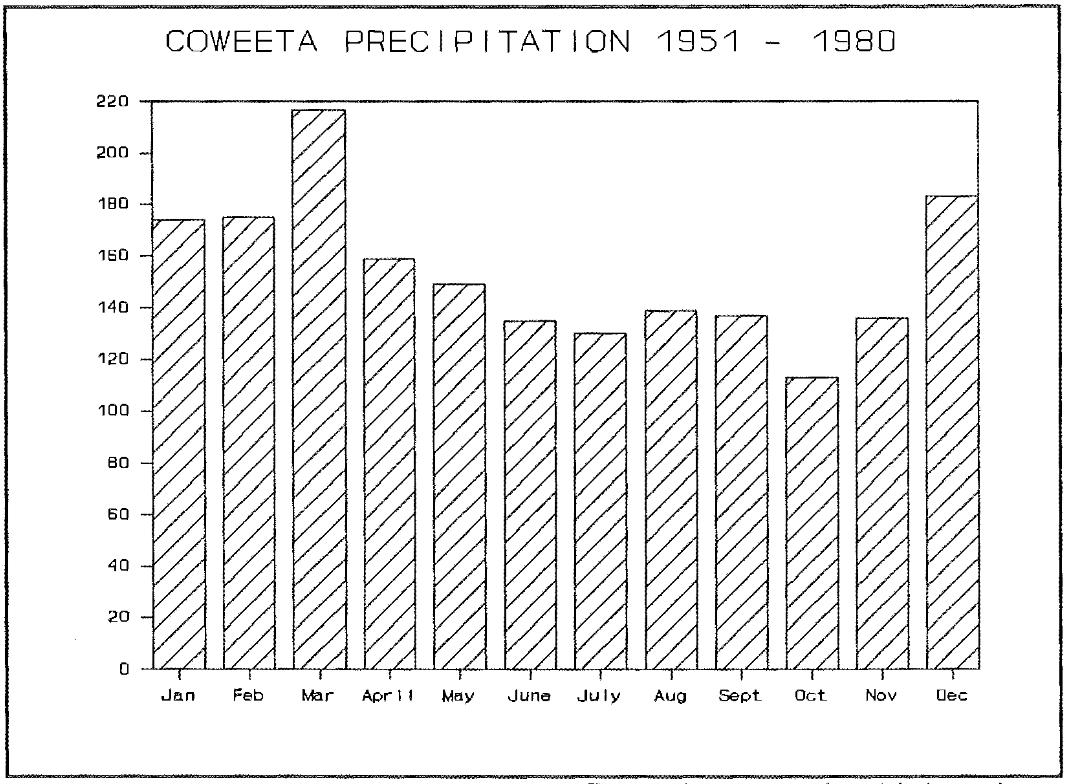



**Figure 2.** Average annual precipitation totals.

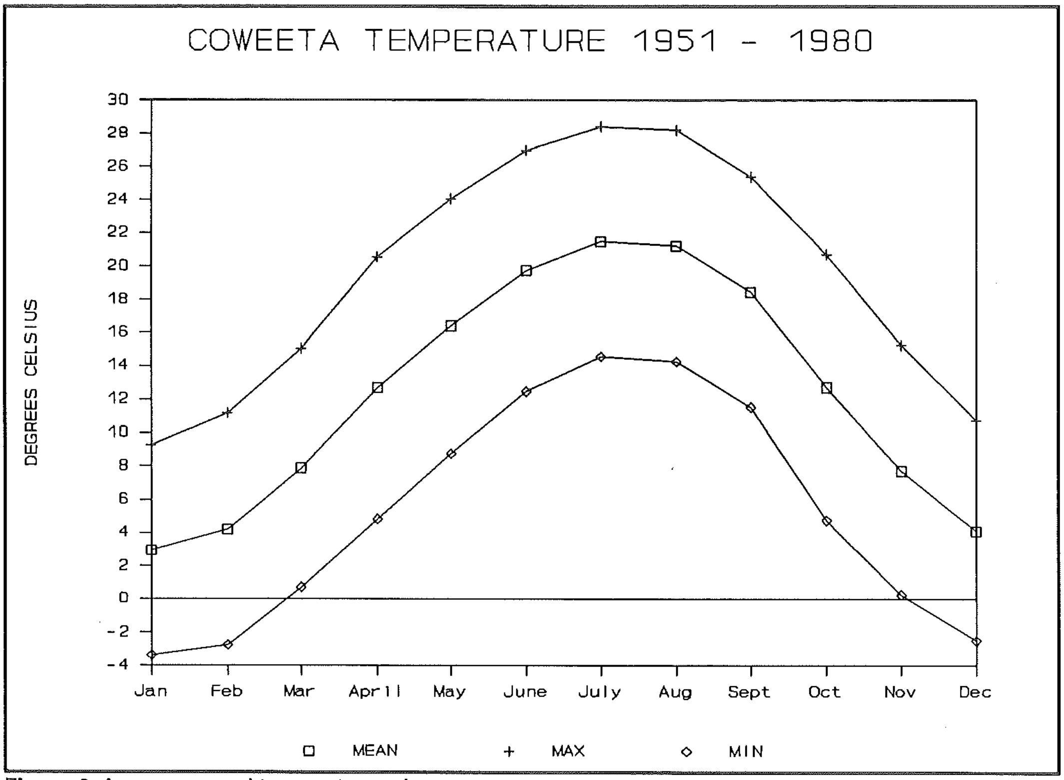
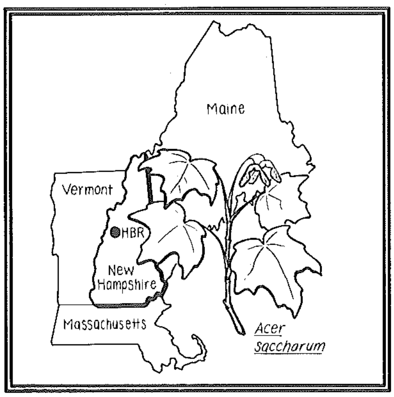



**Figure 3.** Average annual temperature values.

* Data from on-site or nearest weather station.




# Hubbard Brook Experimental Forest (HBR)

## RESEARCH SETTING

The Hubbard Brook Experimental Forest (HBR) is a 3,076-ha bowl-shaped area within the boundaries of the White Mountain National Forest in the Pemigewasset Ranger District in central New Hampshire. The HBR was established in 1955 and is currently operated by the USDA Forest Service. It has rugged terrain and, except for experimental areas, is covered by unbroken forest of northern hardwoods with spruce and fir at higher elevations. Other salient features include nearly watertight bedrock; well-defined watershed boundaries; reasonably homogeneous geologic formations; uniform soil distribution, vegetation and climate; year-round precipitation and stream flow; absence of forest disturbance for about 75 years; and several clusters of three or more similar-sized watersheds which can be experimentally treated and compared.

Early on it was recognized that the watershed-ecosystems at Hubbard Brook had a great potential for multifaceted ecosystem study. Major virtues for this purpose include: (1) water-tight basins which allow the construction of quantitative water and element budgets, considering not only meteorologic input and geologic output, but also internal accumulation within soil and biomass and release from weathering; (2) an accumulating wealth of background information on precipitation and streamwater chemistry, meteorologic and hydrologic data, and biological information regarding many facets of the component terrestrial and aquatic ecosystems; (3) relatively undisturbed forest ecosystems that allow accumulation of valid baseline data on the structure, metabolism and biogeochemistry of natural ecosystems in the mid-aggradation phase of development; (4) a variety of undisturbed stream ecosystems that connect the forest with larger aquatic systems; (5) the inclusion of a small lake in the matrix of the forested Hubbard Brook Valley that permits study of air-land-water interactions (Mirror Lake is a 15-ha body of water adjacent to, but not part of, the HBR). Finally, (6) there is the unusual opportunity to conduct experiments at the ecosystem level and to compare these results with baseline data collected from adjacent, reference ecosystems.

### *Site Characteristics*

The HBR is located near the town of West Thornton, New Hampshire, within the White Mountain National Forest (43°56', 71°41'W bisecting coordinates). The forest is adjacent to U.S. I-93, about 210 km north of Boston. The Atlantic Ocean is about 116 km to the southeast. Access to the HBR is from Route 3, which parallels I-93, and single entry from that road provides opportunity to closely monitor activities in the forest. With exception of the easternmost boundary, all surrounding land is in National Forest; thus, a protective buffer exists around most of the area and there is complete administrative control over the entire Experimental Forest.

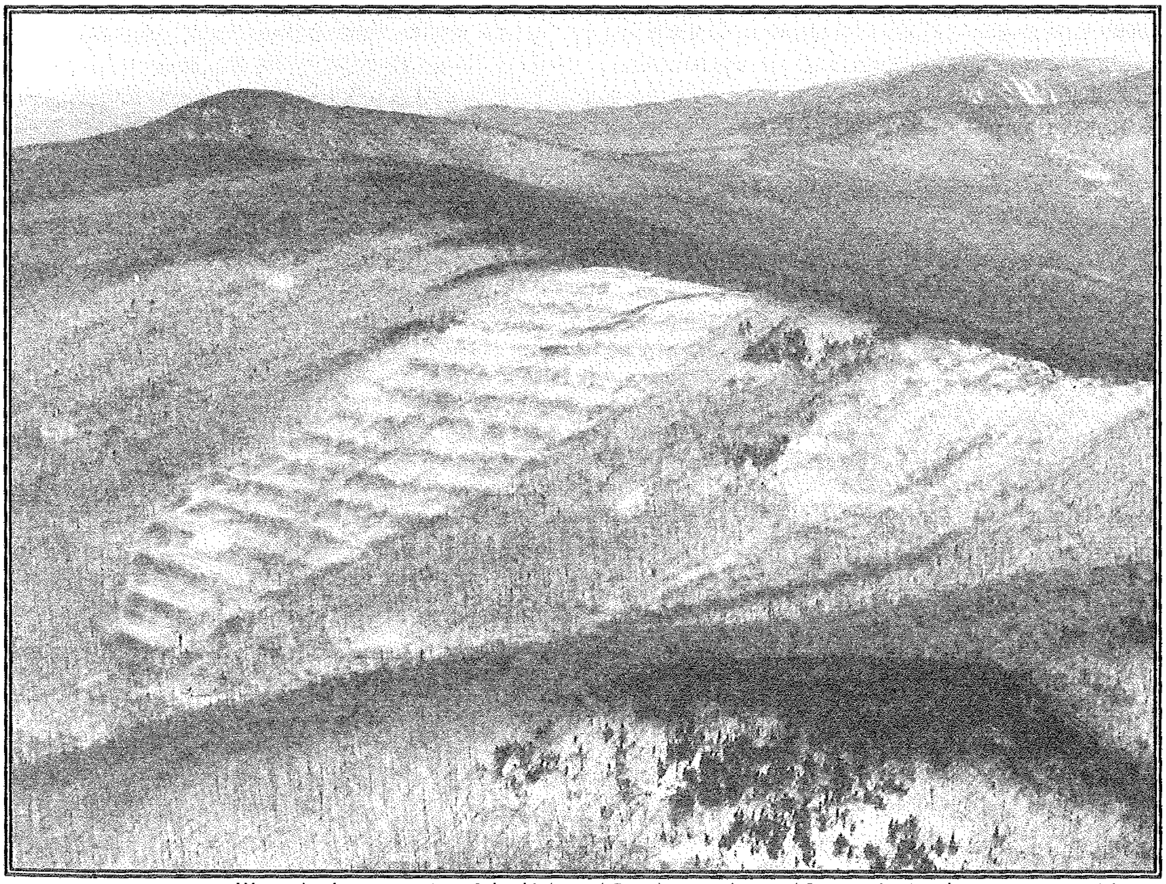
The HBR is representative of the northern Appalachian Mountains: steep, rugged topography;

coarse, acidic, glacially derived soil; largely metamorphosed igneous and sedimentary bedrock; northern hardwood forests on lower slopes and spruce-fir on upper reaches below timberline; and continental climate of long, cold winters and mild to cool summers. Although most of our research in the Hubbard Brook Ecosystem Study (HBES) is conducted at the HBR, many locations in the White Mountain National Forest offer splendid opportunity for specialized research. For example, the Bowl Natural Area, about 26 km from Hubbard Brook, is a virgin, old-growth watershed that has received considerable research attention.

## RESEARCH PROGRAM STATUS

The overall goal of the Long-Term Ecological Research (LTER) project at the Hubbard Brook Experimental Forest is to develop a better understanding of the response of northern hardwood ecosystems to large-scale disturbance, particularly with regard to (1) vegetation structure, composition and productivity; (2) dynamics of dead organic matter; (3) atmosphere-terrestrial-aquatic linkages; and (4) heterotroph population dynamics. Research is being conducted on sites within the HBR with contrasting history of disturbance, using experimental studies as well as analysis of long-term data. Our strategy in the HBR LTER program is to build upon previous and ongoing work conducted at Hubbard Brook through the use of long-term records and experimentally manipulated watersheds.

A variety of long-term monitoring efforts are supported with HBR LTER funds. The largest monitoring effort at Hubbard Brook is the ongoing (since 1963) sampling and analysis of precipitation and stream waters for major solutes at the experimental watersheds and Mirror Lake. Other monitoring efforts include: air quality monitoring, trace metal biogeochemical



*Watersheds 2, 4 and 5 of the Hubbard Brook Experimental Forest. In the right background is Mt. Moosilauke, site of intensive research on spruce decline.* ROBERT S. PIERCE monitoring, measurement of dead and living biomass in the HBR reference watershed (Watershed 6), analysis of vegetation changes in Watershed 2 (biomass and chemistry) 20 years after clearcutting, and the sampling of soils on Watershed 5 eight years after whole-tree clearcutting.

To complement these monitoring programs we have initiated a series of process-level studies designed to elucidate the mechanisms regulating the water, nutrient and energy budgets of northern hardwood forest ecosystems. Thus, the goal of these coordinated efforts is to look inside the watershed "black box" using field surveys, experiments and several simulation models. In the following sections we describe these efforts and some of the early results.

### *Hillslope Hydrology*

The primary objective of our hillslope hydrology research is to understand the mechanics of water movement through the unsaturated and near-surface saturated zones of soils in first-order catchments at HBR. We accept as a fundamental premise that water does not move uniformly through the soil to streams and we hypothesize that different "preferred" flow paths may influence soil and stream water chemistry differently. Our approach to this problem includes detailed field sampling and further refinement of a simulation model. The hillslope hydrology effort supported by the HBR LTER includes an instrumented hillslope, an instrumented soil block, two instrumented stream reaches, three instrumented soil-vegetation macrocosms, and various soil sampling and characterization efforts.

Perhaps the most striking result from this work was obtained during a dye-tracer study of water percolation through an experimental soil block. As expected, some of the water moved through visible soil channels, including root channels, but much of the dye moved through "preferred flow" pathways for which no measured physical differences were observed in comparison to surrounding soil. To some extent the flow pathways appeared to be defined by focusing of the artificial rainfall at the forest floor horizons. In a related effort we have mapped soil channels and noted that the abundant macropore "pipes" follow the plunge and trend of the hillslope and deliver water downslope more quickly in areas where they are abundant than where they are scarce.

On a larger scale, we have examined the dynamics of the near-stream water table in two first-order streams. Depression-focused recharge results in very rapid response of the near-stream water table to rainfall, but this response is highly sensitive to rainfall magnitude and antecedent moisture conditions. Also, in the low-order streams at HBR we commonly observe hyporheic flow that contributes to longitudinal variation in open channel flow.

### *Biogeochemistry*

Within HBR there has been major research activity, as well as efforts to integrate and synthesize data, on the flux and cycling of nutrient and toxic chemicals. Here we will attempt to summarize a few of the highlights from this research. Long-term monitoring of the chemistry of precipitation, stream water, soil water and lake water in the Hubbard Brook Valley continues into its 29th year.

Dry deposition of sulfur was estimated by a watershed mass-balance approach at HBR from 1964-65 through 1986-87. Average total deposition was 420 Eq $SO_4$= ha-yr and dry deposition contributed about 37 percent of total S deposition, varying from 12 percent in 1964-65 to 61 percent in 1983-84. Long-term data from "replicated" watershed-ecosystems showed that temporal variability in estimates of dry deposition was considerably greater than spatial (between watersheds) variability.

In addition to the mass-balance approach, we have estimated elemental dry deposition using measurements of atmospheric concentrations and throughfall flux. For sulfur, estimates obtained by these methods (3.1 and 3.3 kg S/ha-yr for the atmospheric and throughfall methods, respectively) are lower than the estimate of 5.4 kg S/ha-yr, derived from the watershed mass-balance methods for 1989. Reconciliation of these estimates will require more extensive data on atmospheric concentrations and throughfall deposition.

Decreases in volume-weighted concentrations of sulfate in precipitation at Hubbard Brook are related to a decline in sulfur dioxide emissions in the northeastern United States. The decrease in precipitation sulfate has coincided with an increase in precipitation pH in recent years. The decline in precipitation sulfate also is correlated with decreases in stream sulfate.

Since the early 1970s, precipitation concentrations of basic cations have diminished greatly and streamwater concentrations of basic cations are correlated with changes in atmospheric inputs. Regardless of the pathways through the watershed, during the mid- to late 1960s (and likely earlier) atmospheric deposition was a major input of basic cations to the HBR; subsequent reductions have contributed to the acidification of soil and/or drainage water.

Because of the marked decline in their atmospheric deposition, total ecosystem inputs of basic cations to the HBR are currently near the lowest value for the last 26 years, and this decline has greatly increased ecosystem sensitivity to strong acid loading. It would appear that expected recovery of acidified surface waters due to decreased loading of sulfate generally has been retarded by declining atmospheric inputs of basic substances.

The role of organic acids in surface water acidification is a focus of recent controversy. It has been suggested that waters that are currently high in mineral acidity from acid deposition (e.g., White Mountains region) were originally (before acid deposition) high in dissolved organic carbon (DOC) and dominated by natural organic acidity. Thus, acid deposition is hypothesized to have increased concentrations of strong mineral acids with concurrent losses in organic acids and DOC, resulting in little or no change in pH. We have done an ecosystem-level manipulation of the stream in Watershed 9 to test this hypothesis. Experimental acidification of this brownwater stream did not reduce DOC concentrations, and indicated a limited capacity of the organic acid-base system to buffer inputs of strong mineral acids. Thus, the hypothesis was rejected.

We are using the proton budget approach to help integrate our biogeochemical research. The proton budget gives an overview of the important processes and individual element contributions to the acidification and alkalinization of soil and drainage water. We developed proton budgets for the HBR reference watershed (Watershed 6) for two contrasting years: 1974, a year of elevated hydrogen ion loading and 1985, a year of low hydrogen ion loading (Figure 1). These results indicate that atmospheric hydrogen ion inputs were high in 1974 (1555 eq/ha-yr) and represented 60 percent of the total hydrogen ion sources. Inputs were lower in 1985 (to 860 eq/ha-yr) but contributed 90 percent of the total hydrogen ion sources. In 1974 sulfate and nitrate accounted for 59 percent and 30 percent of the precipitation acidity, respectively and, in 1985, 50 percent and 47 percent, respectively.

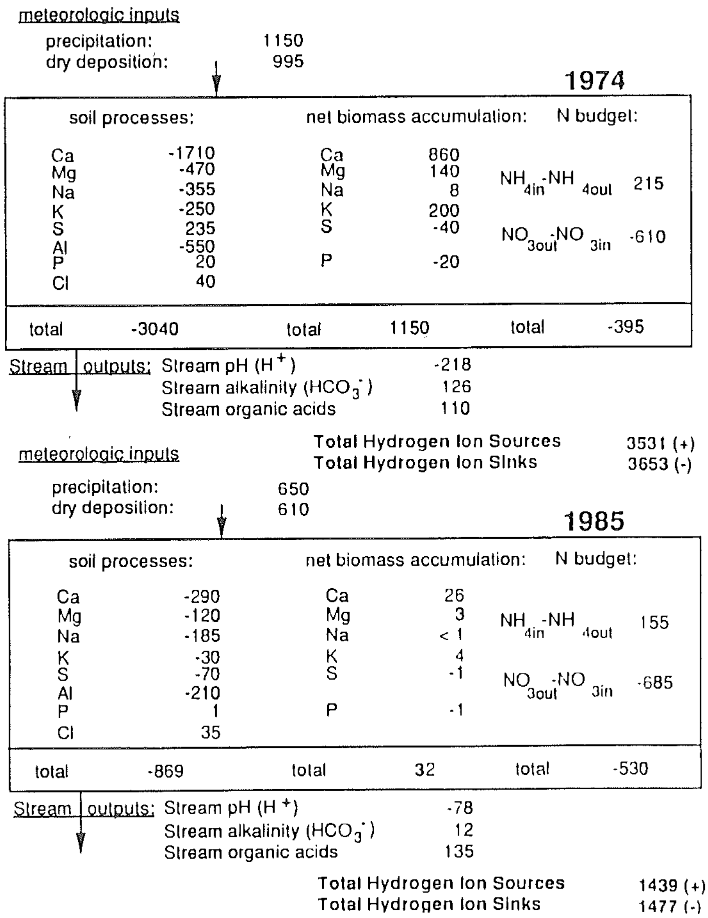



**Figure 1.** H+ budgets for Watershed 6, the biogeochemical reference, NH for high- and low-flux years (1974, 1985). Precipitation fluxes include estimates for dry deposition of S and N.

The accumulation of nutrients in biomass is another important hydrogen ion source. A decrease in ecosystem biomass accumulation over the period of study increased the relative contribution of atmospheric inputs of hydrogen ion to the total hydrogen ion sources. The release of basic cations and aluminum are the most important hydrogen ion sinks for the HBR. The combination of decreasing inputs of hydrogen ion and declining biomass accumulation of nutrient cations has resulted in a marked decline in the total flux of proton in Watershed 6 over the study period.

### *Vegetation Structure & Function*

Based upon early studies of forest dynamics at HBR and other regional sites, Bormann and Likens developed a conceptual model of pattern and process in northern hardwood forest ecosystems. This model provides a detailed framework upon which continuing vegetation studies seek to expand. The overall goal of vegetation studies in the HBR LTER is to improve our understanding of the interactions among vegetation composition and productivity, resource availability and disturbance regimes.

Four complete surveys of the composition and biomass of our control watershed have been completed, the most recent in 1987. Surprisingly, the survey revealed that live biomass of this 75-year-old forest is no longer accumulating. Our next complete resurvey of Watershed 6 is scheduled for the 1992 field season.

On Watershed 5, the removal of overstory trees altered very little the stable, spatial patterns of most species of woodland herbs and shrubs. However, varying degrees of soil disturbance and particular life history traits of different species resulted in some shifts in the distribution and abundance of particular species. The "shifting forest mosaic" at HBR appears to be a reflection of a variety of small-scale successions that result directly from the interactions of the timing and severity of disturbance and the regeneration characteristics of the flora.

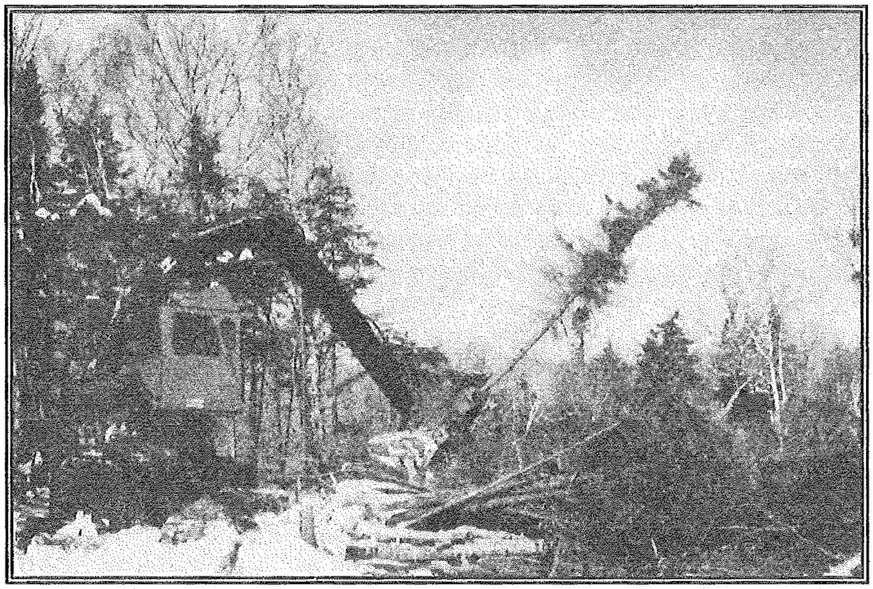
Nutrient retention following large-scale disturbance is maximized by rapid biomass accumulation in vegetation. Biomass accumulation was significantly slower in the first several years of regrowth after disturbance on Watershed 2 than the other clearcut watersheds, presumably because of the lower stem density that resulted after three years of prevention of regrowth on Watershed 2. This initial pattern also appeared to persist into later stages of recovery. The spatial pattern of biomass accumulation on Watershed 2 coincided with elevation and site fertility, high rates of accumulation on lower slopes at the base, but extremely low rates on the upper slopes where severe soil deterioration was observed during the three-year vegetation-free period.

In closed forests, neighborhood competition may be the main factor influencing the attainment of canopy dominance by individual trees. Neighborhood structure in pin cherry dominated stands following whole-tree harvest was heterogeneous and had clear effects on individual growth. Pin cherry growth and survival were highest for individuals experiencing the least neighbor competition. A 1.0-m neighborhood radius explained the most variation in growth of individual focal plants. Competitive effects and responses were both size-specific. Growth of intermediate-sized individuals was most sensitive to neighborhood structure, as small trees were all suppressed and large trees were only affected by larger- or similar-sized neighbors. These results demonstrate that competitive effects are local, strong, and very size asymmetric.

### *Heterotrophic Activity*

Heterotrophic organisms play a wide variety of essential roles that influence the dynamics of forest ecosystems, and we have only scratched the surface in comprehending and quantifying these roles in our studies at HBR. Studies of heterotrophic activity in the HBR LTER build upon several long-term efforts and on the expertise within our group: (1) long-term patterns in the abundance of phytophagous insect populations and their influence on bird communities and forest dynamics; (2) transitions of forest floor horizons between degrading, aggrading and steady state during recovery from large-scale disturbance; (3) C and nutrient dynamics of woody detritus and its role as a medium for roots and saprotrophic fungi; and (4) organic matter processing, the role of organic debris dams, and linkages between primary and secondary production in streams.

The long-term pattern of phytophagous insects at HBR shows that *Lepidoptera* larvae, the most important phytophagous insects in these forests, were in outbreak phase in the early 1970s, with minor peaks in 1982-3; in all other years, caterpillars have been relatively low in abundance. Abundances on four replicate plots sampled since 1986 indicate consistent patterns over a relatively large regional scale, with numbers increasing steadily on all four study areas. Thus, the results to date indicate that irruptive outbreaks of defoliators occur relatively rarely in these northern hardwood forests and that most tree leaf defoliators occur at low abundances most of the time. However, the results of our detailed studies of breeding birdpopulations suggest that population declines during the past 10 to 15 years probably represented corrections from peak populations that corresponded with the insect irruptions of the early 1970s.


*The mechanisms of ecosystem recovery following large-scale disturbance are being examined in detail on Watershed 5 and adjacent catchments at HBR.* C. WAYNE MARTIN

In the summer 1989 we carried out the second detailed survey of biomass and nutrient content of woody detritus on Watershed 2, a site on which all trees were felled and left in place in 1965-6. By analyzing tissue density and chemistry changes in various categories (species, size class, heartwood/ sapwood, position), we can discern the factors influencing decay rates and nutrient fluxes. Decay rates of hardwood boles were very rapid, as only 16 percent of the original mass remained 23 years after felling. We have discovered that certain species and decay classes are significantly more likely to act as a medium for fine roots, but that even at this stage in forest recovery, when rooting in wood is near maximum, only about 1 percent of total fine root biomass is in decaying wood.

Finally, we are testing the hypothesis that Watershed 5, clearcut six years ago, represents an autotrophic stream whereas Bear Brook (Watershed 6, below the weir) represents a detritus-based stream. Given the differing trophic bases, we wanted to examine how microbial secondary production was supported by algal organic carbon versus detrital organic carbon. We observed that Bear Brook has a much higher overall amount of organic matter in storage, with most of the material in debris dams. In Watershed 5, moderate-to-fine sediments represent the greatest reservoir of organic matter; organic debris dams are essentially absent. These patterns confirm the expectation that detrital organic matter should be much more important in fueling secondary production in Bear Brook than in Watershed 5.

We examined algal and bacterial growth on artificial substrates (tiles) and bacterial incorporation of $^{3}$H-TdR in both streams. These studies revealed that short-term accumulation of bacteria and algae on tiles was not significantly different between streams, whereas long-term accumulations differed markedly with higher values in Watershed 6 than in Watershed 5. Surprisingly, neither bacterial abundance nor production responded to changes in algal abundance or production either between streams or as a result of shading manipulations. Continuing experimentation is designed to explore the relationships between bacterial secondary production and various carbon sources.

## FUTURE DIRECTIONS

The continuous monitoring of experimental watersheds at Hubbard Brook provides us with the rare ability to test new hypotheses in a temporally robust fashion. For this reason, the continuation of the monitoring program is a high priority among researchers at Hubbard Brook. In addition, we believe that there are four critical issues emerging in ecosystem science to which HBR can make particularly important contributions:

**Biogeochemistry.** By coupling the long-term data from the HBES with plot- and watershed-scale experiments, important questions concerning the biogeochemical processes operating in forest ecosystems can be addressed. For example, we have initiated studies which are designed to test the effects of elevated nitrogen and changing base cation inputs on soil processes and stream chemistry. The curious, transient increase in streamflow nitrate during the early 1970's sparks particular interest in complex biotic responses (especially belowground) to chronically high N deposition.

These studies address the "nitrogen saturation" hypothesis and the hypothesis that decreasing sulfate deposition does not result in increased surface water pH because of a coincident reduction in base cation deposition. Studies in the planning stage include: development and calibration of a field-based procedure for measuring chemical weathering rates using stable isotopes; a study of soil processes and their effects on short-term changes in surface water chemistry, especially acidification associated with spring snowmelt; and a study of the role of organic acids in the acidification of soils and drainage waters.

**Global Climate Change.** Understanding how possible global warming will affect ecosystems is probably the most challenging research initiative facing ecosystem scientists. The long-term data record at Hubbard Brook is a great asset in model building and interpreting laboratory and field experiments. For example, the impact of climate change on water yield at Hubbard Brook is being simulated by modeling the relationships between precipitation, temperature and stream flow and adjusting the long-term data set to reflect various climate change scenarios. Other studies being contemplated include the effect of removal of a dominant tree species on ecosystem function, and the effects of forest management practices on carbon budgets.

We are also actively involved in experimental and survey work on the mechanisms of production and consumption of radiatively important trace gases (RITGs) in soils and sediments at HBR. We hope to provide a better basis for conceptualizing possible feedbacks between climate change and net flux of RITGs in natural and managed environments.

**Biological & Ecosystem Diversity.** The potential loss of diversity in forest ecosystems due to management practices is of growing concern. Through watershed clearcutting experiments, we have documented the structure and function at many developmental stages in northern hardwood ecosystems, the diversity of plants, animals, and microbes and their relationships to particular successional stages, and the physical-chemical environments in which they occur. The chronosequence of aggrading forest watersheds at Hubbard Brook and nearby sites in the White Mountain National Forest provides an ideal laboratory for studying ecosystem diversity. Diversity in this sense would include not only biological species diversity, but also variability in forest structure, soil properties, microclimate, and hydrologic properties. The initiatives we are considering in this regard include: a critical examination of the influence of different land-use practices on the maintenance of diversity; development of a model of biological and structural diversity patterns in northern hardwood forests; and the establishment of a chronosequence of forest plots clearcut at regular intervals.

**Sustainability.** Increasing demands for forest products and concerns about nutrient losses from forested ecosystems has raised questions concerning the long-term sustainability of forest management practices. Development of land management strategies capable of sustainable yields requires knowledge of biogeochemical processes and rates. The long-term record at Hubbard Brook is useful in providing both average and extreme estimates of many ecosystem variables. Ongoing projects at the HBR are designed to: study the modes and rates of nitrogen accumulation in controlled chemical environments, quantify and model nutrient losses associated with forest harvesting, and measure the importance of dry deposition to forest nutrition. We envision expanding our research in this area to include studies of: (a) weathering release of nutrients and the importance of weathering to sustainability; and (b) the magnitudes of internal transfers of nutrients between ecosystem compartments (e.g., forest floor and mineral soil) following harvesting and the implications to regrowing vegetation. ◘

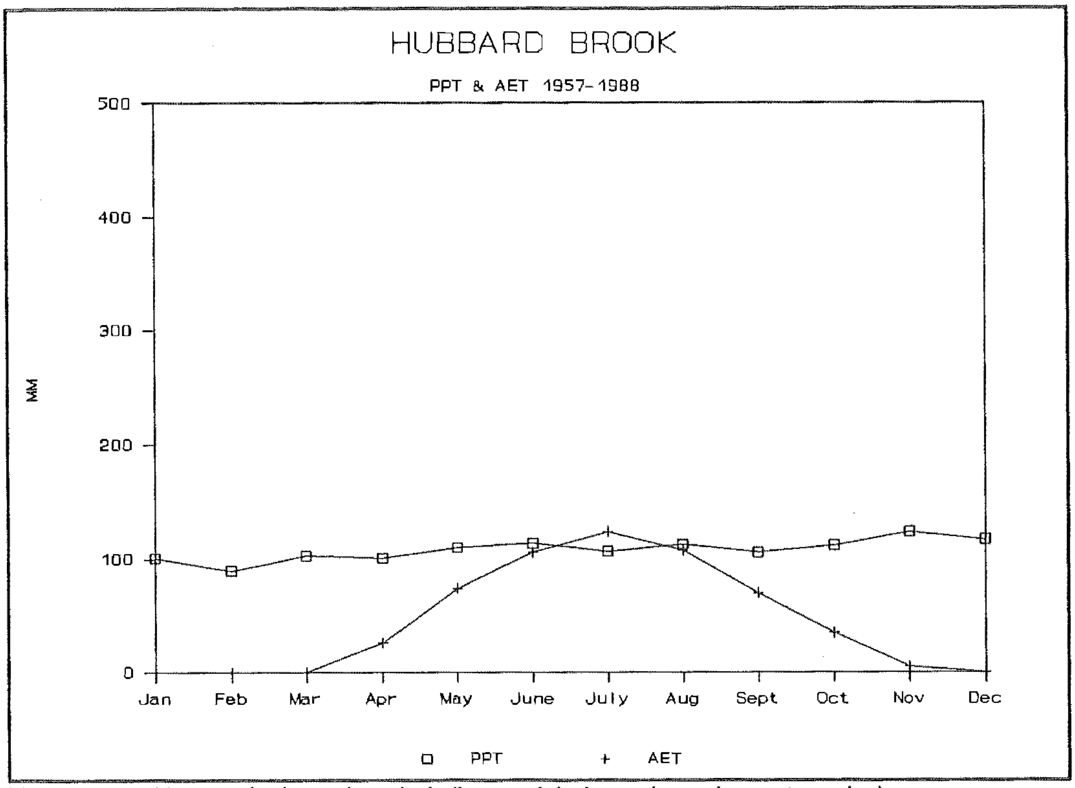



**Figure 2.** Monthly water budget values, including precipitation and actual evapotranspiration.

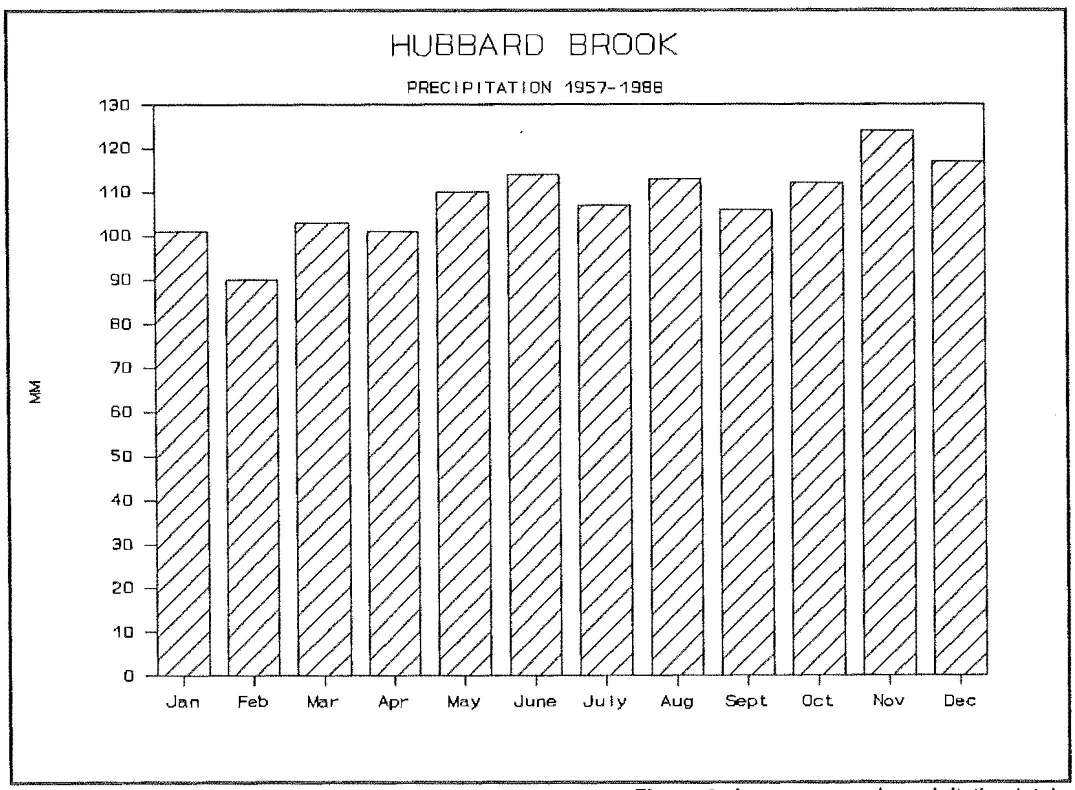



**Figure 3.** Average annual precipitation totals.

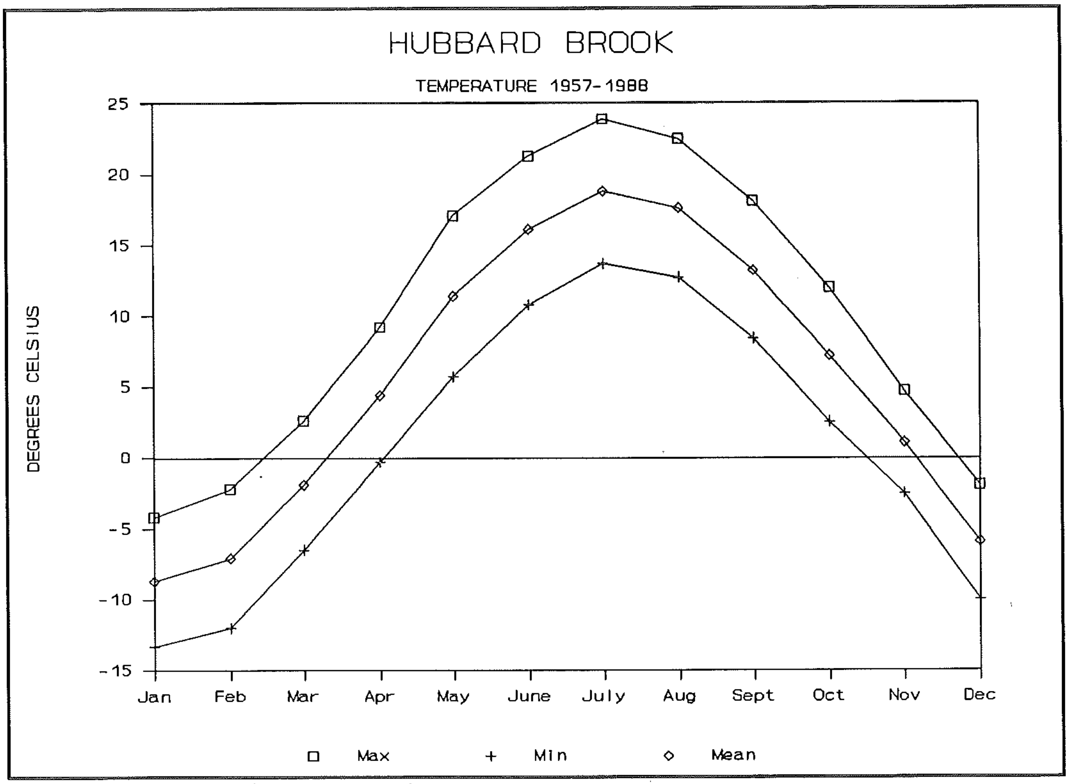


**Figure 4.** Average annual temperature values.

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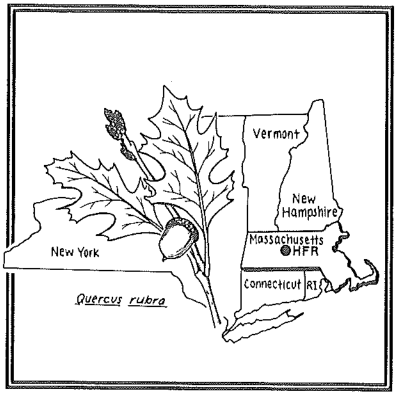
* Data from on-site or nearest weather station.




# Harvard Forest (HFR)

## RESEARCH SETTING

The forests of central New England comprise a dynamic ecosystem that has been shaped through geological and historical time by climate change, natural disturbance and human activity. As documented in the paleoecological record, continual environmental change has resulted in major shifts in the abundance and range of taxa, whereas the temporary loss of hemlock 4,700 years ago apparently from pathogens has been paralleled recently by the elimination of chestnut as a canopy tree and the decline of elm and beech from introduced diseases.

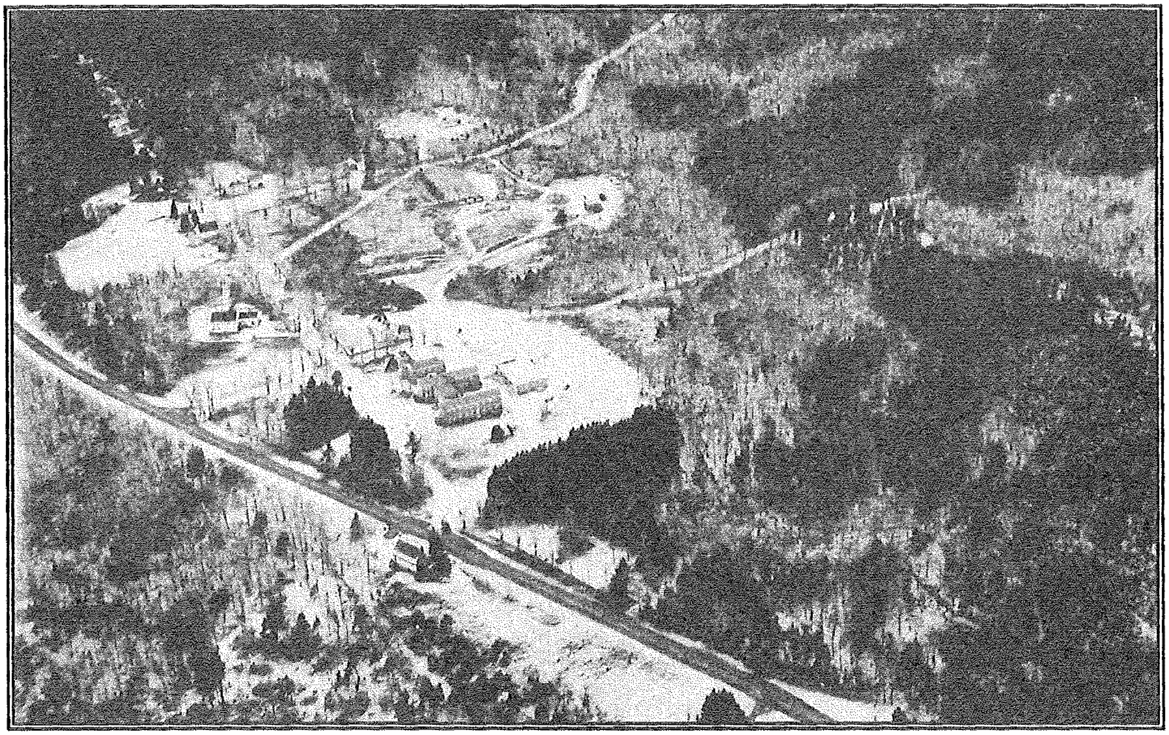
Canopy gaps ranging in size from small- to broad-scale blowdown have been created by individual tree death, windthrow and catastrophic hurricanes. Since European settlement in the early 1700s, extensive deforestation and widespread agriculture have been followed by land abandonment and nearly complete reforestation. The continued productivity of forests through this history of change attests to the resilience of these ecosystems in the face of physical or biological disturbance.

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

The central theme of the research comprising the Harvard Forest LTER is a comparison of historically important physical disturbances and recent and projected chemical disturbances in terms of their effect on ecosystem structure and function. Fundamental questions addressed by the research are:

- How do ecosystems and the organisms comprising them respond to natural, episodic disturbance as opposed to chronic chemical disturbance?
- Can chronic, low-level additions of pollutants result in more lasting alteration of ecosystem function than does the historical regime of disturbance to which components of the system may be adapted?
- Are there significant interactions between physical and chronic chemical disturbance that cannot be predicted on the basis of each disturbance type regarded independently?

Measurements of net trace gas emissions are given



*Aerial view of the Harvard Forest LTER research site facilities.* M.H. ZIMMERMANN

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

The studies required to answer disturbance-response questions are, of necessity, long-term. They must allow for both the cumulative effects of chronic chemical disturbance and the long-term responses of the biotas and soils. Physical disturbance initiates a long-term series of changes in ecosystems that will be compared with responses to chemical disturbance. The core experiments undertaken in the Harvard Forest LTER program include: (1) re-creation of physical types of disturbance, including catastrophic hurricane blowdown, small canopy gap windthrow, and selective standing-death of dominant overstory tree species; (2) simulation of chronic chemical disturbance by altering input of important nutrients or pollutants; (3) examination of interactions between physical and chemical disturbances to assess the role of chronic chemical deposition in changing the normal patterns of system response to physical disturbance; (4) repetition of physical disturbance treatments to assess the role of chance variation in annual weather patterns and species' reproductive behaviors on the composition and function of the recovering ecosystem.

The understanding gained through these studies is being placed in a comprehensive historical context through continued analysis of post-glacial and post-settlement vegetation dynamics, disturbance regimes, and climate change and through the characterization of ambient levels of atmospheric pollution.

The disturbance and response patterns we are studying occur on a variety of spatial and temporal scales, and require synthesis of information from many disciplines. Therefore, we are providing a framework for integration of results through a combination of modeling, remote sensing and geographic information system (GIS) applications.

The research program at the Harvard Forest brings together an interdisciplinary research team

*Experimental pull-down on Prospect Hill simulating hurricane disturbance to the Harvard Forest.* MARCHETERRE

representing four institutions, a diversity of extensively studied and well-documented ecosystem types, a well-equipped facility with an experienced support staff, and a commitment to long-term study and data management.

### *Site Description*

The 1200-ha Harvard Forest in north-central Massachusetts has been operated as a silvicultural and ecological research facility by Harvard University since 1907. The Forest lies in the New England Upland physiographic region, with moderate local relief ranging from 180 m to 420 m above sea level. A bedrock dominated by granite, gneiss, and schist is generally overlain by sandy-loam glacial till soils that are moderately to well-drained, acidic, and that average 3 m in thickness. Local variations in parent materials, textures, alluvial and colluvial deposits, and slope produce poorly drained and excessively drained sites as well. The regional climate is cool (with a July mean of 20°C, January -7°C) and humid, with precipitaton (annual mean 110 cm), distributed fairly evenly throughout the year.

The Forest lies in the Transition Hardwood-White Pine-Hemlock forest region. Dominant species include red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta*), white pine (*Pinus strobus*), and hemlock (*Tsuga canadensis*). On drier soils white oak (*Quercus alba*), black oak (*Quercus velutina*), hickory (*Carya ovata*) and, formerly, chestnut (*Castanea dentata*) increase. Cool, moist, but well- drained sites support a northern mixed forest of yellow birch (*Betula lutea*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), ash (*Fraxinus americana*), hemlock and white pine, whereas red spruce (*Picea rubens*), black spruce (*P. mariana*) and larch (*Larix laricina*) occupy oligotrophic peatlands.

Approximately 7 percent of the Forest is occupied by plantations of diverse compositions and age. Detailed stand records, including land-use history, and repeated growth measurements are available for each plantation and many natural stands. A well-developed network of woods roads provides good access to all areas in the Forest.

## RESEARCH PROGRAM STATUS

Currently in its third year of development, the Harvard Forest LTER program consists of monitoring and background studies, experimental manipulations, intersite studies, and synthesis.

### *Monitoring & Background Studies*

Chemical Climatology & Biosphere/ Atmosphere Interactions. During the first year of our LTER research, installation of the Environmental Measurement Station (EMS) at Harvard Forest was completed. A 30-m sampling tower and an associated instrument building were erected and a 1.7-km underground electrical line was installed.

Instrumentation became operational in October1989 and continuous measurements have been archived since that time.

The following measurements are presently being obtained, routinely processed within seven days, and archived on 8 mm videotape (using Exabyte tape protocols): vertical fluxes (by the eddy correlation method) of momentum, sensible heat, water vapor, $CO_2$, $O_3$, total oxides of nitrogen ($NO_y$), and nitrogen oxide radicals (NO and $NO_2$). Time series for the concentrations/ magnitudes of these quantities are also obtained at the 30-m level. Vertical profiles are acquired every 20 minutes for temperature, water vapor, $O_3$, $CO_2$, and CO. Continuous records are obtained for net and photosynthetic radiation flux, for soil temperatures and the actinometric photolysis rate of $NO_2$, and for the amount and chemical composition of precipitation.

Intensive efforts during 1990 focused on debugging the data acquisition and reduction systems, which must smoothly handle 25 megabytes of a diverse data stream each day, and on assessing the validity of the eddy correlation data. We routinely compute and display a wide variety of diagnostic analyses including orientation of the mean streamlines, heat budget balance, lagged auto- and cross-correlation functions, and power spectra and cospectra. The results indicate that valid measurements of the vertical flux are being obtained for virtually all sampling intervals. We know of no existing comparable data set for eddy correlation measurements of vertical flux, in terms of both duration or diversity.

The study objectives are designed to examine key issues in the role of forests in global and regional environmental change: (1) What are the daily and seasonal net $CO_2$ exchanges from the ecosystem? How are these fluxes controlled by environmental variables such as light, soil moisture, temperature, growth stage, pollutant level, etc.? (2) What are the dry and wet deposition rates for nitrogen oxides and ozone? Where do these chemicals originate (e.g., regional pollution)? What are the likely effects of this deposition on forest metabolism, structure, etc.?

Environmental & Vegetation Change. This project combines paleoecological and historical approaches to studying vegetation dynamics in order to understand the development of the forest vegetation of central New England. Major efforts include: (1) creating palynological and historical data bases from a grid of sites across environmental and cultural gradients in central New England, and (2) studying vegetation change across this grid over the post-glacial (14,000 years), late-Holocene (2,000 years) and post-settlement periods (300 years).

The project will provide a comprehensive understanding of the mechanisms and rate of vegetation change, a greatly improved understanding of the role of natural and cultural disturbances as determinants of the history and pattern of central New England's vegetation, and a recognition of the spatial differences in these factors across environmental and cultural gradients. Specific objectives of the project are:

- to examine spatial and temporal patterns of population dynamics for major tree taxa in response to climate change and disturbance,
- to define gradients in the vegetation and disturbance regime during the late Holocene, and
- to describe the variation in landuse and agricultural practices, to relate these to environmental variables, and to assess the impact of human activity on vegetation patterns.

Tree Population Monitoring & Mapping. A basic interest that cuts across forested LTER site programs is the long-term dynamics and spatial patterning of tree populations as a consequence of stand development, changing environmental conditions, experimental manipulations and natural disturbance. At the Harvard Forest, development of field techniques, analytical routines and cartographic display to deal with existing data and to facilitate the development of new data has been a major priority. The results of this effort include: development of computer routines to encode existing maps of tree locations into GIS and database files; development of efficient field techniques and data-encoding routines to produce stem maps for new areas utilizing triangulation methods; development of data management and error-checking techniques to screen and file data; development of an interface between the stem mapping files and GIS programs; and development of analytical routines for summarizing the data.

## *Experimental Manipulations*

Hurricane Blowdown. In order to assess the response of forested ecosystems to catastrophic wind the Harvard Forest LTER has created simulated blowdowns on which integrated studies are being undertaken. In September 1989 a 0.5-ha area of second-growth hardwoods was pulled over by our woods crew using a skidder and winch. Trees were selected by species and size according to criteria developed from studies of the 1938 hurricane. A cable drawn from the skidder, which was located 100 m off-site, was attached to each individual tree 5 to 10 m above ground and then winched in. The rooting and stem strength of the tree determined whether uprooting or breakage occurred. A larger area (1.0 ha) was pulled down in October of 1990. On both sites quantitative measurements of the force applied to each tree and video analysis of the uprooting/breakage process are being used to determine the biomechanical characteristics of wind damage to trees.

Each simulated blowdown contains areas of deer exclosure and nitrogen addition so that herbivory can be monitored and interactions between physical and chemical disturbance can be assessed. Complete stem maps of the original forest and adjacent controls allow for detailed analysis of damage patterns and regeneration.

In each control and manipulation plot a comprehensive range of measurements will be made, including: biomass increment; composition change in herb, shrub and tree layers; seedling demography; physiological response and carbon gain in seedlings; microenvironment; mineralization rates; fine root dynamics; litterfall; trace gas fluxes; and decomposition and litter dynamics.

Chronic Nitrogen & Sulfur Additions. The goal of this project is to test a series of hypotheses on the responses of forest ecosystems to chronic nitrogen and sulfur additions. Central to these hypotheses is the concept of nitrogen saturation: the removal of nitrogen limitations on biological function. Measurements focus on internal nitrogen cycling processes, on changes in production and foliar nutrient content, on leaching losses of nitrogen and, in particular, on fluxes of nitrous oxide and methane. Measurement of these two "greenhouse" gases is included to investigate possible linkages between regional nitrogen saturation and global climate change. The basic treatments are: (1) control, (2) additions of 50, and (3) 150 kg $N^{ha-1}$ $1.^{yr-1}$ as ammonium nitrate, and (4) additions of 50 kg N as $NH_4$ and a molar equivalent of S as sulfate. Treatments have been carried out in a red pine plantation and a mixed hardwood stand and will be extended to the hurricane blowdown experiment.

Two years of $N_2O$ and $CH_4$ flux measurements have been completed in the intact stands. The most intriguing result to date has been a significant reduction in methane consumption in nitrogen-amended soils. In the first year of N additions, measured annual N mineralization increased by an average of 40 percent of the added N. We hypothesize that this 40 percent increase is the result of rapid immobilization of added N, followed by remineralization within the one-month time period of the incubations. Samples taken in porous cup tension lysimeters through the 1989 season suggest near-zero N loss in the control and low N treatments. Elevated nitrate concentrations were occasionally encountered in the high N plots.

In general, the nitrogen content of leaf litter from dominant species in each forest type has increased with N additions. Woody production over the last three years is being estimated by measurement of tree diameter increment. Results from green foliage analyses indicate that the dominant species show increased N content with N additions, but that carbon fraction contents (lignin, cellulose, etc.) have not changed.

We plan to introduce $^{15}N$ into all fertilizer additions in 1990 so as to provide for a long-term pulse-chase experiment on the fate of added N. The $^{15}N$ will be added in a split-plot design. One-half of each 30m x 30-m plot will receive the label as $^{15}NH_4$, and the other half as $^{15}NO_3$. Additions will be at natural abundance levels in the amended plots.

Ten large (90 m x 90-m) plots have been established as targets for an overflight by the AVIRIS high spectral resolution device. In all plots, total canopy concentrations of nitrogen and carbon fractions have been measured.

Gap Studies of Tree Regeneration & Physiology. (a) *Maple seedlings and microenvironmental patterns.* Gaps 75 $m^2$ and 300 $m^2$ were created in the forest and microenvironmental stations were used to measure air and soil temperature, light intensity, windspeed, and humidity across each gap and intact forest. Seedlings of *Acer saccharum*, *A. rubrum* and *A. pensylvanicum* were transplanted into gap and understory locations. Seedling survivorship, carbon gain, and growth were monitored for two growing seasons.

Diurnal traces and seasonally averaged microclimatic data reveal that the gap-understory gradient is very broad and changes seasonally with solar altitude in complex ways. Significant asynchronies in irradiance and temperature produce different combinations of conditions at different times of the day across the gap. Species exhibit wide variation in survival, carbon gain and architectural modification across the gap environment. The results of this study do not support the gap partitioning hypothesis.

(b) *Response of birches and maples to shifts in resource availability patterns after disturbance.* This research tests the hypothesis that disturbance events influence tree regeneration primarily by shifting patterns and timing of resource availability. These studies will be conducted on sites where disturbances due to hurricane blowdown, pathogen epidemic, and nitrogen deposition are being simulated. The seed and seedling demography of canopy tree species will be characterized on the range of microsites commonly found after hurricane blowdown. We will also monitor the response of existing seedlings and saplings to canopy disturbance, assessing mortality and measuring changes in shoot growth, leaf deployment, photosynthesis rates, gas exchange, and leaf water relations. We will monitor the microclimate, estimate soil water potential and measure carbon dioxide levels. Foliar nutrient concentrations and leaf, stem, and root biomass will be determined after harvest.

The ultimate objectives of these studies are to: (1) identify critical resource attributes, such as timing of availability and degree of congruence among resources; (2) uniquely define, in terms of resources, each type of microsite created by disturbance; and (3) develop a resource-based model to predict regeneration response after disturbance.

(c) *Response of birches to interaction between nitrogen nutrition and light levels.* Because atmospheric deposition changes both the quantity and form of nitrogen input to the forest, a group of experiments was designed to study effects of nitrogen on birch regeneration. An experiment in shade houses is investigating the response of four species of birch to two levels (25 kg/ha and 50 kg/ha) and sources of nitrogen (ammonium vs. nitrate; 100:0, 50:50, 0:100) under two light levels simulating gap and understory conditions. A field experiment is being conducted to test the effects of the amount and form of nitrogen deposition on birch regeneration in a natural setting. Four birch species were planted in the summer of 1990 and are receiving three nitrogen treatments: 1) 50 kg/ha nitrate; 2) 50 kg/ha ammonium; and 3) no nitrogen addition.

A second shade house experiment is now in progress to test whether black birch forages preferentially in patches of nitrate or ammonium, and whether preference for nitrogen form depends on availability of light and total nitrogen. Foliar samples will be analyzed and nitrogen uptake and distribution will be estimated from nitrate reductase activity and measures of total nitrogen and nitrate content in leaves, roots and stems.

<u>Long-Term Litter Alteration</u>. A set of 20, 3 m x 3-m plots will be used in long-term studies of the effects of litter and root inputs on forest soil organic matter dynamics. Six treatments (n = 3) are planned including:

- No Aboveground Litter (screening and raking);
- Double Aboveground Litter (litter added from No Litter plots);
- Forest Floor Removal with Normal Litter Inputs;
- No Root Litter (trenching and barriers);
- No Root Litter and No Aboveground Litter
- Control Plots

Quantitative soil samples were taken from forest floors and B horizons near the reference pits. Oven-dried (50°C) samples will be analyzed for bulk density, percent organic matter, C and N concentrations, pH, cation exchange capacity, and base saturation.

### *LTER Intersite Activities*

<u>Patterns of Forest Disturbance</u>. Research involves an analysis of landscape patterns of vegetation

damage inflicted by hurricane winds and other natural disturbances to the forests of the Luquillo National Forest. Parallel studies are being conducted at the Harvard Forest and the H.J. Andrews Experimental Forest in Oregon. Remote imagery (aerial and satellite photographs) are being used and analysis will be on a Geographic Information System. A generic broad-scale model of hurricane wind interaction with physical and biological features of the landscape has been developed. The model will be used to understand the landscape-level effects of modern storms and to reconstruct the past impacts of historical storms in Puerto Rico and New England.

LTER-Wide Studies of Decomposition Processes. Following an LTER-sponsored workshop on decomposition processes held at the Marine Biological Laboratory, Woods Hole, Massachusetts, a plan was devised to study plant litter decay (long-term belowground litterbag study) and a determination of the relative importance of aboveground and belowground litter decomposition in the formation of soil organic matter. An extensive intersite experiment was planned and will be implemented depending on available funds. Preliminary studies relating to these experiments have been carried out at the Harvard Forest and elsewhere by the group from The Ecosystems Center, Marine Biological Laboratory.

Trace Gas Study. Beginning in October 1989, parallel measurements of soil trace gas fluxes are being taken every three months at HFR and the Luquillo Experimental Forest in Puerto Rico. Sites in Puerto Rico include intact forest, those windthrown by Hurricane Hugo, commercially harvested forest, and forest sites treated with N, P and K fertilizer. Soil nitrogen-cycling measurements are also taken.

LTER-Wide Studies of Coarse Woody Debris. Following the protocol established for the LTER Network a long-term study of decomposition of woody debris is underway at the Harvard Forest. The emphasis at our site is to contrast the dynamics of conifer (red pine) and hardwood (red maple) species, which differ greatly in carbon chemistry and nutrient content.

### *Synthesis*

Synthesis of the wide-ranging perspectives of researchers in the Harvard Forest LTER is being achieved through the integration of approaches within single experiments (e.g., hurricane blow-down and selective species mortality) and through modeling, remote sensing and GIS. Each of the experimental approaches employed in the individual background studies described above are being applied in concert with the large manipulations completed in the fall of 1990 to assess the effect of physical disturbance, chemical disturbance and their interactions across the range of ecological scales from individual organism to the whole ecosystem. The measurement of trace gas fluxes will provide an important assessment of ecosystem function and biosphere-atmosphere interactions.

## FUTURE DIRECTIONS

Results of the experimental treatments will be extended in both space and time to develop a synthetic, landscape-level view of ecosystem dynamics at the Harvard Forest. Existing process models of ecosystem function will be modified to extend predictions in time in order to encompass such important processes as moisture fluctuations, trace gas fluxes, and species changes through succession. Spatial extension will be through remote sensing research (in collaboration with NASA's Ames Research Center) and through extended development of GIS research. As models dealing with soil processes, trace gas fluxes and vegetation change are extended and refined we hope to be able to predict spatial variation in trace gas flux using remote sensing data entered into the GIS as the basis for an areal extension of results in experimental plots. Through the extension of real observations and modeled predictions across space and time we will seek to provide a broad framework for the interpretation of our results.

* HFR Climate Record 1951 - 1980

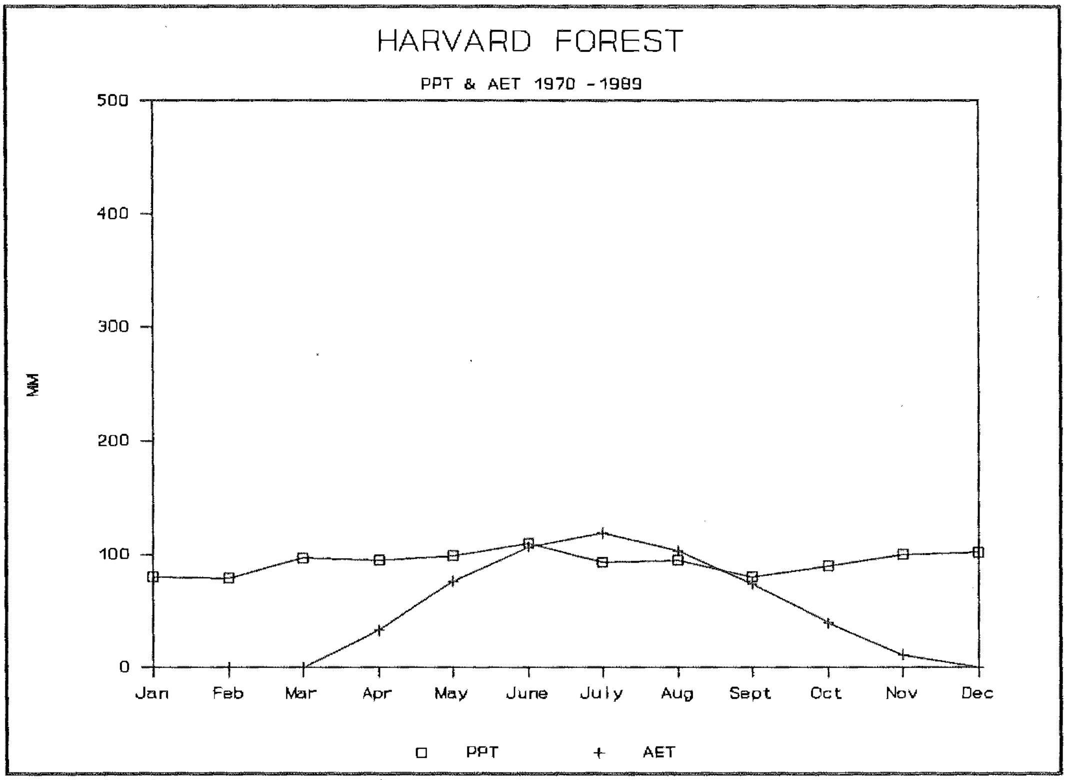



*Figure 1. Monthly water budget, including precipitation and actual evapotranspiration.*

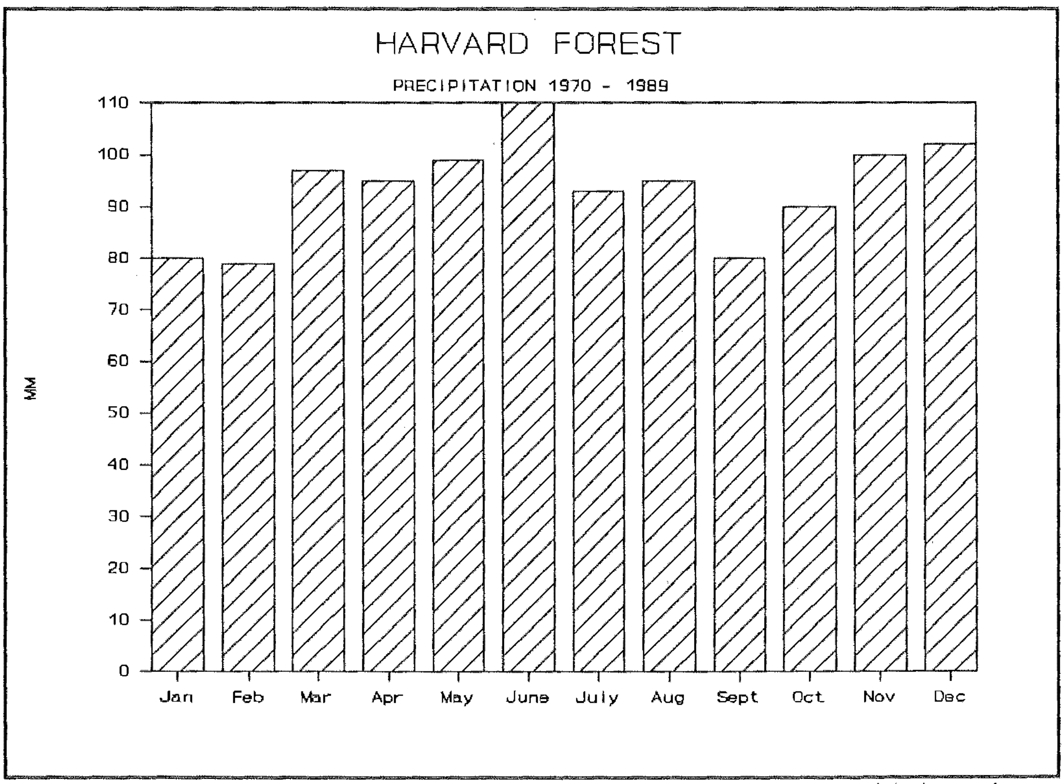



*Figure 2. Average annual precipitation totals.*

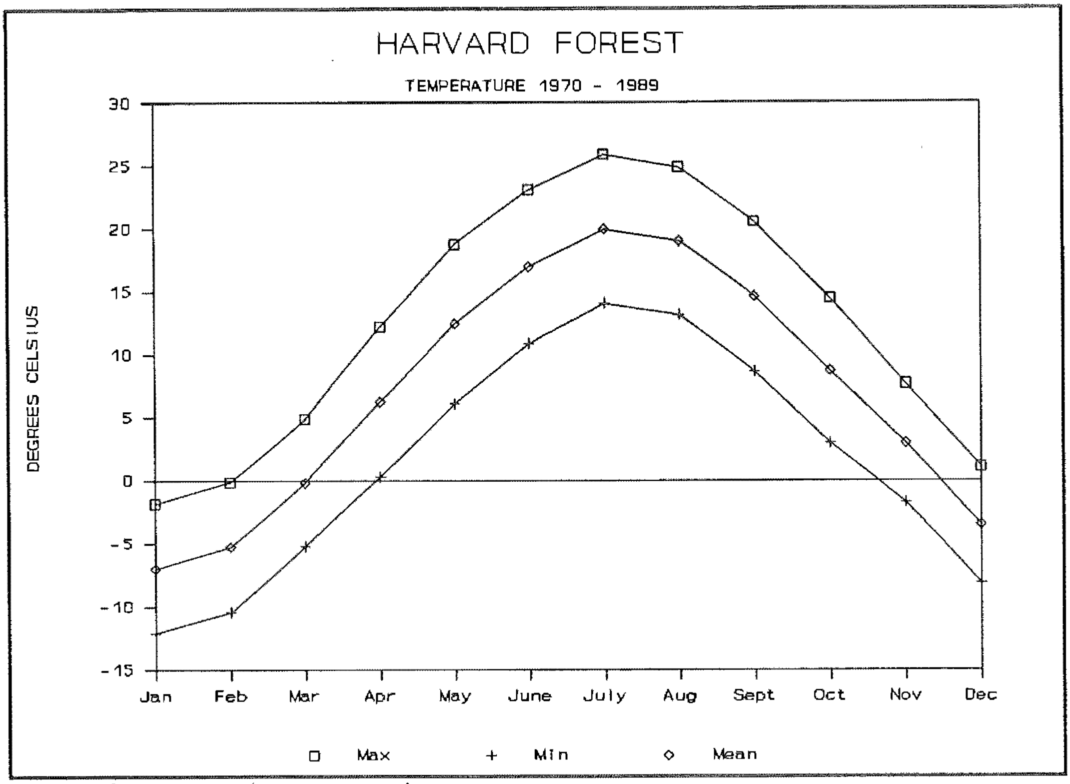
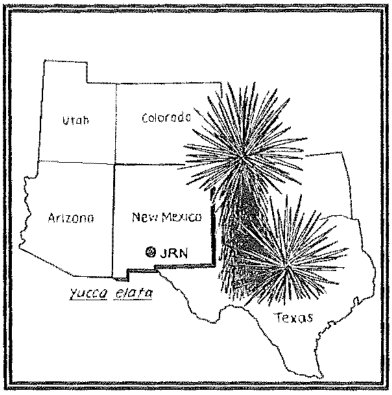



***Figure 3.** Average annual temperature values.*

* Data from on-site or nearest weather station.




# Jornada Experimental Range (JRN)

## RESEARCH SETTING

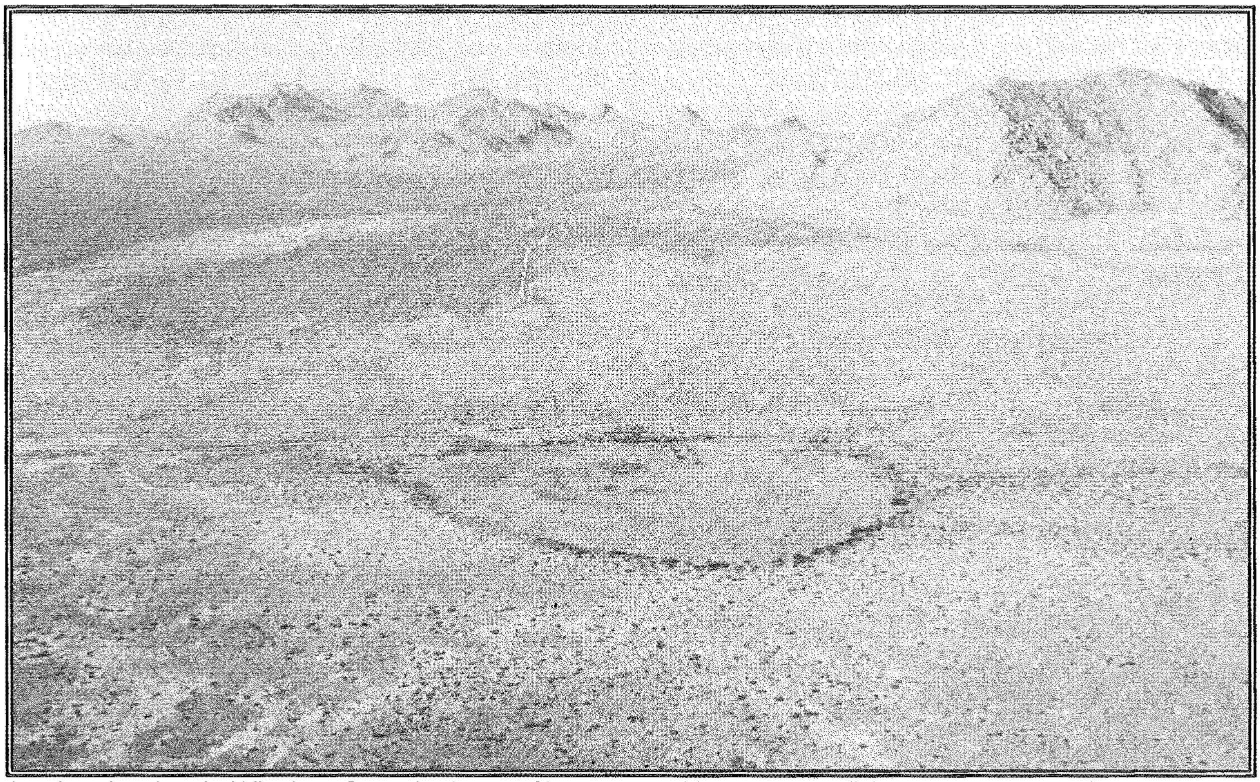
The Jornada Long-Term Ecological Research (LTER) site is organized around a plan for long-term ecological research investigating processes leading to desertification of semi-arid grasslands in the Jornada basin of southern New Mexico and changes in ecosystem properties that accompany desertification. During the last 100 years, large areas of black grama (*Bouteloua eriopoda*) grassland have been replaced by communities dominated by shrubs, especially creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*).

Similar changes have been observed in other areas of the Southwestern United States and in deserts on other continents. This transition appears to be driven by both natural and human-induced environmental changes, which we do not fully understand, and has resulted in fundamental changes in various ecosystem processes, including net primary production (NPP), water flux, and nitrogen cycling. The consequences of such changes are poorly understood, but they are significant to the socioeconomic disruptions that often accompany desertification and to changes in biospheric properties observed at the global level. The Jornada LTER program addresses both the causes and consequences of desertification through a cooperative program among investigators at four institutions (Duke University, New Mexico State University, Oregon Graduate Institute, San Diego State University) and the USDA Agricultural Research Service (ARS).

Increasing human exploitation of arid and semi-arid systems has led to the recent conversion of some marginal areas to desert—a process known as desertification. However, changes in the distribution of desert vegetation have also occurred as a result of natural oscillations in global climate. Arid and semi-arid regions are dynamic landscapes and the study of changes in ecosystem properties at the sensitive margin between arid and semi-arid lands offers an opportunity to observe the extent of global change induced by humans. The presence of large areas of arid and semi-arid land on the Earth's surface endows these ecosystems with an importance that is likely to have been underestimated in past assessments of global biogeochemical processes. Emissions of gaseous nitrogen (e.g., $N_2O$, $NH_3$) from desert soils during denitrification and ammonia volatilization may represent a major terrestrial input of these gases to the atmosphere. Wind erosion produces vast quantities of dust from the world's deserts, potentially affecting global albedo, rain chemistry, soil development and ocean productivity in downwind areas.

### *Site Characteristics*

The Jornada LTER is located 37 km north of Las Cruces, New Mexico in the northern Chihuahuan Desert. The 25,900-ha New Mexico State University College Ranch is contiguous to the 78,266-ha USDA Jornada Experimental Range, creating a block of 104,166 ha wholly devoted to research. This property is a unique site for



*A typical closed-basin Chihuahuan Desert landscape. Mt. Summerford (background) adjoins a creosote-bush bajada which drains into a large playa (center) fringed by mesquite.* WALTER G. WHITFORD

long-term ecological research because virtually all of the ecosystems of the Chihuahuan desert are represented.

The climate of the area is characterized by an abundance of sunshine, a wide range between day and night temperatures, low relative humidity, an evaporation rate averaging 229 centimeters (cm) per year, and extremely variable precipitation. The average annual precipitation is 230 millimeters (mm), with 52 percent occurring during the summer. Droughts are a recurrent climatic phenomenon; the 1951-57 drought is believed to be the most severe in the past 350 years.

Geologically, the Jornada presents a crosssection of the basin and range topography characteristic of the Southwestern United States. Most of the basin is closed, with no exterior drainage, and water occasionally collects in scattered playas. Typically, soils have a caliche layer at depth, but the degree and depth varies with site position and soil age.

The vegetation is representative of that found throughout the Chihuahuan Desert with a flora of about 550 species. We are studying a series of five vegetation communities that are dominant on the Jornada and are hypothesized to differ in their degree of desertification, including: 1) remnant black grama grasslands; 2) playas or low-lying areas with heavy soils (which are periodically flooded) and dominated by tobosa (*Hilaria mutica*) and burrograss (*Scleropogon brevifolius*); and a series of desertified shrublands, including 3) tarbush stands (*Flourensia cernua*); 4) mesquite dunes (*Prosopis glandulosa*); and 5) creosotebush bajadas (*Larrea tridentata*).

For each community type, three permanent plots representing a range of primary productivity have been established to examine patterns of NPP, soil moisture, and soil nutrients as a function of climatic variation. The fauna of the Jornada Experimental Range is the most completely studied of any arid area in the world. We are studying the population dynamics of a number of representative consumers, including rabbits, ants, and termites. Rabbits affect a number of ecosystem properties and processes and are the major (largest biomass) native herbivore within the Chihuahuan Desert. Ants are among the most abundant animals in all deserts. The importance of termites as consumers of dead plant material, producers of soil macropores, effectors of soil organic matter and soil N, agents of soil turnover, and effectors of aboveground net primary production (AGNPP) in the northern Chihuahuan Desert is well-documented.

## RESEARCH PROGRAM STATUS

We suggest that the changes in ecosystem function at the transition between arid and semiarid regions are best understood in the context of the spatial and temporal distribution of soil resources. In our hypothesis, when net, long-term desertification of productive grasslands occurs, a relatively uniform distribution of water, N, and other soil resources is replaced by an increase in their spatial and temporal heterogeneity (Figure 1). This heterogeneity leads to the invasion of grasslands by shrubs. In these new plant communities, soil resources are concentrated under shrubs, while wind and water remove materials from intershrub spaces and transport soil materials to new positions on the landscape. Shrub dominance leads to a further heterogeneity of soil properties because effective infiltration of rainfall is confined to the area under shrub canopies, whereas barren intershrub spaces generate overland flow, soil erosion by wind and water, and nutrient loss.

The cycling of plant nutrients, largely controlled by biotic processes in any ecosystem, is progressively confined to the zone beneath shrubs; this process leads to the development of well-known "islands of fertility" that characterize desert shrublands. In time, the islands of fertility become favored sites for shrub regeneration and yield self-augmented levels of local fertility. Our hypothesis is based on studies in the Jornada Experimental Range of southern New Mexico, but we believe that this model applies to desertification in other areas of the globe.

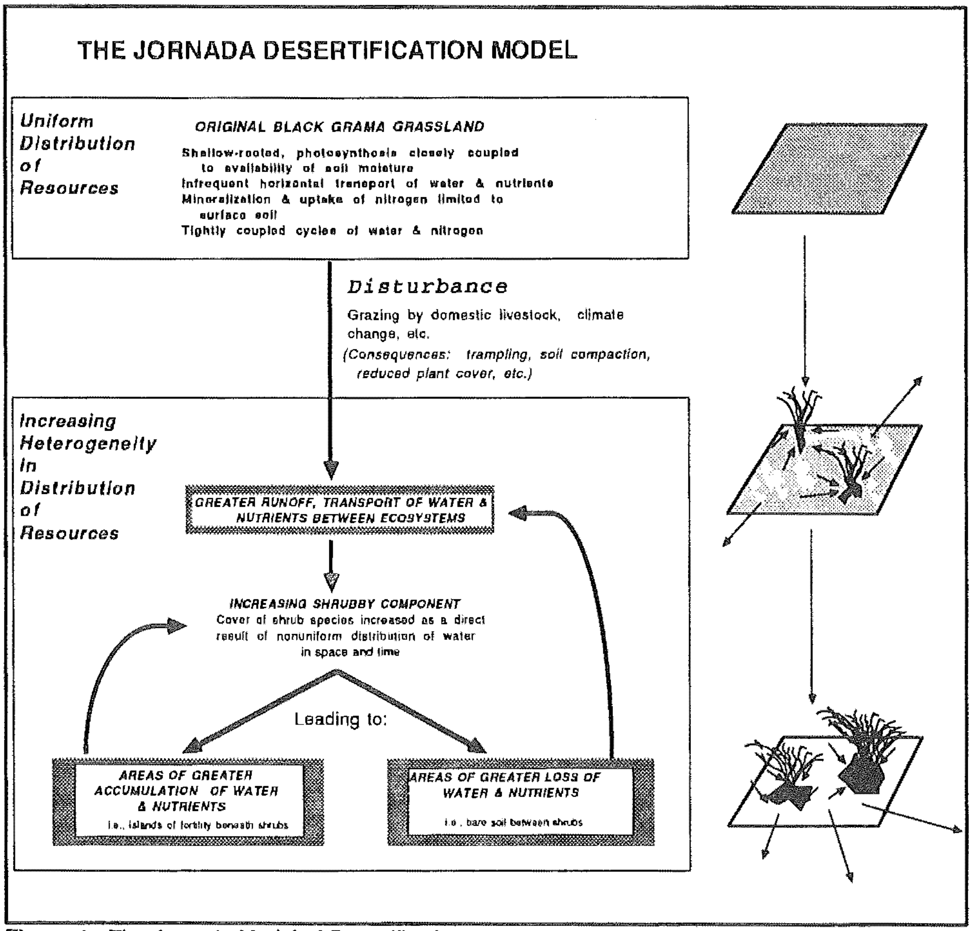



Figure 1. The Jornada Model of Desertification

### *Core Research Areas*

Our central hypothesis is being examined by three levels of study: (1) comparative process studies within representative grassland and shrub ecosystems; (2) studies of transport (runoff, runon, and wind) and the relative linkage among these ecosystems, and (3) landscape-level studies involving spectral vegetation indices from satellite imagery and a computerized GIS for the analysis of spatial data. In order to obtain the requisite data on productivity, nutrient and water availability, organic matter processing, consumer populations, and system responses to disturbance, we are utilizing field experiments, modeling, and remote sensing.

### *Process-Level Studies*

Hydrologic Cycle: The central hypothesis is that variation in resources, particularly water, is the primary cause of the shift from grassland to shrubland, which is further exacerbated by the nature of the shrubs themselves. Detail studies of the temporal and spatial variability of soil moisture (neutron probe) to depths of 3 meters (m) are being made in each of the five plant community types.

Plant Production: We hypothesize that the patterns of total plant production are synchronous in the ecosystems of the Jornada landscape, i.e., high and low production occurs in the same years in all systems. Plant biomass and production data are necessary for both the development and validation of the ecosystem and landscape models. In addition, these data will be coupled with measurements of plant nutrient concentration to estimate element uptake in the various ecosystems. We are using methodologies ranging from hand-held radiometers and satellite remote sensing of canopy reflectance to direct harvesting.

Decomposition: Decomposition and N mineralization/immobilization of annual plant roots are believed to be keys to understanding N availability and the linkage between rainfall and primary production. We are studying decomposition of annual plant roots across the five communities to examine controls on N availability as a function of vegetation type.

Nutrient Cycling: The amount and the timing of N availability play a critical role in determining patterns of AGNPP across this desert landscape. This leads to the hypothesis that during desertification, major changes occur in the distribution of limiting nutrients (e.g., N), resulting in an increase in their spatial heterogeneity. This is associated with increasing shrub dominance. We are testing the above hypothesis by determining the distribution of soil nutrients to a depth of 3 m in each of the five ecosystems. These data will provide baseline information on the total quantity of and variability in the distribution of nutrient reserves in each system. Plant nutrient uptake is being estimated for the dominant plant(s) in each of the five ecosystems.

Elements of special concern (in addition to N) include phosphorus (P) and micronutrients. Studies of Jornada ecosystems suggest that the very low soil levels of Zn and Cu may be limiting plant productivity. A fundamental hypothesis is that available soil nutrients will vary over time as a function of seasonal soil water content. Yearly dynamics of soil nutrient ion activity will be monitored through the use of synthetic ion exchange resins.

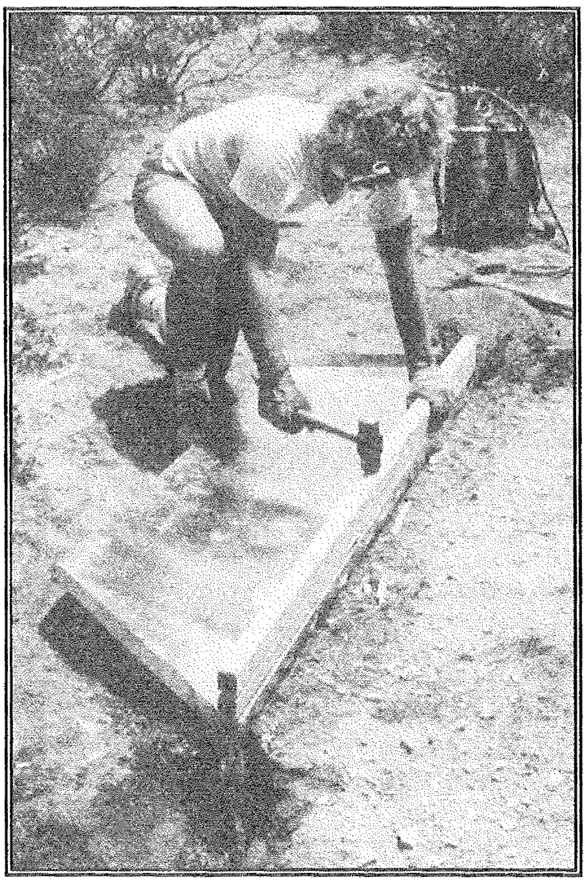
Consumer Studies: The autecological hypothesis of Noy-Meir (1979) predicts that desert animal populations fluctuate in time and space as a function of water availability. This hypothesis also predicts no feedback effects of consumer activities on rates of primary production, nutrient cycling and secondary production of other species. Our data suggest that the autecological hypothesis is not applicable to northern Chihuahuan Desert ecosystems. Indeed, we view consumers as key regulators of ecosystem processes, affecting the patch dynamics of component ecosystems in the landscape and modifying water and nutrient availability across the landscape. The animal populations selected for study by the Jornada LTER are species or groups of species that we have found to affect plant production both directly and indirectly—and/or to affect the redistribution of water and nutrients. The activities of consumers (e.g., burrowing, digging, transport of organic matter) contribute to increased patchiness in water and nutrient availability and, hence, contribute to the desertification process. In addition, many of these taxa may benefit from some degree of desertification; that is, desertification may result in increases in resources that limit the population size of some of the animals.

### *Transport-Level Studies*

Changes in the processes that link ecosystems along drainage basins are central to our model of desertification (Figure 1). We suggest that as a result of increased runoff, there is a greater linkage among ecosystem types; this linkage has altered the extent and location of ecosystem processes in the basin.

Water transport: We have established runoff plots in black grama grassland, and *Larrea tridentata* shrublands. These plots are designed to catch runoff produced on a 2 x 2 m area. These studies are added to the data from runoff plots in creosotebush shrublands established in 1978 and commence the long-term collection of runoff data that has proven so useful in understanding ecosystem function in sites such as Hubbard Brook.

Gaseous Losses: In alkaline soils significant amounts of ammonia can be lost through the abiotic conversion of $NH_4$ to $NH_3$. Soil erosion during desertification may have increased the rates of ammonia volatilization. We are evaluating the possibility that ammonia volatilization losses have increased in areas of the Jornada Basin that have undergone erosion during the transition to shrubland communities. Site-specific rates of ammonia volatilization are being determined in the five reference ecosystems.



*Runoff plots are installed in grass- and shrubland communities to examine the redistribution of water and nutrients as a function of vegetation type and rainfall.*
*WALTER G. WHITFORD*

### Landscape-Level Studies

Baseline Satellite Data: Desertification has resulted in changes in plant community patterns and distributions throughout the entire Jornada basin. To address these landscape-level changes, remote sensing is being used to provide information for estimating plant cover and production and provide long-term records of vegetation change. The proximity of the Jornada to White Sands Missile Range is advantageous for purposes of sensor calibration. We are assessing the potential to resolve vegetative signals from the Jornada ecosystems using digital image data recorded by SPOT, Landsat, and NOAA satellites. Particular attention is being paid to how the varying spatial, spectral and radiometric resolution of these satellite systems influences our ability to determine types and abundance of vegetation.

Geographic Information Systems (GIS): GIS is being used to examine the interrelationships between soils and vegetation types. Data entered into the GIS are spatially referenced to an earth coordinate system and are being related to other data layers, retained for temporal comparisons, and analyzed statistically. Geographic information systems technology is also being used in our simulation modeling efforts.

### Modeling

Modeling is being used to develop a predictive understanding of potential ecosystem responses to simultaneous changes in resource availabilities as depicted by the Jornada Model (Figure 1). Our modeling goals are to examine relationships between intra- and intersite processes to gain an understanding of the mechanisms underlying these responses. Three major tasks are being addressed: (1) describing processes that occur at specific locations on the landscape; (2) characterizing transport of energy and materials between locations; and (3) interfacing local and transport processes in a landscape framework. Our approach is employing a hierarchy of models, using different levels of time and space scales to simulate ecosystem and landscape dynamics.

An ecosystem model developed for the Jornada-PALS (Patch Arid Lands Simulator) is the cornerstone of our modeling efforts. PALS is being coupled to an ARC/INFO GIS system to simulate transport dynamics, including sedimentation, erosion, and water dynamics; this coupled model, termed REGALS (Regional General Arid Lands Simulator), will permit us to explore various questions concerning the spatial and temporal distribution of resources at the Jornada. Our scheme effectively combines the data analyses and manipulation functions of GIS with the powerful extrapolation capability of phenomenological ecosystem models to accomplish a regional landscape model.

### Test of the Jornada Model

Our central hypothesis suggests that restoration of homogeneity in water and nutrient availability in former shrub-dominated systems should result in reinvasion by grasses, whereas shrub establishment should be favored by increasing soil heterogeneity. As a test of our general model we plan to experimentally manipulate soil heterogeneity by bulldozing established mesquite dunes to effectively redistribute the "islands of fertility" contained in these dunes to the nutrient-poor shrub inter-spaces. This will increase the homogeneity of soil nutrients and water infiltration. On half of the dozed plot we are increasing soil heterogeneity by altering infiltration patterns through the construction of microcatchments. Mesquite and grass will be seeded on the plots and plant establishment and changes in soil nutrient and moisture distribution in will be followed as a function of the initial soil heterogeneity.

### Research Results

Jornada LTER I (1982-1987) focused on studies of ecosystem response to spatial and temporal heterogeneity. It was hypothesized that spatial differences in water and nutrient availabilities would impose lags in system responses (e.g., plant production) and that these lags would not necessarily be equal, nor synchronous, spatially. The experimental design centered on two 3-km transects, extending from the middle of a dry lake bed to the base of a mountain. The transects traversed seven perennial plant vegetation zones, encompassing many of the plant communities that make up Chihuahuan Desert landscapes. One transect was fertilized (with 10 kg. $ha^{-1}$ of $NH_4NO_3$) once each year during the rainy season; this fertilization was imposed to homogenize a previously patchy and limiting resource. A variety of short-term studies was conducted that evolved from questions or hypotheses generated from the long-term transect studies.

The transect studies demonstrated that some ecological processes (e.g, plant production, N mineralization) and populations (e.g., soil arthropods, ants) vary greatly, exhibiting sharp transitions over short distances, while others vary gradually. The complex interactions between rainfall, N availability, soil, and geomorphic position and their effects on plant production and decomposition were examined by a series of experimental studies on small plots using irrigation and fertilization.

The Jornada Model (Figure 1) predicts that homogenization of a potentially limiting resource, such as N, will lead to an increase in plant cover and a decrease in plant diversity. Results of the first five years of N amendments in LTER I indicate that these predicted responses are occurring for the annual plant species—N amendments resulted in increased annual plant cover and decreased diversity. With time, we anticipate finding similar responses in the perennial vegetation.

Several experiments examined relationships between water inputs and nutrients and mass losses from dead organic matter. We found little effect of irrigation on mass losses from litter on the soil surface or from dead roots. The exception was that mass loss from surface litter was accelerated by simulated rain events during an extended rainless period. Studies of mass losses from surface litter demonstrated that much of these mass losses are due to fragmentation by sunlight and that fragments are transported into the soil by rainfalls. This interpretation is not consistent with conventional wisdom that decomposition rates in deserts are low and occur for brief periods following rains. These experimental studies also demonstrated that populations of soil biota are limited by substrate availability and not by water.

The findings summarized above have clearly demonstrated the importance and link between water and N availability as driving variables in Chihuahuan Desert shrub ecosystems. These studies have raised questions pertaining to the applicability of these results to desert grasslands and how these processes may have changed during the desertification process.

## FUTURE DIRECTIONS

### *Intersite and Interagency Efforts*

The Jornada LTER is involved in a number of interagency cooperative efforts related to desertification and transport processes. One of the major linkages between deserts and global processes is the long distance transport of dust and its effect on ocean productivity. At present the USGS is conducting studies of water and wind transport at the Jornada. The Jornada LTER has research plots on the USDA-ARS Jornada Experimental Range and is developing a cooperative effort with USDA and the Bureau of Land Management to share data to produce a GIS data system to cover the entire Jornada basin. In addition, the National Aeronautics and Space Administration (NASA) is supporting research to use satellite imagery to estimate shrub canopy dimensions and density. Finally, the Jornada LTER has organized a joint workshop with a group of Chilean scientists interested in desertification processes and long-term comparative studies of U.S. and South American deserts.

Networkwide and intersite research opportunities contribute to the general objectives of the Jornada LTER in several ways. The Jornada has a long history of studies of decomposition and organic matter cycling as a function of climate and soil biota. The intersite decomposition study now in progress will provide important information on factors controlling litter mass loss. At the core of the Jornada LTER effort is a need to quantify and understand the biological factors contributing to soil heterogeneity. A number of LTER sites are now interested in the role of animals in affecting soil heterogeneity. The key plant community change associated with the desertification of the Jornada has been a shift from grass to woody vegetation. The Sevilleta and the Central Plains Experimental Range sites are also interested in grass/shrub interactions and plant community change in semiarid environments.

The present-day Chihuahuan Desert is a mosaic of shrubland and remnant grasslands that are well-represented on the Jornada. It is important to emphasize that the tropical affinities of the flora and fauna and the evolutionary history of subtropical deserts impose functional differences on these areas in comparison to temperate "dry" areas. We should therefore expect greater functional differences between shortgrass steppe ecosystems (Sevilleta, Central Plains sites) and the Chihuahuan Desert, which are separated by a few hundred kilometers, than between the Chihuahuan and the African, Middle Eastern or Australian deserts that are thousands of kilometers distant. This hypothesis may be tested by parameterizing the PALS model for intersite differences in climate and developing predictions that may be tested through gathering of long-term core data sets on productivity and decomposition or from field experiments.

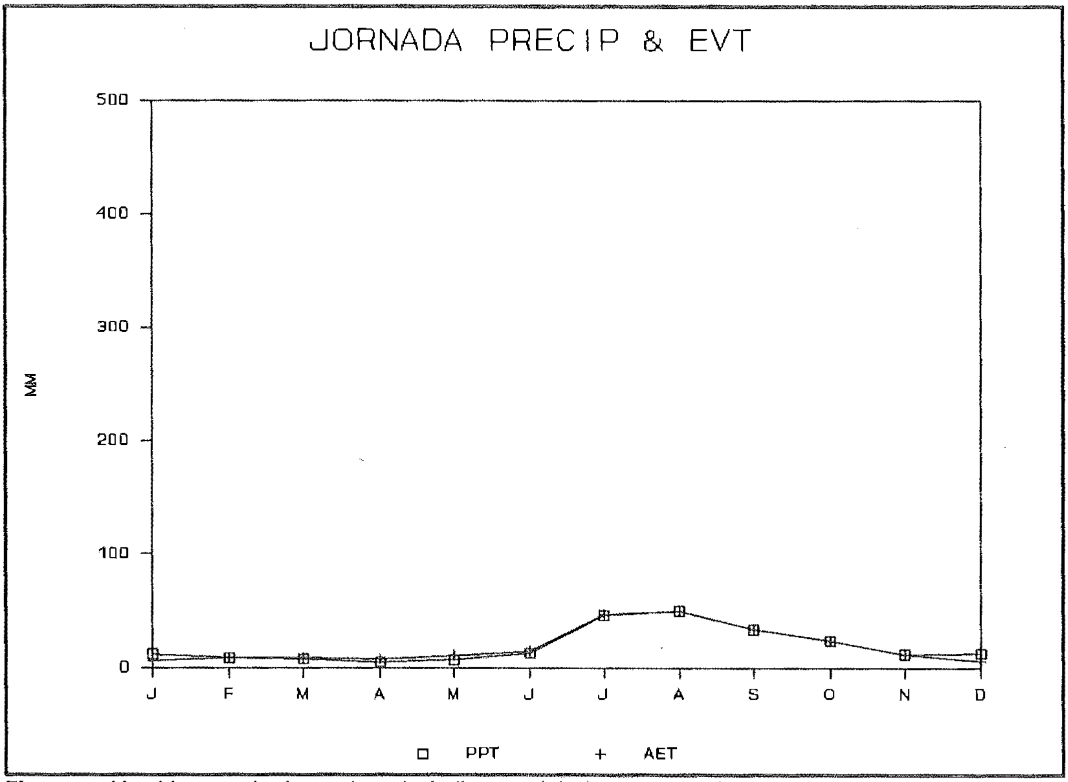



**Figure 2.** Monthly water budget values, including precipitation and actual evapotranspiration.

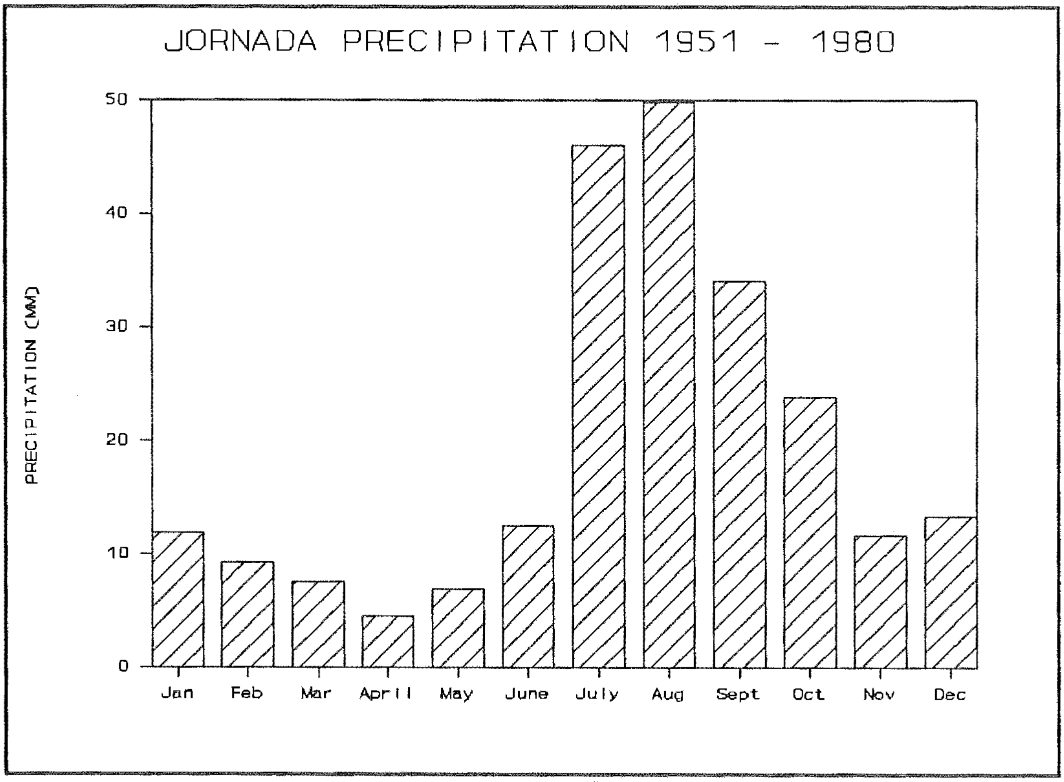



**Figure 3.** Average annual precipitation totals.

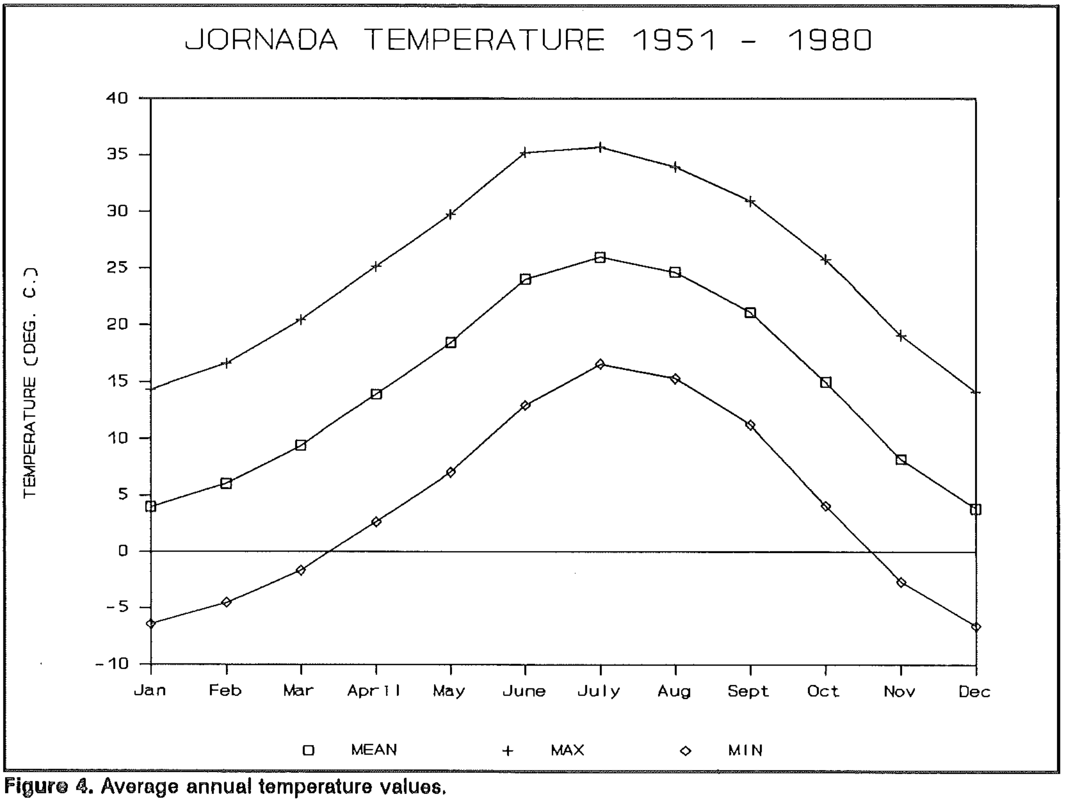
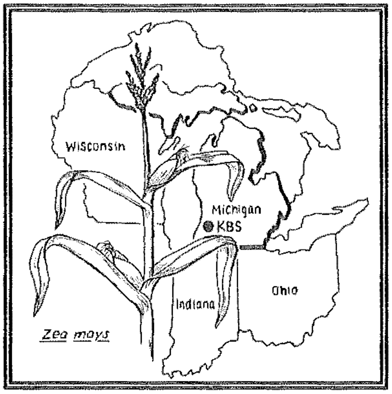



**Figure 4.** Average annual temperature values.

* Data from on-site or nearest weather station.




# Kellogg Biological Station (KBS)

## RESEARCH SETTING

The primary focus of the Kellogg Biological Station Long-Term Ecological Research (LTER) project is the agricultural ecosystem represented in the northern portion of the Midwest corn belt. Our principal LTER interests lie in ecological interactions in major row crops of the region, both annual (corn, soybean, wheat) and perennial (alfalfa, *Populus*). Our aim is to gain a basic, integrated understanding of the organism-level interactions that underlie modern row crop ecosystems.

The global, long-term hypothesis of the KBS LTER Project is that agronomic management based on ecological concepts can effectively substitute for current reliance on chemical subsidies in production-level cropping systems. A major corollary of this hypothesis is that herbicide subsidies can be minimized by manipulating crop-weed interactions, pesticide subsidies can be minimized by manipulating plant-insect-pathogen interactions, and nutrient subsidies can be minimized by manipulating plant-microbe-soil interactions. Figure 1 presents a simple conceptual model outlining these foci.

### *Site Characteristics*

Most of the KBS LTER research effort is concentrated on a 42-hectare (ha) site that has been subdivided into seven different 1-ha cropping systems, each replicated in one of six blocks. Cropping treatments 1 and 2 are corn-soybean rotations that represent conventionally farmed grain production.

One treatment is a moldboard plowed system, the other is a no-till system; both treatments receive standard levels of chemical inputs. Treatments 3 and 4 are corn-soybean-wheat rotations that represent low-chemical-input systems. Both of these treatments have a winter legume cover crop; treatment 3 receives chemical inputs only to control outbreak pest populations and to provide an initial pulse of N at planting, while treatment 4 receives no chemical inputs at any time. Treatments 5 and 6 are perennial biomass plots. Treatment 5 is planted to herbaceous biomass (alfalfa), while treatment 6 is planted to woody biomass (fast-growing *Populus* clones on a five-year rotation cycle). Treatment 7 is a native successional treatment, abandoned after plowing in 1989. An additional never-plowed site, 200 meters (m) from the others, serves as an historical control for soil organic matter studies. All plots contain subplots established to address specific process-level hypotheses (e.g., +/- fertilizer, +/- herbicides, different planting densities).

### *The Larger KBS Landscape*

The KBS LTER site represents a relatively small portion of the Kellogg Biological Station as a whole, but LTER is an integral part of the larger landscape. The Station is the largest of 13 Agricultural Experiment Stations (AES) in Michigan and, in addition to the 42 ha of cultivated land assigned to LTER activities, another 200 ha are cultivated as part of AES

*KBS cropping systems: (front) low- and zero-chemical input wheats; others, no-till and conventionally tilled maize, alfalfa and short-rotation Populus, and native sucession plots.* PHIL ROBERTSON

operations. Included in the AES land base are small-plot research areas typical of AES research stations nationwide, several large irrigated fields associated with the Station's 300-cow dairy herd, a 300 $m^2$ rain-out shelter, and several in-ground, undisturbed-profile weighing and nonweighing lysimeters.

Noncultivated areas of KBS include 240 ha of old fields in various, well-documented stages of secondary succession, 25 ha of old-growth oak-hickory forest, and 300 ha of conifer and hardwood plantings established on eroded farmland in the 1930s. Also on-site are several small lakes and a set of 18 experimental ponds designed to allow near-natural, replicated aquatic experiments. General support facilities include a modern research laboratory and a greenhouse.

Surrounding KBS is a diverse, rural-to-semirural landscape typical of many parts of the U.S. Great Lakes and upper Midwest regions. The diversity of landuse, soil and vegetation types, and aquatic habitats within a 50-km radius of the Station is high. Most of southwest Michigan is on the pitted outwash plain of the morainic system left by the last retreat of the Wisconsin glaciation, circa 14,500 years ago. Soils in the area developed on glacial till, and include well- and poorly-drained alfisols, mollisols, and entisols. Most regional soils are sandy loam and silty clay loam of moderate fertility; principal Station soils are Typic Hapludalfs. Land use around KBS ranges from urban (Kalamazoo, with a metropolitan population of 300,000, is 20 km south of the Station) to rural; vegetation ranges from cultivated and early successional old fields to old-growth oak-hickory and beech-maple forests; and aquatic habitats include more than 200 bodies of water of different morphometries, alkalinities, and degrees of eutrophication.

Precipitation in southwest Michigan (about 920 mm/year-1) is fairly evenly distributed throughout the year. The Station is included in Lake Michigan's snow shadow and receives approximately 2 m of snow each winter. The

Lake's heat capacity tends to slightly retard the advance of spring and prolong fall relative to Wisconsin, on the leeward side of the Lake. Southwest Michigan growing seasons are typically 180 days. The average number of days with appreciable precipitation is about 100 per year. Solar and sky radiation are concomitantly low, especially during the winter.

## RESEARCH PROGRAM STATUS

Areas of active LTER research at KBS range from the molecular to the regional, though most of our strengths derive from expertise in microbial and plant physiological ecology; in insect and plant population dynamics; in plant community structure; and in ecosystem processes in disturbed communities. We have organized the LTER project into four conceptual groups:

- nutrient availability, which considers the degree to which primary production and consequent population interactions are affected by nutrient (primarily N) limitations;
- plant competition and carbon/nitrogen allocation, which considers interactions among crop and colonizing (weed) species as they affect communitywide species composition and resource allocation, including the allocation of C and N to different species in the community and to different sinks in each species (e.g., allocations to above vs. belowground and vegetative vs. reproductive tissue);
- insect herbivory, plant pathogenesis, and gene transfer, which examines questions related to the dispersal of insect pests and pathogens in the agricultural landscape with particular reference to controls on population dynamics and mechnisms of gene transfer in soil; and
- systemwide biogeochemiocal inputs, outputs and modeling, which addresses mechanisms by which nutrients and water are gained and conserved in agricultural systems, and the modeling of ecosystem processes and population dynamics.

Specific questions related to each of our core areas are being addressed in the context of the experimental design described above. Our long-term questions rely for their resolution largely on information collected from each experimental treatment at varying frequency intervals.

At present, core nutrient availability hypotheses are centered on (1) understanding the active fraction of soil organic matter (SOM) and the microbial communities responsible for its turnover, (2) the composition and activity of the soil invertebrate community, and (3) the contribution of symbiotically fixed vs. native and applied nitrogen to SOM cycling and crops. Studies of the microbial communities involve determinations of microbial biomass pools, of fungi:bacteria ratios, and the development of genetic probes to follow specific taxonomic groups in collaboration with the Center for Microbial Ecology at Michigan State University. Soil invertebrate work centers on studying the response of earthworm and nematode populations (fungivorous, bactivorous, parasitic, and omnivorous nematode feeding groups) to cropping

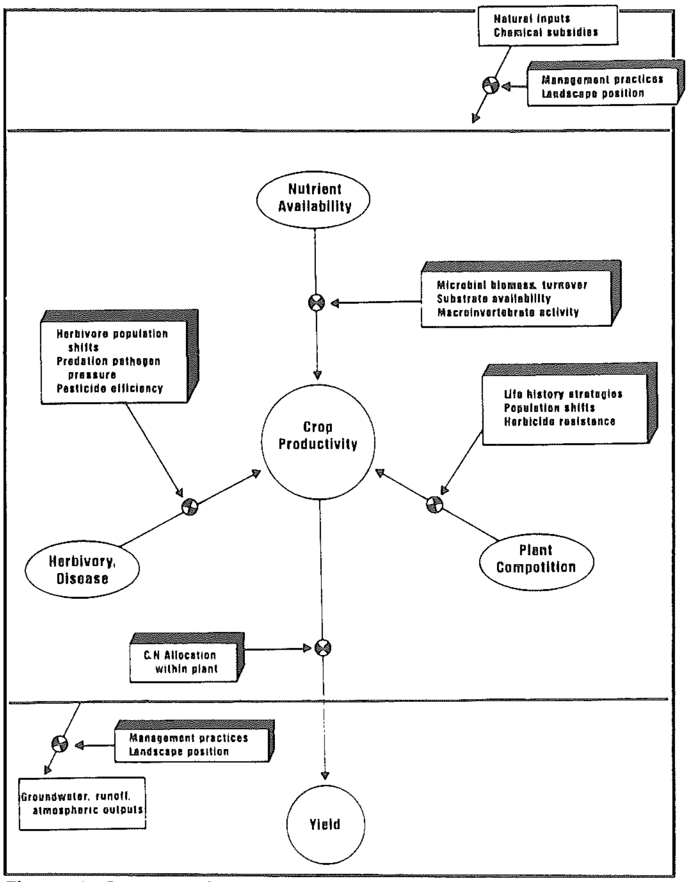
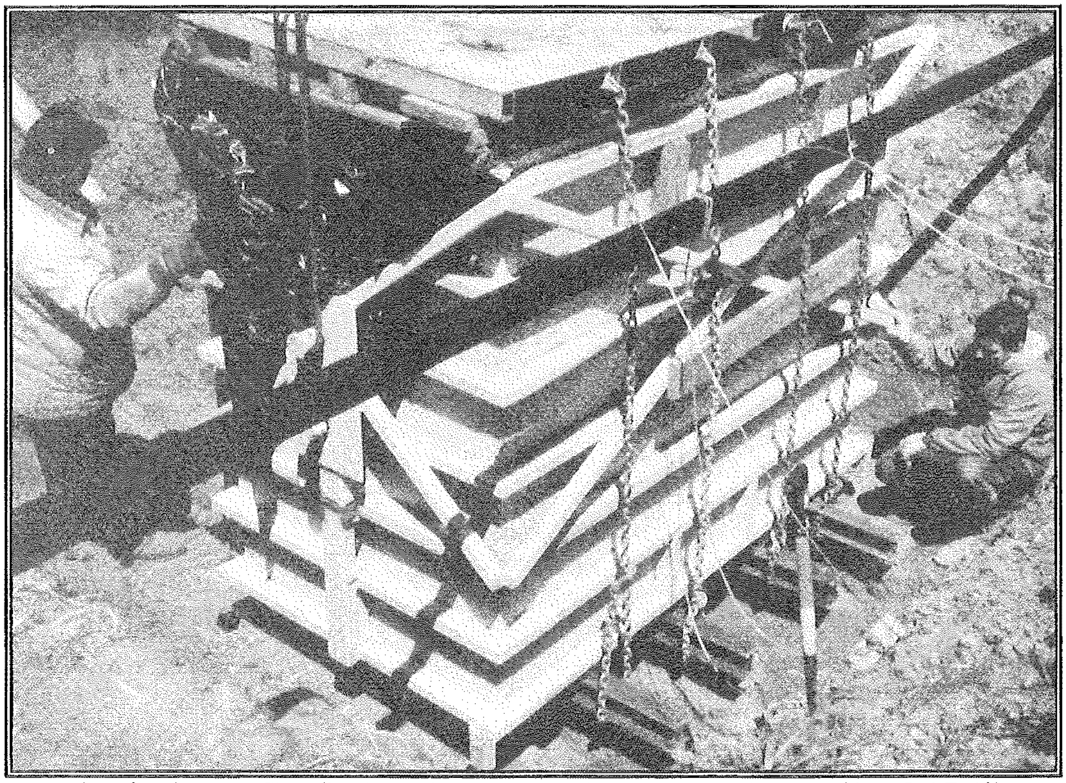


*Figure 1. Conceptual model of the major areas of inquiry in the KBS LTER project.*

disturbance. The N cycle experiments are presently focused on the use of $^{15}N$ to follow the fate of particular sources of N into and through different plant, microbial, and soil pools.

Plant competition and C,N allocation questions are presently focused on (1) crop-weed competition for resources and consequent communitywide allocation patterns, (2) variations in weed distributions and abundances among the different cropping systems, and (3) soil-root interactions. Experiments to determine how plants partition resources and whether crop-weed interactions vary in response to resource levels are underway in a set of experimental subplots within the two high-input annual crop systems, the *Populus* treatment, and the native successional community. Manipulations include crop density, fertilizer inputs, and weed pressure. Weed distribution questions currently center on examinations of the weed seed bank; in particular, on (1) how well the seed bank predicts weed abundances and composition in subsequent years and (2) how changes in disturbance (tillage and cropping systems) affect the distribution and composition of the bank. Work on soil root interactions currently centers on examining hypotheses regarding the effects of soil physical properties as affected by soil disturbance and crop species on root turnover. Turnover is being assayed using minirhizotron microvideo methods.

Insect herbivory, pathogenesis, and gene transfer investigations are now centered primarily on (1) the population dynamics of major insect pests and predators, (2) *Fusarium* dynamics in soil, and (3) the genetic aquistion of a xenobiotic metabolizing capacity by soil bacterial populations. The insect population work focuses mainly on quantifying the distribution and abundances of major pests and predators in each of the different cropping systems; experiments to determine how important insect predators respond to cultural and chemical manipulations in the different systems; and examinations of the factors that regulate pest and predator dispersal rates through the agricultural landscape. The *Fusarium* work focuses on the interactions between a specific model pathogen and target plant species (maize) as affected by the presence of surface litter and water stress. Gene transfer work centers on an examination of the set of genetic events that follow the application of a novel substrate to soil (2,4 D) that result eventually in the capacity of soil bacterial populations to metabolize the substrate.



*Installation of an intact-profile soil lysimeter in a set of experimental plots at KBS.* PHIL ROBERTSON

Systemwide inputs/outputs and modeling work are presently focused on examinations of gaseous N losses from agricultural soils, water movement within complex landscapes, and primary productivity and biogeochemical model development. In the nitrogen gas research we are examining pathways of loss from row crop ecosystems, testing the explicit hypothesis that N-gas losses (both $N_2$ and $N_2O$) will be positively related to soil N status, as will the ratio of $N_2$:$N_2O$. Water movement in landscapes is being addressed by investigating the effect of geomorphic landscape position on the movement of water, and soil; in particular, we are interested in the potential for significant lateral or down-slope water flow as a result of textural discontinuities in the soil profile. Modeling efforts are presently centered on the development of crop-nutrient-water submodels to be applied to the row-crop rotations. A multi-crop rotation model that incorporates components of the Ceres and Century models is presently under development, as is an analytical study of the soil organic matter/soil nutrient flux submodel.

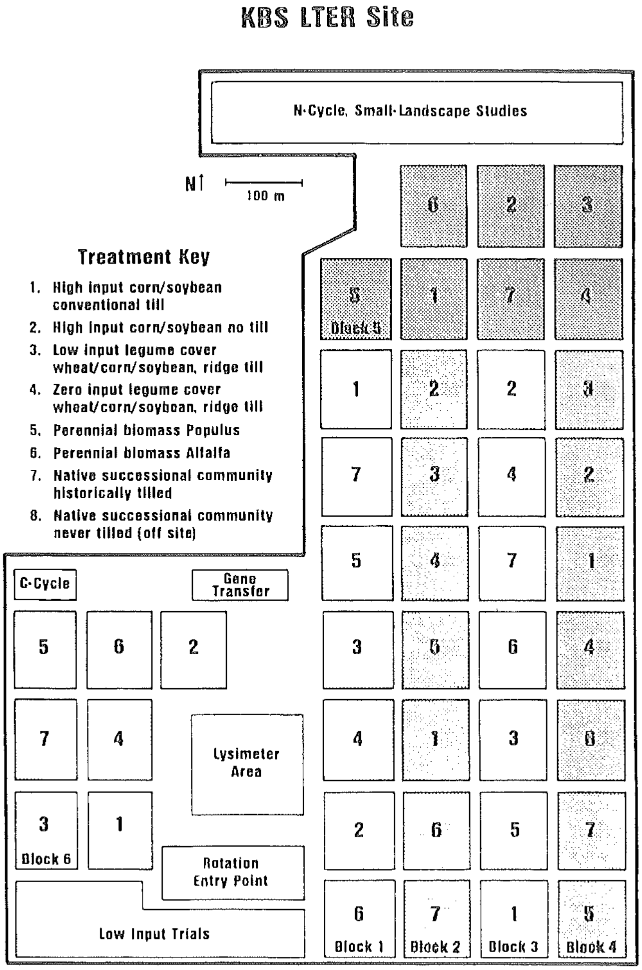



**Figure 2.** Site diagram and description of the main experimental treatments in the KBS LTER project.

## FUTURE DIRECTIONS

Virtually all of the major questions outlined above are in early stages of inquiry, as our cropping system treatments were established in 1989. Thus, much of our future effort will be devoted to addressing the long-term questions posed above.

Since our original proposal, two additional areas of inquiry have developed in which we expect to contribute to the understanding of highly managed, disturbed ecosystems: microbial population dynamics and small-scale spatial heterogeneity. Rapid advances in molecular biology are providing us with the ability to follow specific groups of microorganisms in soil at a variety of taxonomic resolutions. This development, coupled with new mathematical techniques for quantifying spatial heterogeneity in soil, should allow us to begin examining the structure and function of *in situ* soil microbial populations with the same rigor and detail that plant ecologists now use to establish and investigate aboveground plant community dynamics. This will be especially useful for understanding the complex behavior of ecosystems with respect to trace gas production and carbon storage and, in particular, for providing further insight into ways to design managed ecosystems that are economically efficient and environmentally sound.

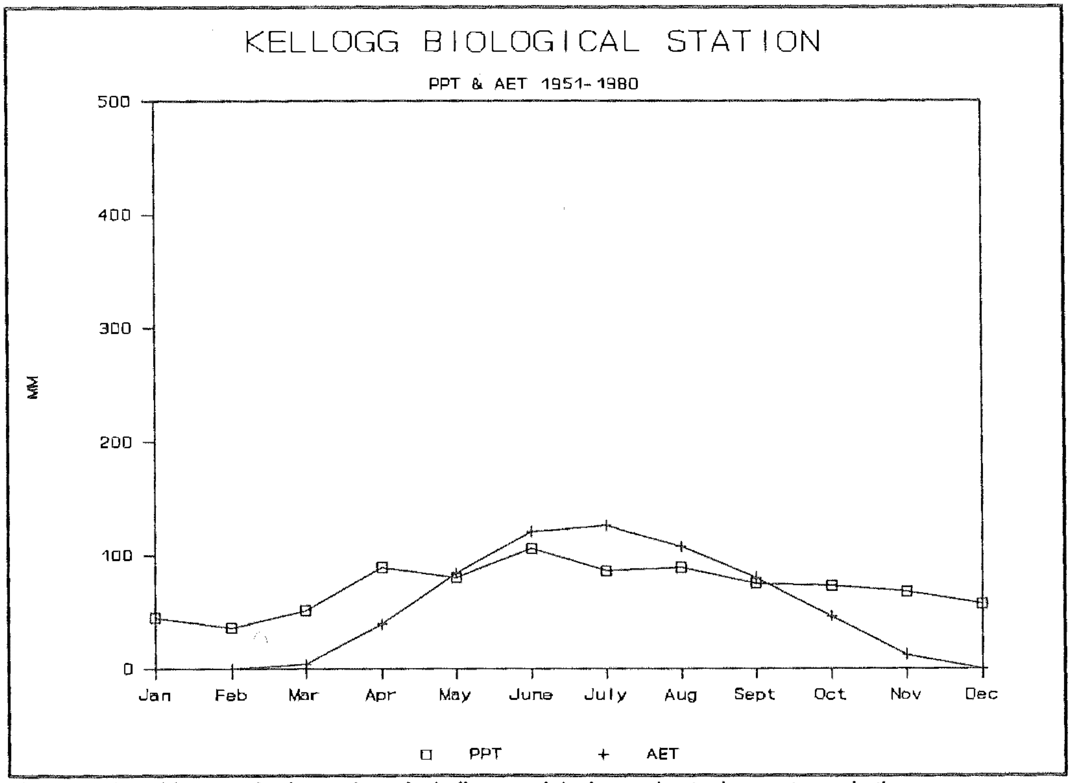



**Figure 3.** Monthly water budget values, including precipitation and actual evapotranspiration.

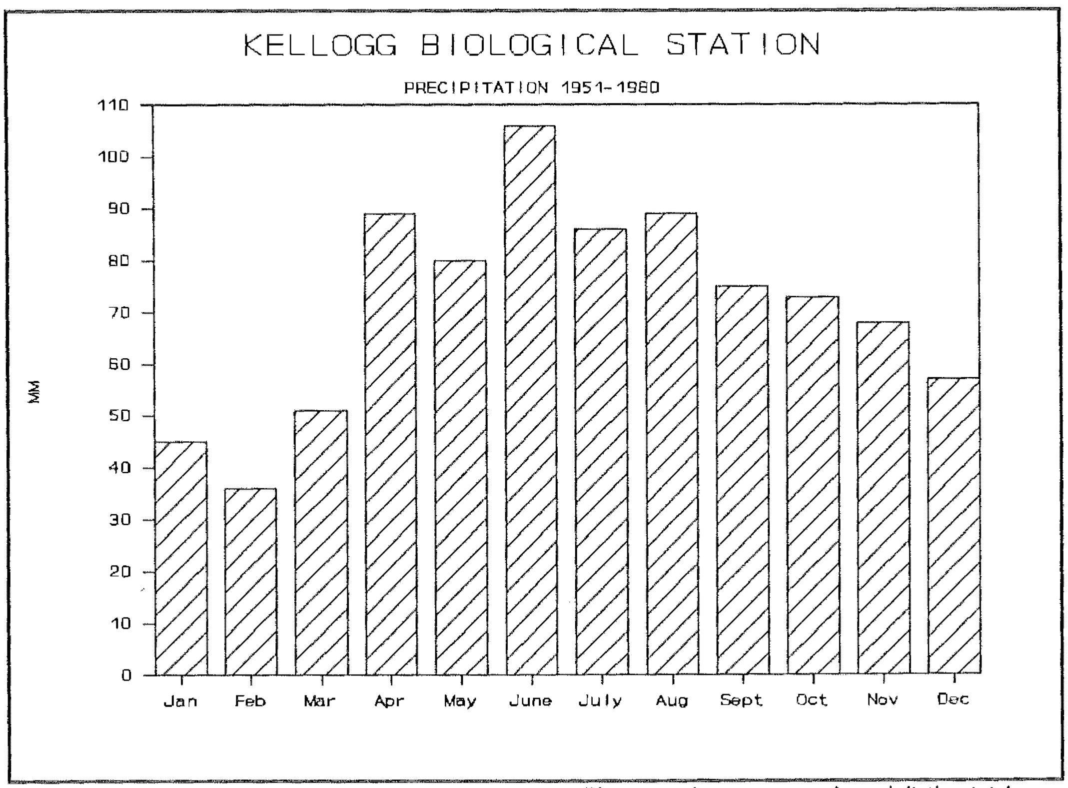



**Figure 4.** Average annual precipitation totals.

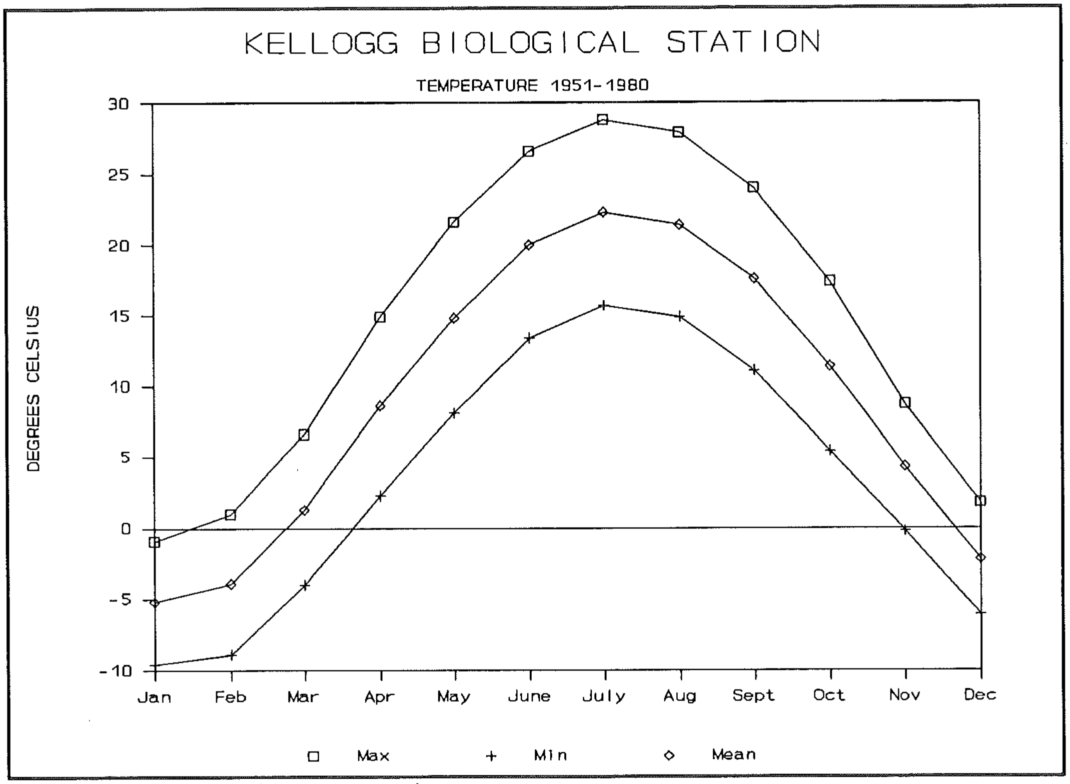
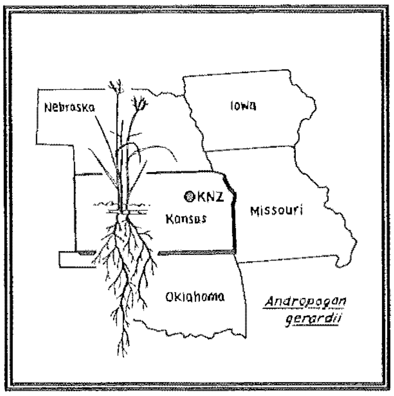



**Figure 5.** Average annual temperature values.

* Data from on-site or nearest weather station.




# Konza Prairie (KNZ)

## RESEARCH SETTING

The tallgrass prairie was North America's major humid grassland. The largest surviving tract of tallgrass prairie is found in the Flint Hills of eastern Kansas, with about 50,000 km$^2$ of unplowed native tallgrass vegetation. Konza Prairie Research Natural Area, a 3,400-ha tract 10-km south of Manhattan, Kansas is the largest parcel of tallgrass prairie in North America set aside for ecological research. Konza Prairie's development as a research site began modestly in 1971 after a portion of the site was purchased by The Nature Conservancy. Today, Konza Prairie is the most intensively studied grassland on earth. No other area has experienced the magnitude of research supported by the National Science Foundation (NSF), the National Aeronautic and Space Administration (NASA), the U.S. Geological Survey (USGS) and other agencies during the last 10 years.

Our Long-Term Ecological Research (LTER) program benefited from the intensive NASA-FIFE research effort operating at Konza from 1987 through 1989. FIFE (First ISLSCP Field Experiment; ISLSCP, the International Land Satellite Surface Climatology Project) has given us an appreciation for spatial scales and spatial patterns that are relevant and appropriate for LTER questions.

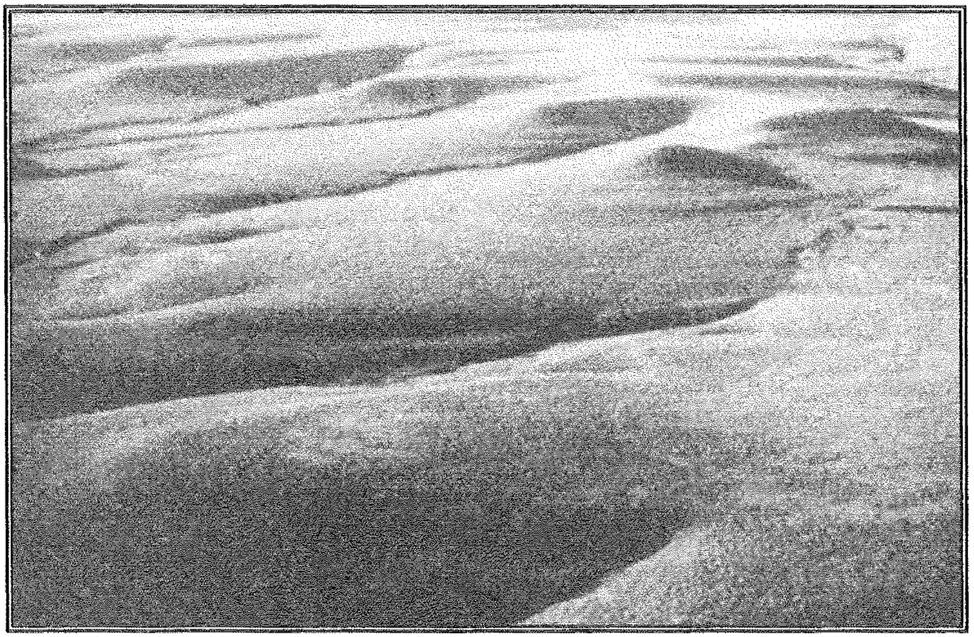
### *Site Characteristics*

Konza Prairie Research Natural Area is representative of the Flint Hills, a dissected upland with chert-bearing limestone layers. The ridges are usually flat with shallow, rocky soils, whereas the larger and wider valleys have deep permeable soils. The steep-sided hills are characterized by exposed Permian limestone and shale strata that prevented cultivation. Elevation ranges from 320 m to 444 m, with most of the land in the range of 366 to 427 m.

This native grassland is dominated by big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), Indiangrass (*Sorgastrum nutans*), and switch grass (*Panicum virgatum*). Slightly more than 6 percent of KNZ is wooded by gallery forest (narrow bands of woody vegetation along the stream channels). Dominant species include bur and chinquapin oaks (*Quercus macrocarpa* and *Q. muehlenbergii*) with green ash (*Fraxinus pennsylvanica*), hackberry (*Celtis occidentalis*), and American elm (*Ulmus americana*) common. The Kansas State University herbarium contains more than 470 species of vascular plants collected from KNZ. Species lists have also been compiled for birds, mammals, reptiles, amphibians, and aquatic invertebrates.

The climate is temperate mid-continental. Annual mean temperature is 13°C with a range of 6°C to 19°C. The January mean temperature is -3°C (ranging from -9°C to 3°C) and the July mean is 27°C (ranging from 20°C to 33°C). Annual precipitation is 835 mm of which about 75 percent occurs in the growing season. Mean snowfall for January is 150 mm; the annual total is 521 mm.

Konza Prairie serves as a benchmark for studies of agricultural and grazing land management-water quality relationships. The combination of NASA- and NSF-sponsored research has provided new insights into methods for studying vegetation-climate interactions. These interactions are hypothesized to be the causal links between traditional ecological and climatological interests and, thus, form a logical research emphasis for a national or international network of biosphere preserves. Facilitating this interaction is an objective of the 1991-1996 LTER effort.



*The Flint Hills of Kansas, Konza Prairie Research Natural Area, are the largest surviving tract of tallgrass prairie. They have unplowed lands because of the abundance of steep and rocky soils. KONZA*

Research conducted as part of the International Biological Program at other tallgrass sites emphasized effects of cattle on ecosystem dynamics. While we are interested in effects of large herbivores, bison were not established on Konza Prairie until autumn of 1987 and, to date, these animals have not been allowed on LTER intensive study sites. Research during the first 10 years of the Konza Prairie LTER program concentrated on fire, the major variable influencing tallgrass prairie. This background research on fire effects, in conjunction with previous research done on grazing, and the new, spatially explicit analytical techniques developed as part of the NASA-FIFE program, now allows study of complex aspects of fire, grazing and climatic interactions.

## RESEARCH PROGRAM STATUS

Konza LTER research encompasses a variety of questions within the realms of organismic, population, community and ecosystem ecology and attempts to integrate them (e.g., explain community dynamics in terms of population processes; explain system productivity in terms of ecophysiological processes; and explain landscape scale phenomena in terms of spatially explicit patterns of abiotic influences and population responses).

This diversity of approaches and interests is one of the program's strengths. Some of our questions or variables do not directly scale up to units necessary to provide a higher synthesis or to integrate ecological information from diverse sites. Nonetheless, such comparisons do provide insights into basic ecological processes, and explicit comparisons of organismic through ecosystem phenomena often contribute to a better appreciation of ecological concepts. For example, the evaluation of disturbance effects led us to the conclusion that the disturbance concept is useful only when applied to a specific level of the biological hierarchy; i.e., a disturbance to an organism or population is not necessarily measurable at higher levels. Moreover, the same "disturbance" produces potentially very different responses depending upon initial conditions of the system and forcing functions such as climatic variables.

Ecologists are only now developing methodologies and procedures to study the consequences of spatial patterns on organismic and ecosystem processes. Evidence is accumulating that spatially explicit interactions are the appropriate level for mechanistic interpretations of many ecological phenomena. Aggregation of this information using different formulae and approaches produces unique perspectives, all of which are potentially important for specific ecological questions. Therefore, we advocate this approach to the long-term study of fire and grazing effects on tallgrass prairie, and our studies involve landscape-level, spatially explicit analyses of organismic, population, community and ecosystem responses to fire, grazers, and climate interactions.

In spite of a rich history of ecological inquiry, important concepts basic to the functioning of tallgrass prairie have been overlooked or unappreciated. Prior to the mid-1960s, ecologists viewed fire as a destructive force, and the importance of fire for arresting forest invasion of prairie was not recognized. Possible reasons include: (1) decades of fire suppression were required for woody species to attain densities to provide an adequate seed source; (2) the droughts of the '30s and '50s suppressed woody expansion even in the absence of fire; and/or (3) in 40 years of existing study the emphasis was on grazed prairie. Fire under moderately to heavily grazed conditions may be a neutral factor. Tests of these hypotheses require a long-term, site specific data base on plant population and community dynamics such as that accumulating on Konza.

Previous landuse practices and biological legacies of previous communities affect current ecological phenomena. Our site exhibits large-scale patterns in plant species composition not attributable to current management treatments. The years 1981-1987 (the first seven of the Konza LTER program) all had annual precipitation values above the long-term average, and results from the period were affected by this unusual climatic pattern. Only in 1988 and 1989 were data representative of responses to below-average rainfall. Ironically, our own LTER group initially failed to recognize this potential "wet bias" in our results. Wet years favored plant production in general (and certain species in particular) which, in turn, increased the C:N ratio of the soil and, therefore, the soil N immobilization potential. As a result, stream chemistry exhibited directional changes and the production of the gallery forests (located "downhill" from the prairie) may have been similarly affected by a reduction in available N.

The extent to which demographic responses of individual plant and consumer species were influenced by this suite of wet years is not yet known. Only a long-term data base will demonstrate these patterns and relationships. This work becomes particularly relevant given anticipated directional changes in climate. Historical effects or biological legacies will be important in understanding the biotic response to climatic change. While some effects of drought on tallgrass flora are known, we are just beginning to develop predictive models for other system components.

### *Experimental Design*

Konza Prairie is a complex landscape consisting of grazed and ungrazed watersheds burned at various intervals designed to study fire and grazing effects on community and ecosystem processes. Each watershed encompasses complex topoedaphic gradients created by the limestone and shale layering of the Flint Hills landscape. Initial LTER questions focused primarily on the effects of late spring burns of varying frequencies on upland and lowland communities, or on the characteristics of one-, two-, four-, or 20-year burns. Not all treatments were replicated for LTER measurements, but replicated short-term intensive studies were used to statistically validate LTER findings. Our interest in grazing-fire-soil fertility interactions resulted in the establishment in 1986 of the LTER Belowground Plots, which do provide long-term, statistically valid comparisons among treatments. Ironically, while such information may be statistically valid, the generality of the results from small plot studies may be questioned because of the potential for "founder effects" on the system response.

Given our central questions involving fire-grazing-landscape interactions, the watershed series remains the best "experimental unit" for most of our research. We believe that grazing intensities (none, moderate, heavy) and topoedaphic effects can be nested within a watershed unit. In the past, we tended to study the extremes of annually burned versus long-term unburned prairie. We are continuing certain measurements and observations on those treatments, but substantial information suggests that annual burning or extended periods of fire suppression on any particular site were low-probability events, unlikely to persist for extended periods. Thus, expansion of the experimental design to include native grazer treatments and detailed analysis of fire-bison-topoedaphic interactions will focus only on sites burned at four-year intervals because this regime is most similar to estimated natural or pre-European settlement fire frequencies, and because expansion of sampling to include grazing and topoedaphic effects on *all* burn frequencies is not feasible.

Measurements on a watershed burned every four years means that data are actually gathered on sites burned in the year of study, or that have been left unburned for up to three years. By using four watersheds in this effort, at least one watershed will be burned each year; thus, major patterns of fire-grazing-climate interactions will be detected. As before, we will have to use short-term experimentation on replicated watersheds or plots to provide statistically robust interpretations of our observations. We also plan to use remote sensing and geographic information systems (GIS) to offer spatial pattern measurements at various scales for the treated watersheds.

We plan to introduce bison to the new intensive study sites in autumn of 1991. All LTER plots are permanently marked, and a cessation of measurements on certain sites does not preclude their resumption, either intermittently or more intensively, at a future date. Fire treatments will be continued on all Konza Prairie watersheds.

## *LTER Hypotheses & Questions*

### Controls of Net Primary Productivity (NPP)

- Ungrazed tallgrass prairie exhibits energy, water and N limitations, with the intensity of the limitation determined by the specific combination of climate, topography and fire frequency.
- Grazing negates the effects of fire as an ecological variable but often induces similar effects.
- Grazed vegetation exhibits a susceptibility to water stress. Thus, production will be diminished in the second year of drought and recovery from drought effects will be slower on grazed sites.
- Soil nutrient availability will improve during drought on grazed sites.
- Because grazed vegetation will lack the root surface area to exploit higher levels of available nutrients in soils once water is no longer limiting, the production response on grazed prairie will be less than that observed on ungrazed sites.
- Light and moderate grazing, like fire, will stimulate foliage productivity in most years; however, heavily grazed sites will most resemble floras from the shortgrass prairie and/or contain elements of the flora of the Southwest.

### Organic Matter Dynamics

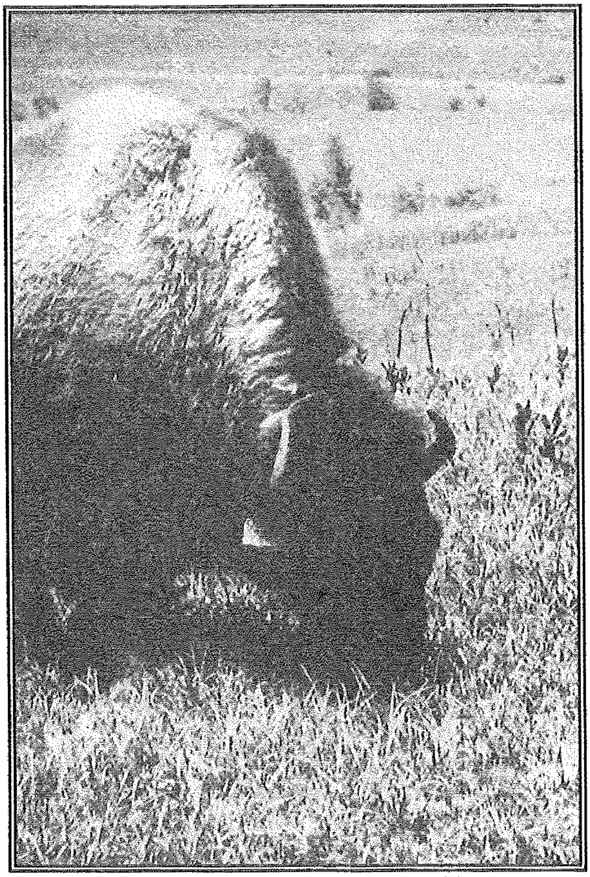
- Sustained annual burning will result in a decline in soil organic matter.
- Since plant nutrient availability is dependent upon decomposition, microbial immobilization of nutrients and turnover of the active fraction of soil organic matter, fire will result in tighter coupling of plant and microbial N dynamics.
- The input of higher C:N ratio plant material will result in an increase in the proportion of fungi compared to bacteria.
- Grazing in tallgrass prairie reduces the C input and the C:N ratio of the above- and belowground plant biomass: grazers may negate the fire effect. The decrease in C quantity and quality (C:N ratio) as a result of grazing reduces the soil N immobilization potential. Microbial biomass C and N is also reduced with grazing frequency.

### Nutrient Dynamics

- Nutrient outputs from watersheds are less than inputs except during years marked by high-intensity, low-frequency runoff events (floods). Long-term drought will result in an increase in N concentrations of groundwater and (if present) streamwater.
- Sustained experimental phosphorus enrichment of tallgrass prairie will eventually stimulate the appearance of N-fixers.
- Soil and stream water nitrate concentrations will increase in response to grazing intensity due to the reduction in soil N immobilization potential.
- Aboveground NPP will be maximized by an intermediate intensity of grazing because of the increase in soil inorganic N availability.

### Population Studies

- Bird, small mammal, and grasshopper densities are governed by resource/competition interactions, as mediated by experimental treatments.
- We hypothesize that certain forbs should benefit from short-term drought, which may improve soil



*Grazing is a natural part of the tallgrass prairie ecosystem. Bison were added to part of the prairie in 1987.* KONZA

nutrient status via reduced immobilization and/or reduced plant competition for nutrients while deep soil water remains available. Thus, although frequent burning may result in declines in many forb populations relative to $C_4$ grasses, this may be offset by an enhancement of forbs in drought years due to enhanced nutrient availability.

- Grazers can increase species diversity by either increasing habitat heterogeneity or by reducing the competitive dominance of the dominant perennial grasses. The former mechanism should primarily influence species richness, whereas the latter is predicted to strongly influence the evenness component.
- The interacting influences of native ungulate grazers and fire over the topographic gradient will result in unique patterns in species abundance, distribution, and diversity at different spatial scales. We predict that local abundances and within-population diversity of plant species can be explained by predictable effects of fire, grazers and their interactions on plant growth dynamics and sexual and vegetative reproduction.
- Grazing by bison will result in different responses among co-occurring plant species and shifts in plant community structure, and these grazing effects may be a result of both *direct* effects on plants and *indirect* effects on mycorrhizal abundances and resulting shifts in competitive relationships between $C_3$ and $C_4$ species.

## Studies Related to Global Questions

Ecosystem-Climate Relationships. We are addressing several questions revelant to issues of global climate change. These include the following: How do fire, grazing and fire-grazing interactions influence processes and patterns in tallgrass prairie and the response of the prairie to climate forcing functions? What will be the ecological response (biophysical, ecosystem, community, population, organismic) to climate change given current land use? How will modification of experimental treatments (representing Flint Hills landuse patterns) influence the persistence and characteristics of the system? How much control does the biota have on microsite and local climate, and how might these controls be modified by fire and grazing intensities or frequencies? Can patterns observed for the tallgrass prairie be extrapolated to other LTER sites?

Ecology has traditionally focused on the organism-to-ecosystem hierarchies, but efforts are now underway to predict ecosystem to landscape and regional scales. Ecologists must be able to scale research questions to the landscape level in order to integrate the importance of their research to the regional scale and to broader scales where implications for climate change are meaningful. Understanding the landscape controls or constraints on ecological phenomena therefore become a critical LTER question.

The Ecological Significance of Spatial Patterns. How do position in the landscape and landscape interactions affect ecological phenomena in tallgrass prairie, and what is the importance of the interaction of edaphic and climatic variables on biotic processes? How do landforms affect processes in tallgrass prairie? The neutral hypothesis (spatial patterns do not affect the variable of interest) has been implicitly negated by all Konza researchers. Analysis of the importance of geomorphic patterns and landscape position on ecological processes is underway at scales ranging from plant leaf to watershed levels.

### *New and Continuing Research*

In addition to continuing the long-term study of tallgrass prairie patterns in relation to fire/climate, we are expanding the LTER study significantly to (1) assess the role of fire/bison grazing interactions on populations, community structure, net primary production (NPP), organic matter, and nutrient dynamics; (2) conduct a more spatially explicit analysis to patterns of variation across topographical gradients; and (3) analyze patterns at larger spatial scales by linking analysis of population, community, and ecosystem properties with patterns detected at the landscape level using remote sensing, GIS and simulation modeling. The central question and goal of the research is to understand how grazing influences biotic and ecosystem processes and patterns imposed by fire frequency over the landscape mosaic, all of which are subjected to a variable (and possibly directional) climatic regime.

### *Intersite & Network Activities*

Researchers from our site were among the first to participate in multisite LTER studies, helping to develop the data management system now used at a number of LTER sites, and comparing the N and P sensitivity of streams in five different biomes. Konza LTER is cooperating with four other LTER sites and the LTER Network Office in developing a distributed intersite climate dtaabase for ecological research. This system could serve as a prototype for access to other ecological data. The list of ongoing multisite projects involving Konza Prairie and LTER investigators is rapidly increasing. Eight of 19 federally supported projects on Konza Prairie during the current five-year period have involved at least one additional site. In addition, several proposed multisite projects involving Konza are pending at NSF.

We are currently working at a number of spatial scales above our individual site. We have established relationships with a network of tallgrass prairie sites including at present: Fermilab (Illinois), Tucker Prairie (Missouri), The Land Institute (Kansas), and three Nebraska sites (Allwine Preserve, Arapaho Prairie, and Niobrara Preserve), as well as a group interested in comparing native prairie and agroecosytem properties. An example of this regional interaction occurred in 1986-87, when LTER data sets were used in a preliminary evaluation of the status of nearby tallgrass prairie sites used for military training activities.

Konza personnel are active participants in the LTER and associated networks. Collaboration currently exists for several initiatives, including modeling, data management, stable isotope and stream studies, remote sensing/GIS, decomposition and organic matter dynamics, and global climate change.

### *Related Research Projects*

The NASA FIFE project (1987-present) represents a study of a size and scale previously unknown to ecologists; it dwarfs even the grasslands International Biosphere Program (IBP) work in terms of number of scientists involved, funding, data acquisition, and data management. The significance of this effort to current LTER efforts cannot be overstated. If ecologists are to become active participants in the global change arena, they must be able to interact with biophysicists and atmospheric scientists and be capable of providing data appropriately scaled for vegetation-atmosphere studies. Biological processes and ecological constraints have extremely large influences on regional climate, for both the short- and long-term. This fact has yet to be integrated into general circulation models. Until such information is incorporated, these models cannot provide realistic long-term predictions.

Thus, the Konza Prairie group has an important responsibility to the scientific community. First, we must provide proof-of-concept projects and studies using the FIFE data and, second, we must preserve the FIFE data base (FIS) to guarantee its availability to ecologists. Our current cooperative study with CSU, and our own NASA projects, should contribute towards the first goal. We are also exploring avenues of obtaining a functional archive of FIS with personnel at NASA.

Collaborative research with CSU is examining the influence of tallgrass prairie biota on $CO_2$ and $H_2O$ exchange with the atmosphere. This examination is at a finer scale than the FIFE project and thus complements and builds upon that experiment. Measurements of foliage N content, leaf chlorophyll, plant water status, net photosynthesis, transpirational water loss, and aboveground biomass have been made on transects spanning topographic gradients. These data are being correlated with canopy spectral reflectance measurements made at CSU to provide the key links in the modeling efforts of CSU colleagues. The influence of fire on these relationships is also being studied. Ultimately, these data will be combined with landuse patterns to develop a regional model of biosphere-atmosphere interactions that can be nested within global climate models.

Work has begun on a time-domain reflectometry (TDR) system in conjunction with the transect studies. TDR provides real-time measurements of soil moisture along a topoedaphic gradient, and these data, in conjunction with photosynthesis, water stress, production and N data should provide a robust perspective of plant-nitrogen-water relationships, as mediated by the Flint Hills topography. Should the system provide useful data not obtainable with current methods (neutron probes), we will attempt to install a system for the LTER transects.

With support from NSF, Konza researchers are conducting a study entitled, "Phase-space ordination and the complexity of successional trajectories." The complexity of the successional trajectory will be quantified using long-term data sets at Konza Prairie, Cedar Creek, and Sevilleta LTER sites.

An effort is underway by the USGS and State of Kansas Cooperative Studies to characterize soil water and groundwater conditions within a watershed. Four transects perpendicular to the stream channel were instrumented with 58 lysimeters and 20 observation wells in late winter of 1988. Lysimeters were installed in the A, B and C soil horizons to sample the unsaturated zone, and observation wells were installed in the Morrill and Eiss Limestone Members (Lower Permian). Water samples analyzed for dissolved organic C and nitrate had greater concentrations in the unsaturated zone than in groundwater, indicating a decrease in these constituents during transport from soil to groundwater. Future work will focus on the reasons for the Dissolved Organic Carbon (DOC) and nitrate decrease and the identification of DOC biomarkers that can be used as tracers in the transport of water and natural compounds from the soil to groundwater.

## FUTURE DIRECTIONS

The availability of GIS and remote sensing techniques now allows us to make full use of Konza's robust experimental design, and several projects are already underway. A Konza Prairie geomorphology map is being digitized onto the GIS. Maps indicating soils, elevation, slope and aspect, and watershed boundaries are already on the GIS. Our current holdings of satellite images will be augmented with additional TM scenes as these become available.

Additional funding is being sought to acquire a functional archive of the FIFE data set, which contains over 30 gigabytes of data on KPRNA and adjacent areas. In conjunction with this project, we are seeking outside support to re-establish some of the fine temporal resolution biophysical measurements of mass, energy, momentum and $CO_2$ flux originally obtained by the FIFE project.

An analysis of gallery forest wood growth dynamics is planned. This dendrochronological study will allow us to compare forest wood production with our prairie foliage NPP record, and test several predictions regarding controls on the respective systems. The dendrochronological analysis will also complement LTER studies on the dynamics and spatial patterns of woody plants by providing information on wood, plant population structure and past recruitment patterns. These data will also be integrated with climate/ hydrological pattern issues studied by the "Wet Group."

Spatial modeling at the landscape or regional scale demands a high degree of concurrent processing in order to simulate efficiently (and naturally) the nested spatiotemporal hierarchies intrinsic to ecological processes. Accordingly, we intend to implement an integrated soil-water-vegetation model on a fine resolution parallel processor. We shall be able to map the Konza Prairie landscape by specifically programming the topology of the processors to mimic our link-node representation of watersheds. Climatic variables, disturbances and other forcing variables are introduced into the "landscape" through a host computer which represents a cutting-edge technology that holds great promise for ecological modeling.

National Science Foundation-sponsored research projects recently initiated on Konza Prairie include a study of the role of mycorrhizal relationships in determining plant population and community patterns, research designed to identify the mechanisms of persistence of tallgrass prairie forbs (important for biodiversitiy in tallgrass prairie) within a "sea of grass," and studies of trace gas flux from experimental watersheds. These projects, and others like them which involve a multidisciplinary approach and collaboration with researchers from other academic institutions, are evidence of the value and success of the site-based LTER program at Konza Prairie. Our future short- and long-term research efforts at Konza will continue to build upon our rich tallgrass prairie data base as well as LTER Network initiatives. Together, these provide us with opportunities to address complex ecological issues that demand information at temporal and spatial scales only accessible through the LTER program.

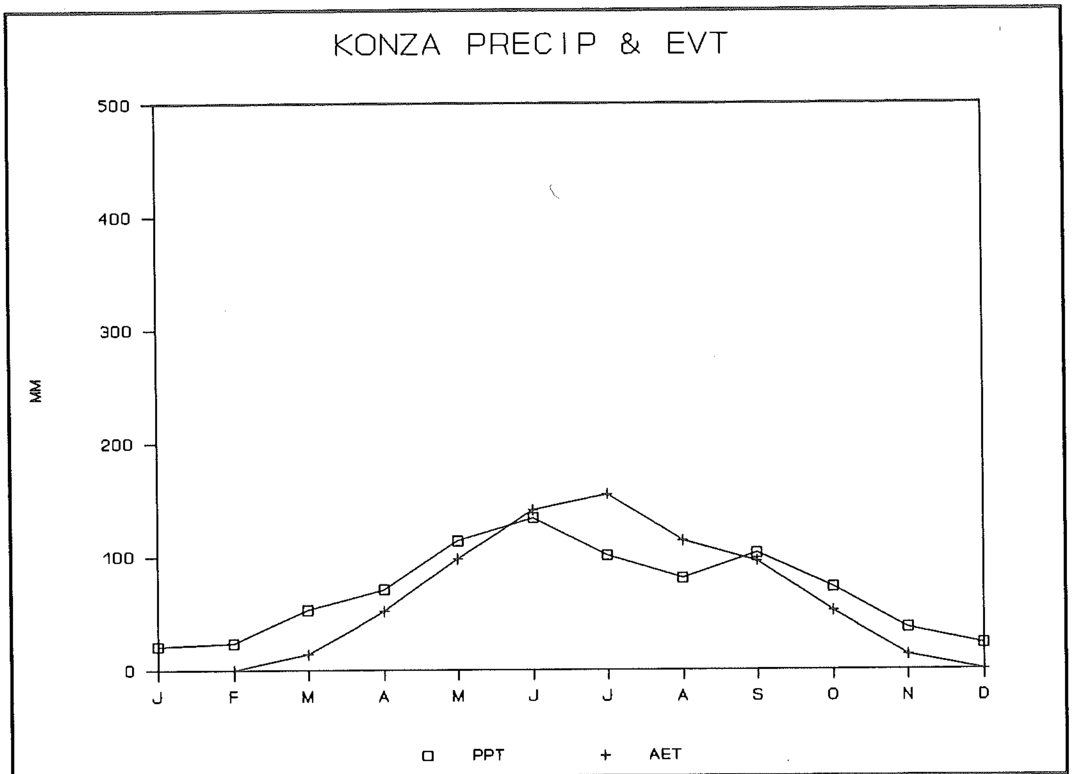



**Figure 1.** Monthly water budget values, including precipitation and actual evapotranspiration.

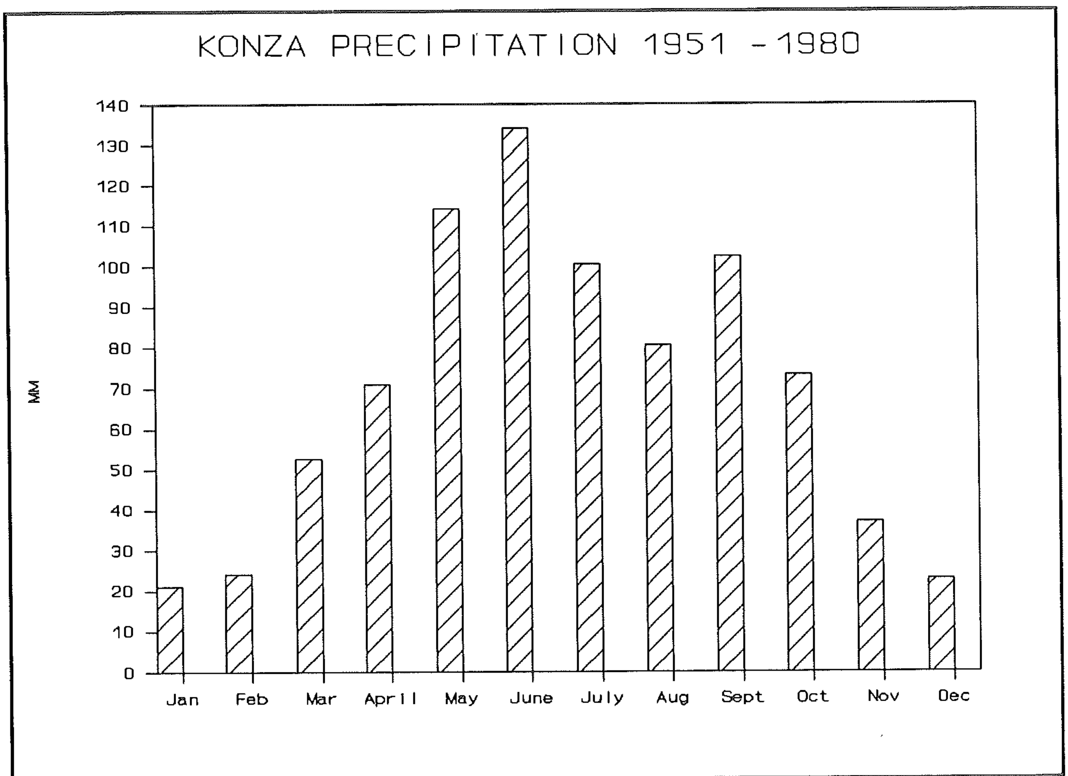



**Figure 2.** Average annual precipitation totals.

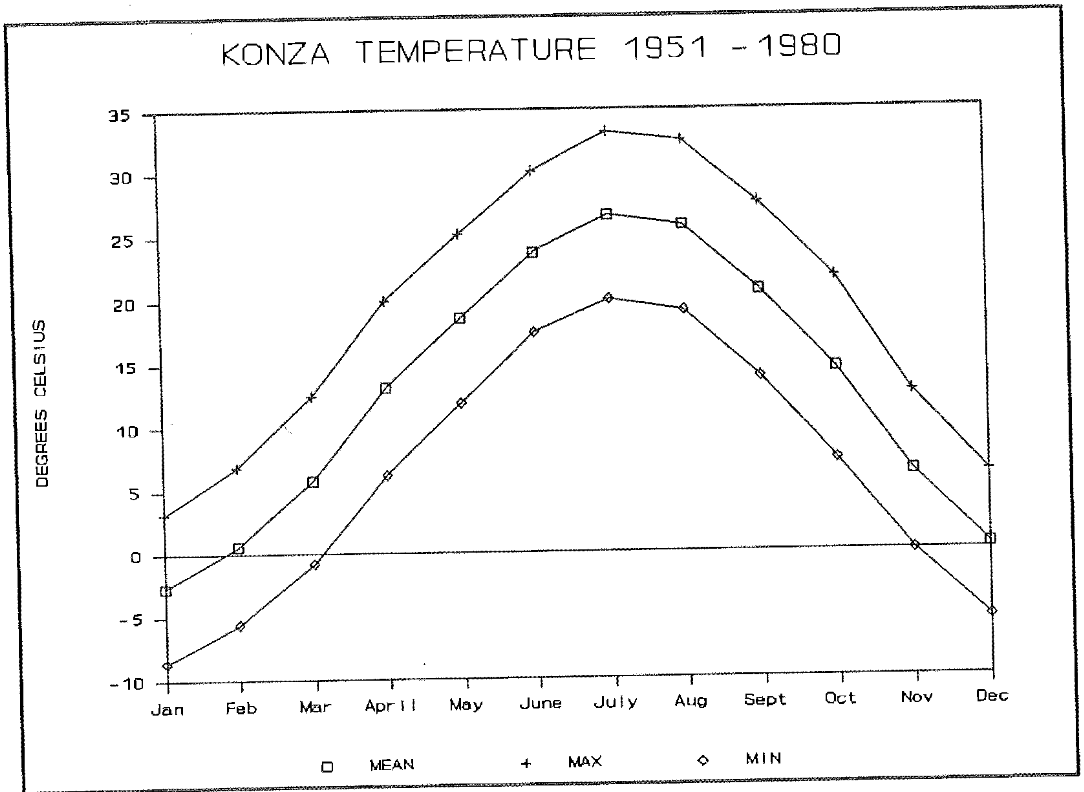
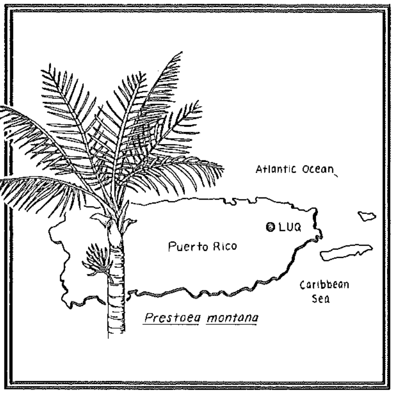



**Figure 3.** Average annual temperature data.

* Data from Manhattan, Kansas.




# Luquillo Experimental Forest (LUQ)

## RESEARCH SETTING

Periodic visits by hurricanes and tropical depressions in the Caribbean and their interaction with steep topography offer an opportunity to study long-term responses of complex ecosystems to natural disturbances. Researchers from the University of Puerto Rico, the Institute of Tropical Forestry, and 15 other institutions are conducting long-term studies of the relationship between disturbance regime and forest structure in the Luquillo (loo-KEY-yo) Experimental Forest LTER site in Puerto Rico. The objectives of these studies are: (1) to investigate the relative importance of different types of disturbance within the four life zones constituting the landscape of the Luquillo Experimental Forest, and (2) to analyze the importance of the biota in restoring ecosystem productivity after different types of disturbance within representative watersheds in one of these life zones.

Research at the site began over 100 years ago with a series of botanical explorations. Over 400 publications record the results of this activity up to 1980. Portions of the research site were protected by the Spanish Crown as early as 1860 and transferred to the U.S. government in 1898. In 1939 the USDA Forest Service established a research station whose mission was to study and manage the forest ecosystems of the Luquillo Mountains. Today, the Institute of Tropical Forestry is among the oldest tropical forestry research institutions in the hemisphere and is the oldest among U.S. government facilities, including those in Hawaii and Costa Rica.

The Luquillo Experimental Forest (LUQ) was established by the USDA Forest Service in 1956 to recognize the growing importance of research work undertaken there. Early research sponsored by the Forest Service at Luquillo emphasized long-term studies of tree growth and the management of tropical forests. In 1963, the U.S. Atomic Energy Commission (AEC) established a research project at the El Verde Field Station to study the structure and function of the forest ecosystem and to investigate the effects of gamma irradiation on ecosystem processes. This research program continued uninterrupted under the auspices of AEC and later the U.S. Department of Energy for 25 years. Since the initiation of the Luquillo LTER program in 1988, approximately 100 scientists and about 60 graduate students have used the site each year for research. Over 100 research projects are currently being undertaken.

To preserve genetic diversity and remnant virgin tracts representing the forest types indigenous to the area, an 850-hectare "Baño de Oro" Research Natural Area has been established within the Luquillo Forest, and the El Cacique Wilderness Area has been proposed. The Forest has also been designated as a research site for the U.S. Geological Survey's (USGS) Water, Energy, and Biogeochemical Budget (WEBB) program. An investigation of the controls of primary productivity along an elevational gradient has been initiated through the National Science Foundation's Minority Research Centers of Excellence (MRCE) program.

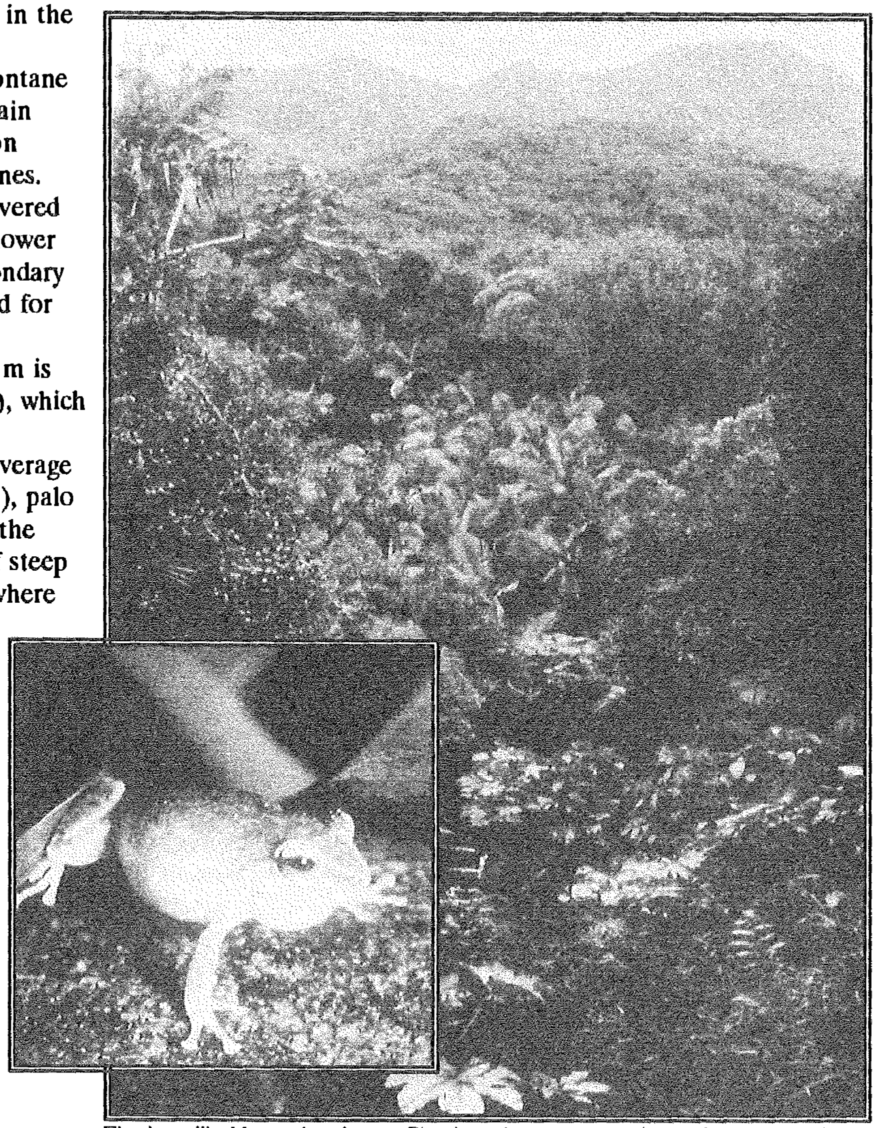
## *Site Characteristics*

The Luquillo Experimental Forest, encompassing elevations between 100 to 1,070 m in the Luquillo Mountains in eastern Puerto Rico, is a National Forest and a Biosphere Reserve, and contains several research natural areas within its 11,231 ha. Four life zones occur in the Forest (subtropical wet forest, subtropical rain forest, lower montane wet forest, and lower montane rain forest), and four major vegetation associations occupy these life zones. The higher elevations remain covered with virgin forest, although the lower elevations are forested with secondary growth, having been once cleared for agricultural purposes.

The dominant tree below 600 m is the tabonuco (*Dacryodes excelsa*), which is best developed on protected, well-drained ridges. Above the average cloud condensation level (600 m), palo colorado (*Cyrilla racemiflora*) is the dominant tree except in areas of steep slope and poorly drained soils, where the palm *Prestoea montana* occurs in nearly pure stands. The dwarf forest occupies ridge lines and is composed of dense stands of short, small-diameter trees and shrubs that are almost continually exposed to winds and clouds. Both the palm and dwarf forests are dominated by only a few plant species. Tree height, number of species, basal area, average tree diameter at breast height (dbh), and complexity index decrease with elevation; stem density increases.

The Luquillo mountain range intercepts several global airsheds, including northeast trade winds, cyclonic activity originating in East Africa, northern fronts produced at high latitudes over continental North America, and cloud systems from the Amazon Basin. Annual precipitation in the Forest ranges from 2,500 to over 5,000 mm, while mean temperatures range from 25.5°C at the lowest elevation to about 18.5°C above 1,000 m.

More than 225 tree species are native to the Forest (23 of these are endemic, and 88 are rare), and 47 tree species have been introduced. About 50 species of native orchids and 150 species of ferns exist in the Forest. Also, 100 vertebrate species occur, including 11 native mammals (all bats), eight lizards of the genus *Anolis*, 16 small frogs of the genus *Eleutherodactylus*, and nine shrimp species. Sixty-six bird species occur in the Forest, which contains all of the existing habitat for the endangered Puerto Rican parrot.



The Luquillo Mountains. **Inset:** *Eleutherodactylos portoricensis.* R. GARRISON

*Landslides are an important disturbance type in the Luquillo Forest.* ROBERT B. WAIDE

## RESEARCH PROGRAM STATUS

Hurricane Hugo (September 1989) created opportunities for the Luquillo Experimental Forest LTER program (LUQ) to study forest regeneration processes, as well as those stemming from regional and global-scale environmental change. The history of disturbance is well-known through measurements of long-term observation plots established by the U.S. Forest Service in the 1940s, although ecosystem responses have not been thoroughly investigated for each type of disturbance.

The major forms of disturbance in this humid tropical forest are natural treefalls, landslides, hurricanes, and selective cutting. The integral role of disturbance has been emphasized by computer simulation of actual relative abundances of tree species, using a forest dynamics model that incorporated treefalls and hurricanes.

Components of the LTER program include the examination of:

- pattern, frequency, and intensity of disturbance (treefalls, landslides, and hurricanes);
- environmental properties that are expected to vary with disturbance size, age, and origin (light, nutrient availability, moisture, temperature, and soil organic matter);
- biological properties that are expected to vary with environmental properties (species composition, growth, nutrient dynamics, reproductive success, carbon fixation, and food web structure); and
- system properties that emerge from the effects of disturbance pattern and frequency on the mutual interaction of abiotic environment and biota (nutrient cycling, phases of recovery, rates of recovery, and displacement from and return to steady state).

Tropical forestry research in Puerto Rico has already produced observations that suggest certain patterns of biotic response to both large- and small-scale phenomena. For example, the estimated age of large colorado trees (*Cyrilla racemiflora*) and palms (*Prestoea montana*) can be related to hurricanes in 1867 and 1932, respectively. Studies show that frequently measured forest parameters such as biomass, tree density, number of tree species, basal area, wood volume, wood density, above-ground primary productivity, and complexity index will change in predictable patterns over periods of 40 years following hurricanes. Variation in annual rainfall that is unrelated to hurricane events can also elicit biotic responses, since periods with more frequent and higher rainfall increase the probability of landslides and can result in a doubling of annual stream runoff. Because hydrologic fluxes are critically important to many ecosystem processes, infrequent but large fluctuations in rainfall will have significant effects on ecosystem functions such as organic matter export, nutrient cycling, and productivity. Long-term records are necessary to measure and understand such infrequent events.

### *Long-Term Field Studies*

Research related to the LTER program at Luquillo has been focused on three major areas. Mathematical modeling is an integral part of each of these research areas.

**Disturbance Regime:** Frequent human-related and natural disturbances to the Forest have created a mosaic of areas in various stages of succession, where the major forms of disturbance are natural treefalls, landslides, hurricanes and selective cutting. By far the greatest disturbance in recent years has been Hurricane Hugo, which significantly affected the Forest in September 1989.

Using aerial photography, satellite imagery, and long-term plot data, we are determining the frequency, size class distribution, and spatial distribution of the major disturbance types in the Forest. Mathematical models of hurricane characteristics are being used to generate information on the effects of historical storms. Research results suggest that disturbance intensity is regulated in part by stage of vegetation development. Topography and bedrock characteristics are also important in regulating the frequency and spatial distribution of disturbance because of the high relief, diverse hillslope aspects, and varied geologic conditions.

*Table 1. The range of tree (> 10 cm dbh) mortality and turnover time as a result of background and catastrophic mortality in the Luquillo Experimental Forest. Hurricanes of the intensity shown have a return time of 60 years. In the absence of hurricanes, background mortality results in a turnover time for trees that is less than the hurricane return time. Hurricane and gap data are from the LTER site at Bisley.*

| Type of disturbance | Tree mortality | Turnover time (stems/ha.100 yr) |
|---|---|---|
| Background (all causes but hurricanes) | 1973-2650 | 49 |
| Treefall gaps | 100-266 | 380* |
| Hurricanes | 472 | 116 |

* based on the average mortality (144 trees/ha.100 yr)

**Environmental Correlates of Disturbance:** Past and ongoing research serve to quantify the changes in environmental parameters that occur after disturbance in order to understand regeneration mechanisms. An extensive data base on general climate and gap environments exists for the tabonuco forest, as well as data on light availability, soil moisture, and soil nutrient levels for tropical forest disturbances in general. Hourly, daily, and monthly records of insolation, illumination, temperature, humidity, rainfall, wind, evaporation and carbon monoxide levels from the Rain Forest Irradiation Project at El Verde are available for the period 1963-1966 for comparison with present-day records. Data on these parameters in gaps and through vertical profiles within tabonuco forest are also available.

**Biotic Response to Disturbance:**

*Plant succession* - The processes by which a disturbed patch of forest regenerates is a major focus of the LUQ LTER. Revegetation after disturbance alters abiotic and biotic variables with the amplitude and direction of change strongly dependent on the severity and scale of the initial disturbance. Disturbance within the Luquillo Forest can be categorized along a continuum of area from small to large gaps, and along a continuum of severity from tree falls to hurricanes and landslides. Pathways of succession vary depending on initial conditions and the type and severity of the disturbance.

*Nutrient cycles* - Baseline data collected before Hurricane Hugo allowed us to examine changes in ecosystem storages and fluxes as a result of the hurricane. The reorganization of system structure and the transfer of large amounts of mass between ecosystem compartments had profound short- and long-term effects on nutrient cycles. Monitoring of the affected ecosystem components over the life of the LUQ LTER will permit evaluation of the long-term effects.

Nutrients stored in vegetation serve as an index to the rate of nutrient recovery and indicate mechanisms for nutrient conservation after disturbance. An initial inventory of above- and belowground C, N and P in both disturbed and surrounding undisturbed vegetation was conducted prior to Hurricane Hugo. A total nutrient budget is being estimated by the inclusion of soil analyses.

Comprehension of the dynamics of soil organic matter is a critical factor in understanding fluctuations of soil nutrients after disturbance. Changes in soil organic matter, C, N, and P over time provide information on the relative role of root vs. leaf litter on soil organic matter formation, on the impact of different leaf litter application rates on soil organic matter formation, and on the influence of different types of disturbance and time since disturbance on soil organic matter formation.

*Plant and animal population studies* - Population studies of key plant and animal species are critical to the understanding of both community and ecosystem processes. Studies consisting of systematic observations on life history and organism-environment relationships were initiated for animal and plant species as part of the routine work at the LUQ LTER. However, after Hurricane Hugo these studies acquired new meaning and value to the program. The two traditional study sites of the program (Bisley and El Verde) became the two poles of a new environmental gradient, that of hurricane disturbance. Paired studies of animal and plant populations (coquis, lizards, bats, birds, shrimp, walking sticks, palms, tabonucos, ausubos, and others) are now providing critical information about how organisms cope with various intensities of disturbance, i.e., how they respond to natural stress gradients. Addressing organismal response to hurricane disturbance in paired studies across a gradient of damage is central to the main question of this program, i.e., how the forest biota copes with, and maintains homeostasis in, the stressful conditions of the Forest.

## FUTURE DIRECTIONS

The evaluation of hurricane effects has once again underscored the importance of environmental gradients in the Luquillo Forest. We are in the process of surveying large forest areas for damage and have expanded our traditional focus on two sites (El Verde and Bisley) to include sites with intermediate levels of response to Hurricane Hugo. The addition of the WEBB, Global Change, and MRCE programs to the LTER represents a significant leap towards understanding landscape gradients both in the Forest and on a regional scale in the Caribbean Basin. We see our program evolving towards a closer examination of the many gradients that operate in the Forest.

We anticipate a greater effort in the accurate depiction of the geographic and topographic location of studies (possibly using global positioning systems) and the measurement of local environmental conditions at each of these locations. Only through such a strategy will we be in a position to apply the powerful tools of modeling and GIS being developed in this first phase of research. These modeling and GIS tools provide the capability to accurately extrapolate our measurements to the landscape and study patterns over time scales that range from the instantaneous to millennia.

## * LUQ Climate Record 1951 - 1980

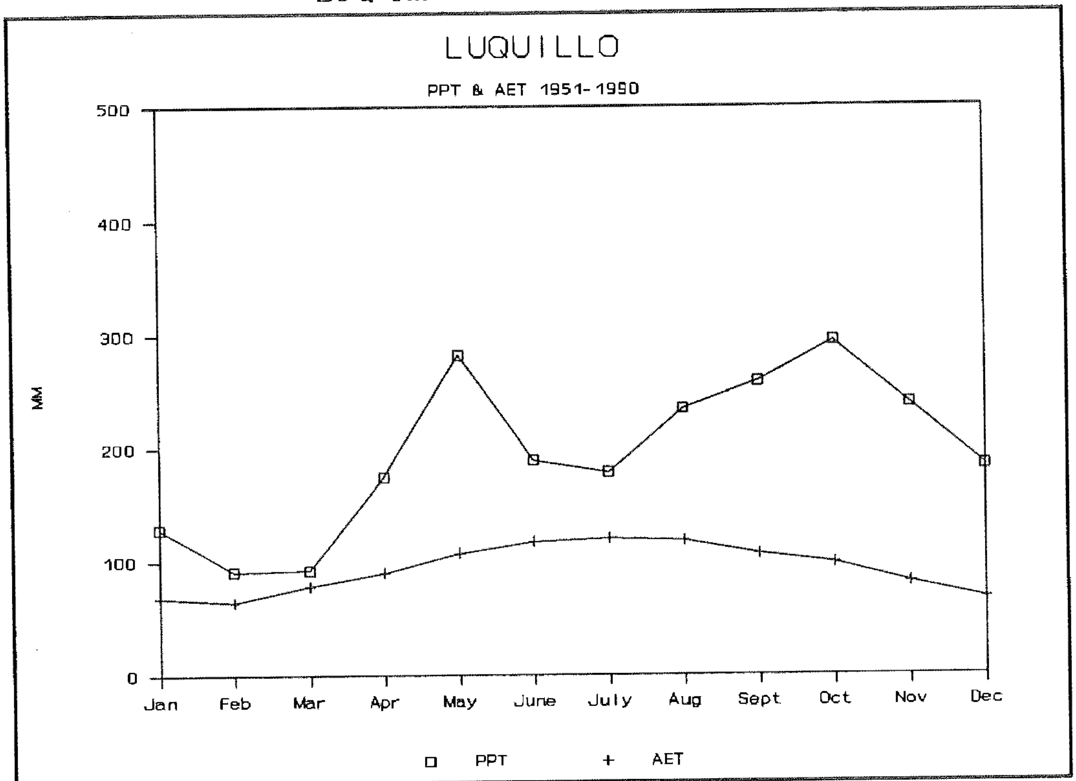



**Figure 1.** Monthly water budget values, including precipitation and actual evapotranspiration.

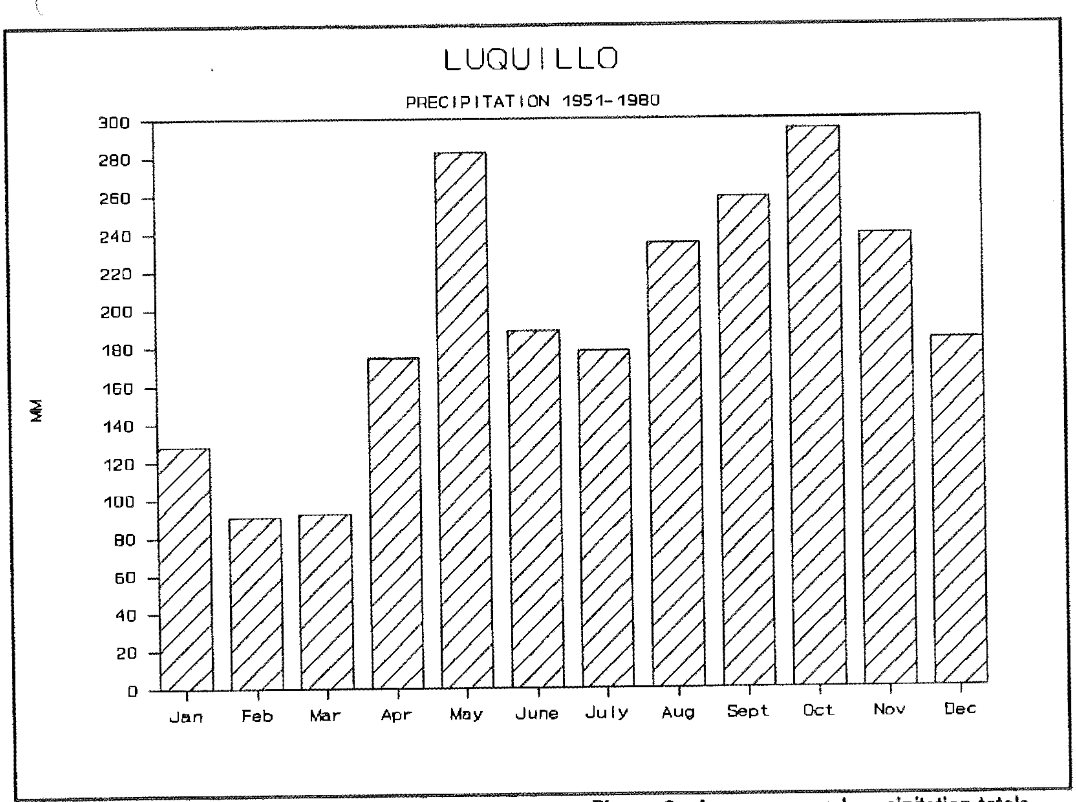



**Figure 2.** Average annual precipitation totals.

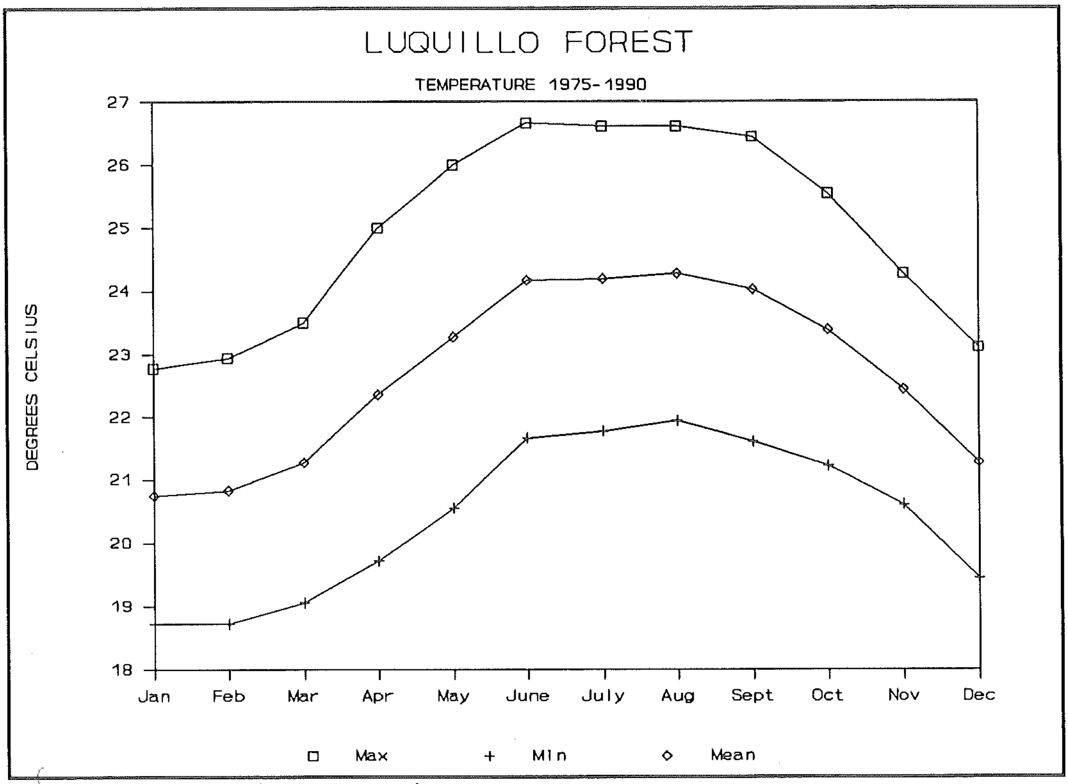
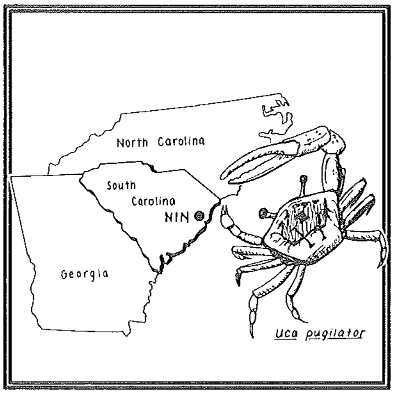



**Figure 3.** Average annual temperature values.

* Data from on-site or nearest weather station.




# North Inlet Marsh (NIN)

## RESEARCH SETTING

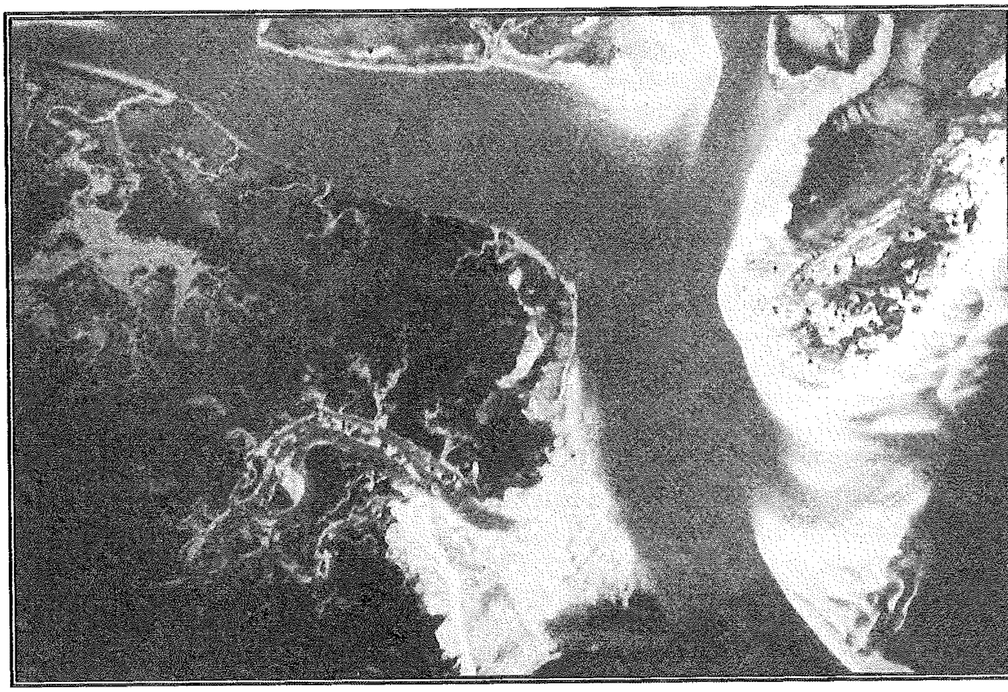
The North Inlet Marsh Long-Term Ecological Research (LTER) site research is focused primarily on a pristine estuary typical of the southeastern United States. The North Inlet coastal landscape is composed of a well-defined estuary with a major inlet connecting to the Atlantic Ocean and minor tributaries entering Winyah Bay, the largest drainage basin in the southeast. The primary water exchange (79 percent) occurs through Town Creek, with inputs from Winyah Bay occurring primarily with southwesterly winds and during high river discharge into the Bay. The estuarine-marsh complex is surrounded to the north and west by maritime forest and, to the east, is separated from the Atlantic Ocean by sandy beach ridges. Most of the highlands surrounding North Inlet Estuary are preserves owned by the Belle W. Baruch and Tom Yawkey foundations.

The watershed is approximately 25 km$^2$ (6,139 acres), with 3,697 acres to the north draining a moderately developed residential watershed into the upper portion of North Inlet Estuary and, to the west, 2,442 acres draining a forested watershed. Residential development is less than 2 percent of the watershed land area. The maritime forest consists of long-leaf pine, loblolly pine, laurel oak, red maple, turkey oak, and live oak. The swales contain mixed bottomland hardwoods with cypress and tupelo in the wetter areas. The swales aggrade into freshwater marshes which are typically occupied by white marshgrass, cattails, giant cordgrass, and bulrush, and the brackish water marshes by needle rush, black rush, and giant cordgrass. The open dunes have at least 24 species of higher plants, including sea oats, *Spartina patens*, *Panicum*, *Iva*, and *Myrica*.

### Site Characteristics

The estuarine-marsh area consists of 32 km$^2$ of immature (20 percent) and mature (80 percent) salt marshes intersected by numerous interconnecting tidal creeks. The estuarine marshlands are dominated by *Spartina, Juncus*, and *Salicornia*. Over 130 species of fishes and 200 species of macroinvertebrates have been identified which occupy different habitats within the estuary-marsh complex. These habitats include mud flats, sand flats, shelly bottoms, mud bottoms, open beaches, and oyster shells.

Marshlands range from ocean salinities to freshwater. The average channel depth within the estuarine-marsh area is 3 m. The greatest depth (7.4 m) occurs in Town Creek adjacent to the inlet. The freshwater input to the system from the adjacent watersheds is less than 1 percent of the tidal prism, and this low freshwater inflow contributes to an average annual salinity range of 23.6 parts per thousand (ppt) to 35 ppt in the estuarine-marsh complex. Freshwater inflow generally occurs from November to May. The tide is semi-diurnal with a mean range of 1.4 m and the estuary has a tidally pumped circulation. The maximum spring tide range is 2.5 m, the neap tide range about 1 m. The maximum tidal current is 1.7 m per second. There is no significant vertical



Infrared image of North Inlet, South Carolina from 8,000 feet (Atlantic Ocean, right) clearly delineates different components of the system: sandy beaches and shoals (white); *Spartina* salt marsh (dark); flooded creeks and marsh (intermediate).

stratification of salinity or density.

The present topographic configuration reflects the modification of the pre-marsh landscape by the slow rise in sea level (approximately 2 mm per year). The pre-marsh landscape has been preserved as a series of regressive beach ridges which are now found within the maritime forest and underneath the immature and mature marsh. The swales within the forest are approximately 1 m lower than the adjacent ridges and are drained by intermittent blackwater streams which flow either toward Winyah Bay (mesohaline bay-brackish marsh) or toward North Inlet marsh (tidal creek-high salinity marsh).

Subsurface flow is the major hydrologic transfer within the forest and to the streams. With the gradual rise in sea level, salt water is slowly invading the forest along the low-lying swales. The swale basin is being gradually converted from a terrestrial swale into an estuarine swale. With time, the new or immature marshes are buried by clay brought in with the tides. When this occurs, the basin is converted from a sandy immature marsh into a muddy mature marsh. Groundwater flow from the forest to marsh or within the marsh is minor.

Surface flow, primarily driven by tidal processes, is the major hydrologic transfer within the marsh. Because of the tremendous increase in tidal exchange runoff, as the system converts from forest to marsh the creek channels widen and deepen. Seaward of the immature marsh, the active beach ridge, or shoreline, is also migrating upslope across the marsh in response to the gradual rise in sea level.

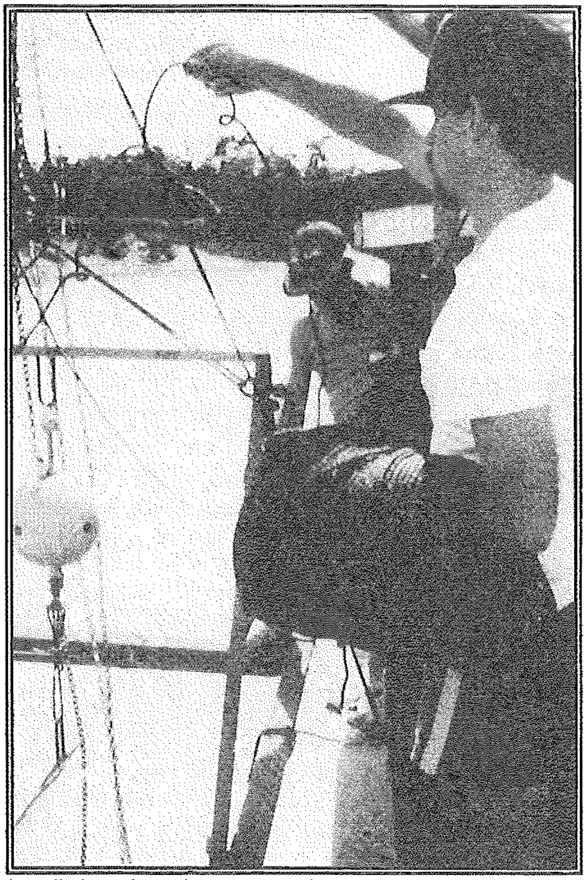
The climate of the North Inlet coastal landscape is controlled by the low elevation and coastal location. The climate is temperate (average 18°C) to subtropical with annual temperatures ranging from 8 to 27 °C. Precipitation in the study area averages 130 cm per year. Annual precipitation patterns are highly variable due to the episodic occurrence of tropical storms and hurricanes. Tropical storms or hurricanes impact the South Carolina coast approximately once every 2.6 years accounting for an average 10 to 15 percent of the total annual precipitation at North Inlet, and as much as a quarter of the annual rainfall. Wind speed and direction vary with season. Northeasterly (fall and winter) and southwesterly (summer) winds are the most common. Predominantly southwest spring winds are the most variable.

North Inlet is important to the LTER Network in that it represents one end of a continuum of sites ranging from the mountains to the sea. The estuary is the last land-encompassed body of water receiving extensive run-off from terrestrial habitats before it reaches the sea. Unlike terrestrial LTER sites, the estuary is dominated by the rhythmic surging of tidally driven waters. This extremely dynamic environment presents resource management questions that differ from other sites. Many of the major economically important marine species spend part of their life cycles in the estuary before returning to the ocean. What are the management strategies which must be developed to address the complexities of dealing with this wide diversity of species competing for the same estuarine resources?

## RESEARCH PROGRAM STATUS

Estuarine systems are influenced by critical temporal controls operating over semidiurnal to decadal scales (e.g., short-term tidally forced fluctuating water heights, longer-term meteorological processes, and episodic disturbances). The gradual rise in sea level is converting relatively stable habitats on decadal to century time scales. These habitats include a relatively stable terrestrial component at the highest geomorphic position in the landscape, slowly-aggrading tidal marsh (immature marsh) adjacent to the terrestrial component, relatively stable tidal marsh (mature marsh) and, at the lowest geomorphic position in the landscape, open water (river, bay or ocean). Exchanges among these landscape habitats occur primarily via streams, tidal creeks, or inundating tidal water (sheet flow). The importance of these linkages among the coastal landscape habitats are poorly understood. While it is readily acknowledged that estuarine systems are very dynamic, no studies have adequately quantified the temporal variability important in determining controls of system processes and the exchanges among the landscape habitats. Initially research activities were focused on quantifying temporal variability within selected habitats of the coastal landscape. Emphasis was placed on quantifying variability of important components at a variety of temporal scales within the five LTER-designated core areas.

During its 12-year history, LTER research at North Inlet has evolved from emphasizing detailed studies of the separate five core questions to attempting to integrate the data from these earlier studies into a better-defined systems approach. Although systems-level modeling was incorporated in the early research plans, the need to establish a broad database, representing as many subunits of the estuarine system as financial resources would support, was paramount to a long-term study of temporal variation. Earlier efforts were directed toward establishing statistically valid sampling protocols and to establish an understanding of biotic diversity with time and space. With time, well-established cyclic patterns of species abundance, life history data, variation in nutrients and other chemical species, and the abiotic characteristics were determined. Long-term trends could not be determined based on a short-term database. In the process of establishing a database, it was possible to modify



*Installation of an electromagnetic current meter used to take time series measurements of current speed and direction. (Courtesy of TIDINGS)* the sampling protocols based on scientific evidence. One of the important aspects of long-term research which was not fully appreciated when this project was begun was the importance of developing a functional data management system.

The fundamental question that research at North Inlet LTER seeks to address is: What is the relationship between the observed coastal landscape structure and the underlying physical, chemical, and biological processes that create, maintain, and change it? Because patches vary over geomorphic and hydrologic (tidal inundation) gradients which can vary from hours to centuries, we have subdivided the landscape into spatiotemporal domains and we are focusing on the internal and external controls within each domain as they regulate the observed structure and important ecosystem processes which maintain that structure.

Research is organized around the following questions:

- What are the structural and functional attributes of neighboring ecosystems which affect estuarine processes?
- Are primary production, trophic structure, nutrient dynamics, and marsh development internally or externally regulated?
- Are the abiotic and biotic parameters which characterize North Inlet's structure changing with time?
- What constitutes a "disturbance" to an estuarine ecosystem and how does the system respond to extreme events?
- At what scales do disturbances operate in the coastal landscape?

### Patterns & Control of Primary Production

*Spartina.* A comparative study of the production and demography of *Spartina alterniflora* continues since its initiation in spring 1984. This study conclusively demonstrates a large annual variability in marsh primary production. Aboveground production has declined at all monitoring sites since 1985, when it was 438 g C/m$^2$/yr, to a low of 197 g C/m$^2$/yr in 1988. The cause(s) of variation of primary production are being investigated. The positive correlation we observed earlier between aboveground production and summer sea-level anomalies continues to be a valid predictor of growth. Our working hypothesis is that variation in soil salinity is the proximate cause of variations in primary production. Sediment salinity and $NH_4^+$ levels may be correlated with growth rate. Aboveground growth rates at two high marsh sites are highly correlated and equal in magnitude, indicating that the factor(s) regulating growth are regional in scope. However, stem density at one site is two times greater than the other site, indicating that allocation between vegetation reproduction and growth differ between sites, although total production is equal.

A canopy photosynthesis model, which was calibrated for the *Spartina* marsh and solved for four years beginning in 1985, is being used to derive a carbon budget for the vegetated marsh. Preliminary results suggest that net ecosystem production has varied between a high of 828 and a low of 361 g C/m$^2$/yr. This quantity of carbon fixed by the plant community cannot be accounted for in respiratory losses. Most of this carbon is exported from the marsh; the remainder is buried.

*Phytoplankton.* Annual areal phytoplankton production steadily dropped from 345 g C/m$^2$/yr in 1985 to 220 g C/m$^2$/yr in 1987 (64 percent) and remained the same in 1988. The drop is significant, but is insignificantly correlated with light reduction, temperature of summer surface waters, and annual budgets of nitrate-nitrite, ammonium, and phosphate concentrations; however, we have measured higher productivity rates in previous years when the annual mean nutrient concentrations were lower. Daily chlorophyll *a* measurements track with our regression of chl *a* against $^{14}C$ productivity, which is measured quarterly. Chl *a* measurements are an accurate and easy method for estimating phytoplankton productivity. Diurnal production can be reasonably modeled ($r^2 = 0.73$, $n = 213$, $P < 0.01$) using water temperature, light attenuation (lagged three days), $NH_4$-N (lagged one day), $NO_3$-N (lagged five days), and $PO_4$-P (lagged one day).

*Macroalgae.* All eight of the dominant macroalgal species and most of the other 45 species in North Inlet can complete their life cycles within the estuary and do not require external recruitment of spores. Photosynthesis versus irradiance (P-I) curves do not vary diurnally. Thus, P-I curves generated at any time during a day can be used to model daily photosynthesis provided that solar irradiance (APR) is monitored for the whole day.

Photosynthesis in the dominant species became light saturated at surprisingly low irradiances. Photoinhibition occurred in most species usually at irradiances just above saturation.

Annual net production of macroalgae averages 280 g C/gdw/m extrapolated over the whole estuary, which is significantly greater than that of phytoplankton. An average of 84 percent of the production occurred between December and April, a period when primary production by other plant communities is depressed. A model to determine diurnal photosynthesis is most sensitive to the components of biomass and $P_{max}$. Production of *Ulva curvata* (and perhaps other species) is nutrient dependent only when light is not limiting. Thus, production peaks in early spring (March through April) when light is optimal and nitrogen abundant.

Benthic microalgae. Preliminary studies suggest the existence of a strong periodicity in benthic microalgal production rates with both tidal stage and time of day being significant contributors to this periodicity. The implication is that single point in time measurements are meaningless unless the effects of time of day and tidal stage are taken into account.

### Spatial & Temporal Distribution-Trophic Structure

Biweekly collections of three size fractions of water column organisms and two size fractions of benthic organisms made since 1981 have yielded a unique dataset for examining seasonal patterns and interannual variations in estuarine animal population parameters. Abundance, biomass, and length data for zooplankton (< 1 mm), motile epibenthos or macrozooplankton (1-20 mm), fishes and large crustaceans (> 20 mm), meiobenthos (< 0.5 mm), and macrobenthos (> 0.5 mm) have revealed new information about both the temporal dynamics of the populations and the environmental factors which influence them. Other studies have provided information on white ibis nesting and feeding patterns. A combination of long- and short-term sampling programs and experiments has resulted in the elucidation of habitat requirements, recruitment, predation, and migration patterns and processes.

Most taxa and life stages occur during predictable, well-defined periods; however, abundances are highly variable and unpredictable. Taxonomic composition and dominance within assemblages vary little among years. Except for the benthic taxa which appear to be increasing in abundance throughout the years, most taxa are not changing in overall abundance. For many taxa, larval production and settlement of major taxa are continuous for three to five months, but timing of peak abundances is usually irregular. Recruitment patterns of most water column taxa involve movements between the ocean and estuary; ingress of larvae and egress of immature adults probably result in a large net export of biomass. Studies at nearby Pumpkinseed Island show that the white ibis breeding population imports substantial amounts of N and P to the island from inland freshwater wetlands, but the amounts imported vary from year to year.

Rainfall and salinity have been documented as primary environmental factors which affect both the aquatic and avian community. Annual variations in the size of white ibis breeding populations have been linked to amounts of rainfall during the preceding winter and early spring. Rainfall levels affect the availability freshwater crayfish, primary food of the ibis. Large year-to-year variations in abundances of some fish and crustacean taxa have been associated with significant salinity changes, particularly during the winter.

Within years, population dynamics and distribution patterns are highly variable. In the water column assemblages, maximum faunal abundance and diversity occur during the summer months, but the peaks are highest in the winter for the benthos. Taxonomic and life stage composition of water column assemblages differ greatly between winter and summer but less so in the benthos. Benthic populations decline in the spring when bottom-feeding predators enter the estuary. Short-term (tidal, diel, diurnal) variations in abundance of water column taxa are large and often predictable. Dominant planktivores consume a wide variety of prey but select certain prey types. Major seasonal and ontogenetic shifts in prey preference and habitat requirements for many dominant taxa result in dynamic and complex interactions between the fauna and other ecosystem parameters.

Table 1. Continuously monitored variables measured as part of the North Inlet Marsh LTER program.

**Climate Meteorological Station**
Continuous Recording of
-Precipitation
-Wind speed
-Barometric pressure
-Solar radiation

**Physical Measurements**
Continuous
-Conductivity
-Water temperature
-Discrete (daily water sample)
-Salinity
-Light penetration (secchi disc)

**Chemistry**
Water Column
Daily at 10:00 a.m.
Locations: Two
Constituents:
Dissolved organic N, P, C
Particulate N, P, C, $PO_4$, $NH_4$
$NO_3/NO_2$, Chlorophyll ATP

**Interstitial**
Location: Goat Island, Bread and Butter Creek, Town Creek
4 cores per transect (12 depths, 2.5 cm per depth)
Constituents: $NH_4$, $PO_4$, TDP, TDN, DOC, Cl, $CO_2$, $SiO_3$,CA, Mg, K, Na, Fe, S, pH, Eh, alkalinity
Frequency: Nov, Feb, May, Aug

**Spartina**
Monthly using harvest method
Location: Creekside, mid marsh, high marsh
Monthly using nondestructive measurements of density and heights (1984 - present)
Location: Oyster Landing and Clambank

**Fauna**

| Community | Habitat | Gear | Mesh |
|---|---|---|---|
| Zooplankton | Oblique, bottom to surface | 30-cm ring | 153 um |
| Motile Epibenthos | Within 30 cm of bottom | sled | 365 um |
| Fishes, Crabs, | Shore zone | seine | 6 mm |
| Shrimps | < 1 m depth channel, > 3 m depth | trawl | 6 mm bag |
| Meiobenthos | Subtidal, upper 10 cm of sediment | core | 32-um sieve |
| Macrobenthos | Subtidal, upper 30 cm of sediment | core | 500-um sieve |

**Cruises** - Biweekly (12-15 days)
When low tide occurs between 1100-1400 hrs
All collections within 6-hr period
Replicates at each of two stations
(inlet and creek)

### *Patterns & Control-Organic/Inorganic Matter*

Water samples taken daily over a nine-year period have been analyzed for various dissolved inorganic compounds, dissolved organic substances, particulate matter, and chlorophyll *a*. Freshwater inflow to North Inlet through rainfall and upland runoff is less than 3 percent of the tidal prism. Thus, nitrogen inputs to North Inlet via rainfall and upland runoff (non-point source) are minimal. Biological processes account for the primary nitrogen source for North Inlet, with nitrogen fixation being the dominant source. Approximately 38 $g/m^2/yr$ is fixed by the biota on the marsh surface; however, at present the amount fixed by phytoplankton is unknown.

Another factor is exchanges with both Winyah Bay and the coastal ocean, with a net annual export occurring. Losses from the system include sedimentation and denitrification; 3 $g/m^2/yr$ are calculated to be lost via sedimentation and approximately 1 $g/m^2/yr$ appear to be lost by denitrification. In North Inlet the predominant nitrogen form is dissolved organic nitrogen (60 percent), with particulate nitrogen (34 percent) making up a substantial fraction. It is estimated that approximately 10 percent of the particulate nitrogen is living biomass. Ammonium comprises 76 percent of the inorganic nitrogen while only comprising 5 percent of the total nitrogen present. Nitrate-nitrite is less than 1 percent of the overall nitrogen available in North Inlet.

Unlike most river-dominated estuarine systems, North Inlet has strong seasonal nitrogen patterns which reflect temperature variation rather than freshwater runoff variation. All mean monthly nitrogen fractions were higher during summer months than during maximal runoff periods.

Nitrogen fixation and remineralization are strongly regulated by temperature and thus may be regulating the seasonal variation observed in mean monthly nitrogen fractions. On an annual basis the nitrogen fractions vary substantially. Total nitrogen mean annual concentration steadily declined from 1981 to 1987. In general, inorganic nitrogen interannual variation is inversely correlated with interannual variation in salinity. Higher concentrations of nitrogen during wetter (less saline) years suggest that freshwater import of nitrogen may be important on an annual basis, but even during those years most seasonal dynamics are internally regulated.

Nutrient budgets for an adjacent loblolly pine forest exhibit a net annual flux of ions, with exports exceeding imports by two to 64 times. Important in the export process is intrusion (approximately 37 times per year) by estuarine waters. During the January 1, 1987 syzygy, saline waters penetrated several miles into the terrestrial watershed. Increased ionic concentrations and shifts in ion balance in soil solutions from the terrestrial watershed occurred. Enhanced mobilization of $NH_4^+$ lasted six months and excess salts were detected greater than a year after the intrusion.

### *Patterns & Frequency of Disturbance*

During the past four years two major disturbances occurred: a drought in 1986 and Hurricane Hugo in September 1989. A workshop was held in 1988 which dealt with the comparative effects of drought on the coastal area of South Carolina and the upland forest at the Coweeta LTER site. Hugo was the most destructive hurricane in the history of South Carolina. Both the immediate and long-term effects of this event are being studied.

Some of the modeling effort accomplishments to date are: development of a graphical database, implementation of a water budget computer program, construction of a cypress tree growth model, development of a subtidal benthic carbon model, preliminary evaluation of system response to sea-level rise as a function of global climate change, statistical summarization of all LTER variables, initial development of a tidal freshwater nutrient flux model and a marsh grass production model, and the conceptual design for a spatially articulate habitat distribution model.

In addition to research related to the five core areas, significant effort was expended on developing a data management system, inventorying the biota, archiving samples for future reference, and strengthening intersite relationships. Numerous investigators from other institutions either conducted LTER-related research on-site or used LTER data.

## FUTURE DIRECTIONS

A new emphasis on process-based interactions and feedbacks within the North Inlet ecosystem is proposed. The coupling of ongoing long-term sampling programs with process-based experiments and transect analyses across ecological gradients is also planned. Now that we have a good description of the long-term temporal variability in ecosystem structure, research emphasis will shift toward experiments designed to explain that variation. These process-oriented studies will concentrate on the Oyster Landing Basin (OLB) where marsh habitats are encroaching into the coastal forest. Transects within this watershed will be sampled to monitor spatial and temporal variations in nutrients, the deposition of organic matter, plant and animal biomass, fish migrations, and water movements. Select locations along a transect will provide insights on very long-term processes such as marsh evolution. These measurements will be combined with experiments on nutrient cycling, sedimentation, decomposition, primary production, fertilization, trophic dynamics, and recruitment in a coordinated effort that emphasizes exchange and transformation processes.

Ecosystem models at a variety of spatial and temporal scales will be developed. They will characterize and summarize the complexity of the major structural and functional habitats within North Inlet, test hypotheses, structure our field experiments, and, ultimately, be incorporated into large landscape/climate models. Models will focus our attention on general systems dynamics and the chemical, physical, and biological interactions which regulate system level processes. This focus will, in turn, place the North Inlet LTER site in a strong position to evaluate the impacts of disturbance events (e.g., hurricanes, global climate change, and regional land-use change) on system processes at various scales.

We will also extend key long-term datasets into a second decade (Table 1). This continuity with the past provides the measurements of long-term variations in the estuarine structure, the indices by which change is observed. Statistical analysis of the short-term variability in these long-term data sets has found that certain environmentally controlled parameters, such as chlorophyll concentrations or seasonal fish migrations, are reasonably predictable, while other more biologically controlled parameters, such as the zooplankton abundance or recruitment success of benthos, are unpredictable and likely to vary greatly within and between seasons.

Having studied the variation in over 100 variables for nine years, we can now optimize our sampling resources by (1) sampling less frequently at certain times of the year, (2) combining routine sample collections with small sub-basin experiments, (3) using high-resolution satellite images to sample certain parameters over large spatial scales, and (4) structuring the field sampling, data analysis, and model designs around a hierarchical system of spatial and temporal processes.

The fundamental question addressed by research on integration across scales is: What is the relationship between the observed coastal ecosystem structure and the underlying physical, chemical, and biological processes that create, maintain, and change it? To answer this question for the North Inlet landscape we propose to subdivide the entire system into manageable spatiotemporal domains and focus our attention on the internal and external controls within each domain as they relate to the observed structure. To understand how a system operates at different scales and how these scales can be measured and modeled for North Inlet, we must first categorize the LTER program within the global environment.

The patterns observed at North Inlet are controlled at many levels of organization but the two most influential domains are the microscale and the mesoscale. The dominant processes operating within these two domains are articulated into external and internal controls. Internal controls are biotic feedbacks which affect ecosystem structure. For example, succession is a landscape process which results from the interactions between recruitment, predation, productivity, and competition. External controls are the environmental forcing functions such as sea-level rise and hurricanes, which operate concurrently with internal controls, and which are also confined to restricted spatiotemporal domains. This spatiotemporal scaling of interactions is the guide we will use to dissect the North Inlet ecosystem into more manageable habitat domains for the development of population, process, ecosystem, and landscape models. These controls dictate the changes we have observed at North Inlet over the past 12 years. They are the fundamental forcing functions that shape the North Inlet structure. It is our intention to begin shifting emphasis from a static description of ecosystem structure to a more analytical, dynamic understanding of how processes interact over time and space, as well as what controls them.

Research currently underway on the short-term influence of a major disturbance (Hurricane Hugo) will be expanded to examine long-term system effects on North Inlet Estuary. The impact of the severely damaged adjacent forested areas on the estuary is also being studied. ▫

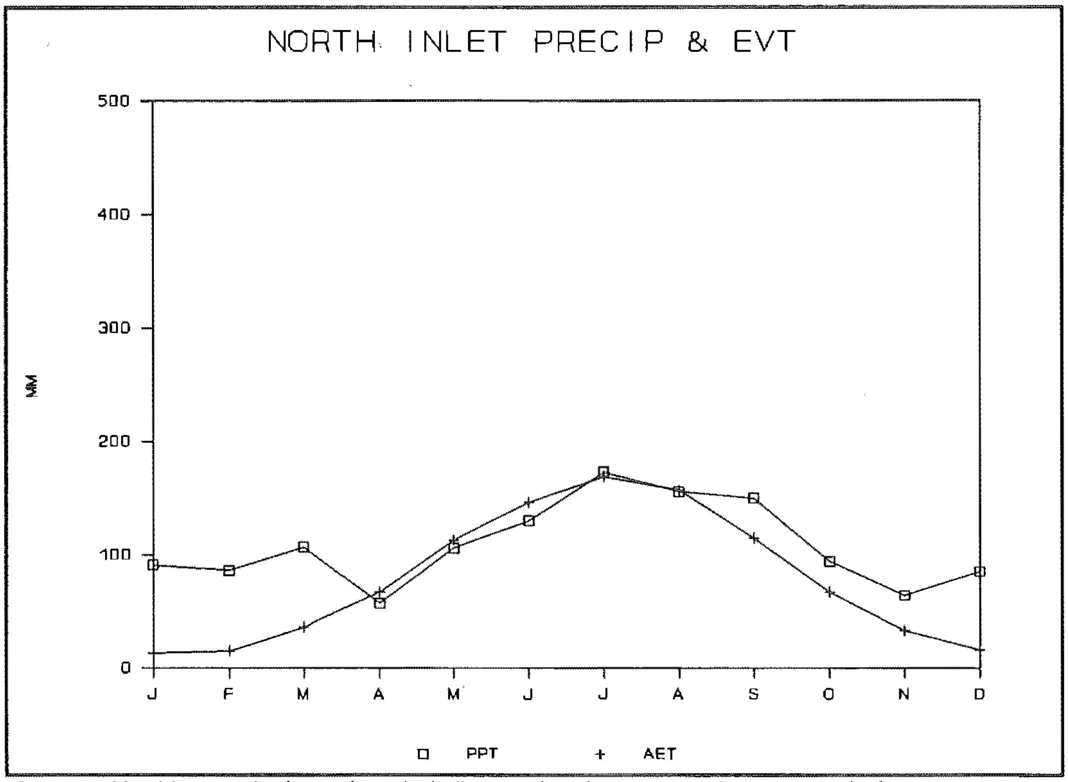



**Figure 1.** Monthly water budget values, including precipitation and actual evapotranspiration.

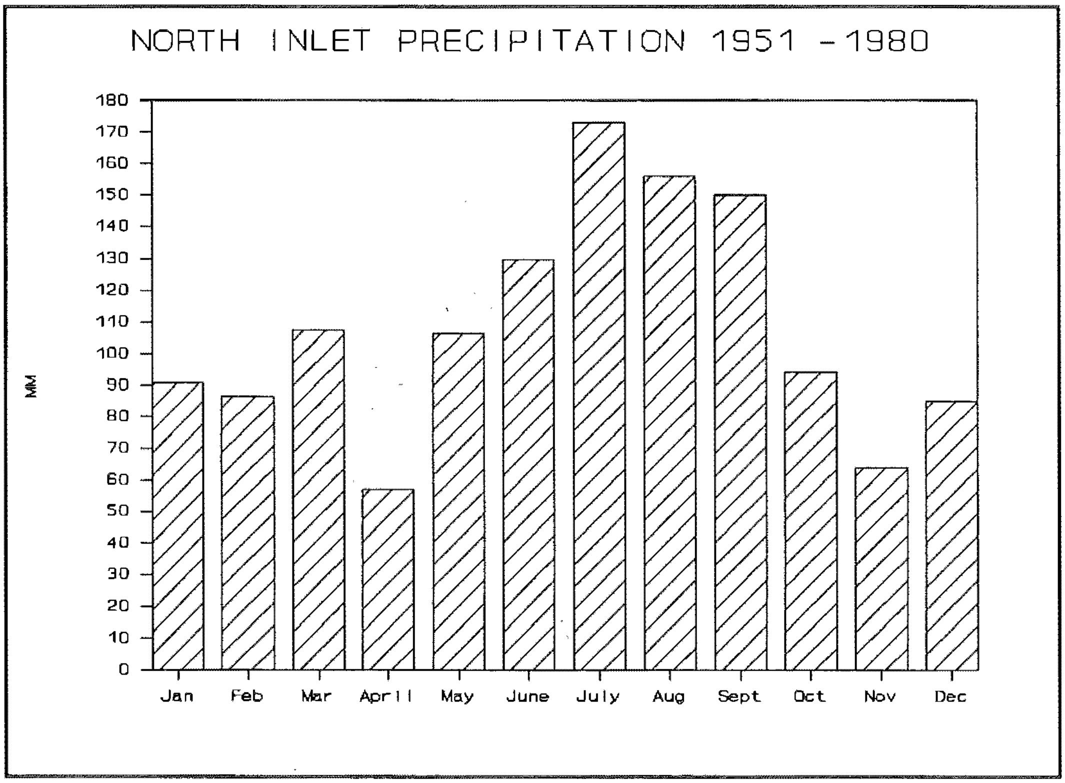



**Figure 2.** Average annual temperature values.

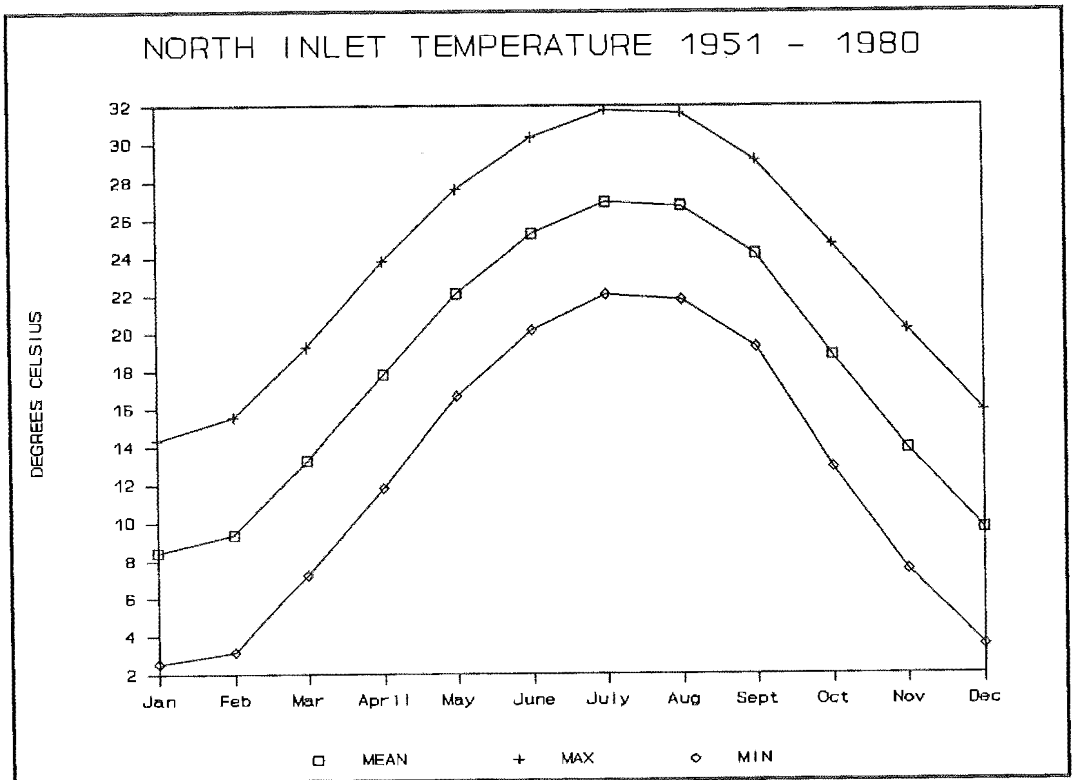



**Figure 3.** Average annual precipitation totals.

* Data from on-site or nearest weather station.


# North Temperate Lakes (NTL)

## RESEARCH SETTING

Our Long-Term Ecological Research (LTER) research on north temperate lakes extends beyond the traditional boundaries of ecosystem studies to encompass multiple temporal and spatial scales. We consider a suite of adjacent lakes that share a common climate but differ dramatically in their physical, chemical, and biological characteristics. We employ a long-term perspective that permits us to place analyses of seasonal and annual patterns into the broader context of year-to-year variability and to evaluate the implications of such variability for community and ecosystem processes. We use a nested series of spatial scales ranging from within individual lakes to the entire Northern Highland Lake District. This permits us to consider how processes occurring in a lake are related to factors in adjacent systems and the surrounding landscape.

Lakes provide ideal systems for long-term ecological research. Their boundaries are relatively distinct, and adjacent lakes, although sharing a common setting, may differ greatly in their fundamental properties. Thus, comparisons of lakes can be used to isolate at least partially important control factors for lake processes. Their distinct boundaries make lakes particularly useful for analyses of landscape-scale patterns. Likewise, many in-lake processes operate on shorter time scales than their analogs in terrestrial habitats (e.g., population growth and succession). This facilitates the observation of repeated sequences of processes within a few years as well as experimental manipulations. These advantages are coupled with a long tradition of limnological work—a substantial amount of which was conducted on our LTER lakes in the first half of this century—which has laid the groundwork for our research.

### Site Characteristics

The Northern Highland Lake District, with an area of approximately 10,000 km$^2$, has one of the highest concentrations of lakes in the world. Within Vilas County alone, where our LTER site is located, there are over 1,300 lakes, covering 16 percent of the surface area. Within a 10-km radius of the Center for Limnology's Trout Lake Station there are 68 named and 38 unnamed lakes. Lakes range in size from 0.1 to over 1,500 ha, in depth from 1 to 33 m, and in fertility from oligotrophic to eutrophic. Other representative limnological conditions include: rainwater dominated, groundwater dominated and drainage lakes; dystrophic lakes; lakes with varved sediments, winterkill lakes, temporary and permanent forest ponds, and reservoirs. Lakes are influenced by strong seasonality and are usually ice covered from late November to late April. The district is also the source area for several major river systems. The county surrounding the station has approximately 640 km of permanent streams and numerous intermittent streams.

Lakes within the Northern Highland exhibit near-natural water quality conditions. The Northern Highland and American Legion State Forests protect 80 percent of the land area and

*The main laboratory at the Trout Lake Station (Center for Limnology, University of Wisconsin-Madison) provides a base for the North Temperate Lakes LTER site. Winter 1989-90.* TIMOTHY KRATZ

about two-thirds of the lake frontage. Many lakes have totally forested watersheds and no private frontage. There is no heavy industry and only a sparse population density. Detailed investigations have indicated minimal effects of acid deposition on the lakes. Outdoor recreation and forestry form the economic base for local communities.

Climate is cool with a growing season of about 195 frost-free days. The average annual temperature is less than 5°C. The area receives approximately 76 cm of precipitation, about 30 percent of which falls in spring, with June and following summer months being the rainiest. This area receives 127-152 cm of snow which covers the ground for about 120 days each year.

Other research activities complement and are complemented by the LTER research. First, other research at the Center for Limnology is extensive. Also, the Station is within 15 km of the Wisconsin Department of Natural Resources' major warm water fish research site, the Five Lakes Experimental Fisheries Area, which has been collecting fisheries data continuously since 1946. Finally, the Trout Lake Station lies in close proximity to the University of Notre Dame's Environmental Research Center. Numerous activities at the two facilities are conducted in close collaboration. Together the Trout Lake Station and the Notre Dame Center form a site within the Experimental Ecological Reserve Program. In addition, cooperative work is underway with the U.S. Environmental Protection Agency, the U.S. Department of Energy, the U.S. Geological Survey, and the Wisconsin Department of Natural Resources.

## RESEARCH PROGRAM STATUS

### *Major Objectives*

Within the synthetic goal of understanding the ecological complexity generated by multiple processes acting over many temporal and spatial scales, we aim to develop a series of broad-scale evaluations of factors controlling lake processes. These evaluations are interrelated but can also be considered independently. They can be classed generally into five major objectives:

- to perceive long-term trends in physical, chemical and biological properties of lake ecosystems;
- to understand the dynamics of internal and external processes affecting lake ecosystems;
- to analyze the temporal responses of lake ecosystems to disturbance and stress;

- to evaluate the interaction between spatial heterogeneity and temporal variability of lake ecosystems; and
- to expand our understanding of lake-ecosystem properties to a broader, regional context.

The first four objectives have played a key role in our research over the past five years; the last objective is new. Conceptual extensions within the first four objectives include (1) a focus on global climate change, (2) expanded evaluations of microbial processes, and (3) more detailed assessments of land-water interactions.

### *Approach to Questions*

Perceptions of Long-Term Trends: Our goal has been to develop a set of ecological measurements that will allow investigators to observe and analyze patterns of long-term change in the physical, chemical, and biological features of lake ecosystems. Long-term measurements at various ecological levels and several temporal and spatial scales are intended to capture the structure and function of lake ecosystems and enable analyses of interactions among the principal ecosystem components. We established a data management system to make modern and historic data easily available to researchers.

We have focused on a suite of lakes and surrounding terrestrial areas linked through a common groundwater and surface water flow system that share common climatic, edaphic, and biogeographic features. Our seven primary lakes (Trout, Big Muskelunge, Allequash, Crystal, Sparkling, and Trout and Crystal Lake Bogs) located within 5.3 km of the Trout Lake Station in north central Wisconsin, were chosen to represent marked differences in size, morphometry and habitat diversity, in thermal and chemical features, in species richness and assemblies, and in biological productivity.

The choice of primary lakes makes groundwater one major focus of our project, because of its importance in regulating differences in the chemical composition of lakes and in linking terrestrial and lake ecosystems. We also have secondary lakes for comparison with the primary lakes on specific research questions of individual investigators. The two most important are Little Rock Lake, the site of a USEPA-funded experimental acidification, and Lake Mendota, the site of a Wisconsin DNR-funded, whole-lake biomanipulation experiment. Lake Mendota, our only study lake outside of the Northern Highland area, is included also because of its rich historical data, including 145 years of ice-cover data to analyze climatic patterns.

We sample most major physical, chemical and biological parameters. Sampling frequency is tuned to the dynamics of individual parameters. Sampling is most intense at spring overturn, maximum stratification in summer, fall overturn, and winter stratification. Nutrients, pH, inorganic and organic carbon are sampled monthly. Temperature, dissolved oxygen, chlorophyll *a*, primary productivity, and zooplankton abundance are measured every two weeks during the open water season and every five weeks under ice cover.

Parameters that vary over longer time scales are measured annually in August. These include macrophyte distribution, fishes (abundance, biomass, and community structure) and benthic invertebrate abundance. In addition, groundwater levels in selected wells are measured monthly and groundwater chemistry is measured quarterly. Parameters measured at our automated land-based weather station include air and soil temperature; precipitation; longwave, shortwave, and photosynthetically active radiation; wind speed and direction; and relative humidity. Our raft-based station on Sparkling Lake records air and water temperature, wind speed at three elevations, and relative humidity.

Dynamics of External & Internal Processes: Long-term patterns in lakes are generated by a complex interplay between the external and internal processes we study. Because internal and external processes operate on a variety of time scales, interactions among them lead to complex patterns, often with time lags between cause and event. Understanding how lakes are affected by the interaction of processes occurring on different time scales, particularly when there are time lags, is a major goal of our LTER program. External processes being studied include climatic and hydrologic factors combined with land-water interactions. Climate exhibits substantial year-to-year variation and distinct long-term cyclic behavior. Hydrologic differences among NTL LTER lakes are associated primarily with differences in groundwater inputs.

These differences exert important influences on both water and chemical budgets. Land-water interactions involve linkages between terrestrial and aquatic systems in which numerous processes operate at fundamentally different time scales (contrast the growth and decomposition of trees versus phytoplankton). For an example of internal processes, a lake's primary production during midsummer is controlled directly by the extent of turnover during the previous spring and by the amount of grazing exhibited by herbivorous zooplankton during that period. Each of these processes in turn is linked with longer-term factors such external nutrient loading and the year-class strengths of zooplanktivorous fishes.

<u>Responses to Disturbance & Stress</u>: Our efforts have emphasized acid deposition and species invasions of rainbow smelt and rusty crayfish. Our work has considered the role of turnover events as disturbances in plankton communities. Using a series of temporary ponds at the NTL LTER site, we also have tested explicitly the hypothesis that the importance of biotic interactions in determining community structure increases with the extent of time between disturbances.

<u>Spatial & Temporal Variability</u>: We consider multiple scales of spatial and temporal variability and interactions not only between spatial and temporal variability, but also between perceptions of variability and scale of observation. Variability is a characteristic of all ecosystems, yet there is little understanding of how systems differ in variability patterns, or what factors lead to these differences. Remote sensing and geographical information systems allow us to sample and analyze different systems at the same spatial scale. Use of these tools can be particularly powerful in analyses of landscape structure of diverse systems.

Temporal variability arises through the interplay between internal dynamics and fluctuations in external driving forces. Spatial heterogeneity may interact with temporal variability in determining community and ecosystem features. Spatial heterogeneity may decrease the connectedness of a system and act as a buffer against disturbance or altlernatively may prevent the re-invasion of a species lost after a disturbance.

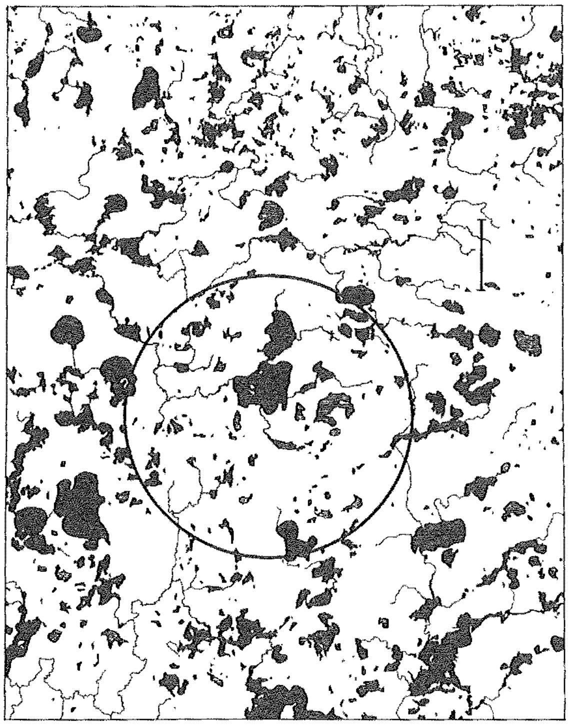


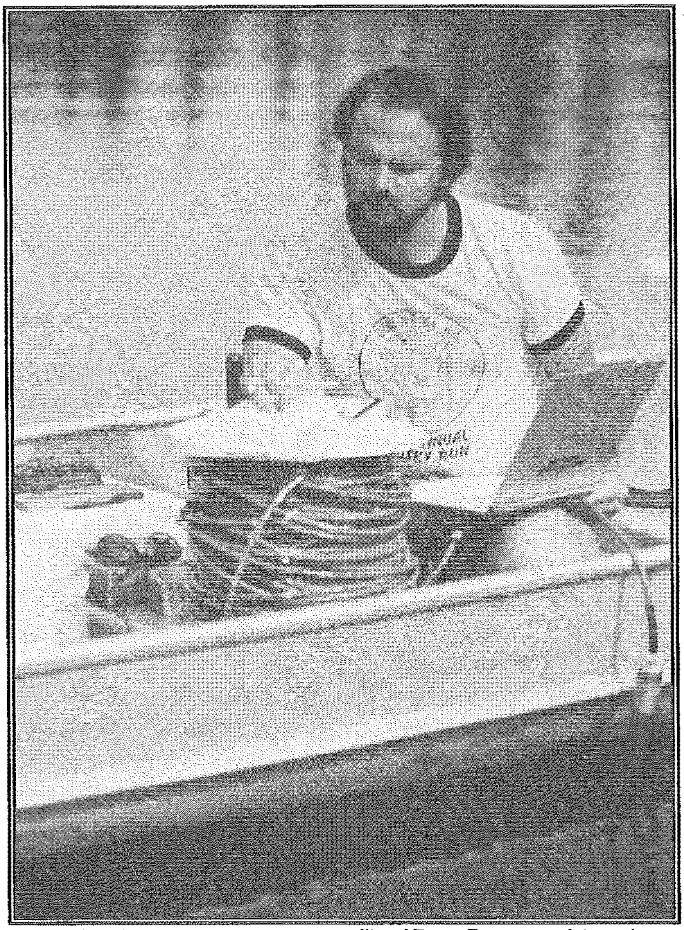
Figure 1. Lake and stream map of the North Temperate Lakes LTER site in the Northern Highlands Lake District of northern Wisconsin and the upper peninsula of Michigan. The Center for Limnology's Trout Lake Station is located in the center of the 10 km circle, which includes the primary LTER study lakes. CARL J. BOWSER and JOHN J. MAGNUSON

<u>Broader Spatial Scales:</u> Of particular interest is the issue of how to make useful predictions across scales. We wish to scale-up from the seven LTER lakes to the Northern Highland Lake District to assess: (1) how well we can transfer our understanding of processes within the LTER lakes to a larger region, (2) regional impacts of global change, (3) regional diversity, and (4) effects of regional changes in conservation, forestry, land development, and recreation policies.

Problems of scale have always been part of ecology. We do not believe that simply extrapolating across scales will be an effective means of predicting across scales. For example, analyses of satellite and acoustic remote sensing scenes makes clear that interesting differences result when the natural world is viewed at different scales. We examined the distribution and morphometry of our lakes from the grain of a

Landsat TM image (30 m) to that of an AVHRR image (1 km). Information was lost at the coarser grain which is important to the interpretation and evaluation of a lake district. Many features are only observable at the finer scales (97 percent of the lakes disappear between the 30-m and the 1-km scales) and significant bias develops in the parameterization of the objects of interest.

In many ways we face the same dilemma as molecular biologists using their methodology to predict the behavior of communities of organisms or as population ecologists using their methodologies to predict the functioning of organ systems. For the present, it seems clear that (1) structural analyses must be conducted across scales at least until we obtain a better understanding of how our view of the natural world is affected by scale of observation; and (2) we must develop sets of appropriately scaled models to cover a range of spatial grains and extents. To address the second problem, we will develop a spatially explicit regional hydrologic model and a model predicting chlorophyll concentrations and water color of lakes from landscape features.



*Measuring the water temperature profile of Trout Bay, one of the primary lakes in the North Temperate Lakes LTER Program.* *TIMOTHY KRATZ*

### Site Research Results

- Ice duration over a 142-year period on Lake Mendota demonstrates a decrease in ice cover at the end of the little ice age and shorter durations in El Niño years over the last 50 years. In addition, the last 10 years show a decrease in ice duration, which when simulated into the future for a doubling of greenhouse gases, results in occasional winters without ice cover.
- Events in Crystal Lake leading to periodic (every five years) strong year classes of yellow perch which through food web dynamics produce a five-year oscillation in water clarity from a Secchi disc depth of 10 m to 6 m.
- Sparkling Lake's water budget was estimated by stable isotopic techniques to be one-third of the total input and transports 19,000 kg/year of road salt into the lake from an adjacent state highway.
- Sediment cores and sponge spicule sizes were used to estimate trends in lake silica concentrations over the last 10,000 years; dissolved silica concentrations have decreased four- to tenfold, indicating significant decreases in silica loading and perhaps the weathering rates of the tills.
- Annual $C_{14}$ primary production was remarkably similar in Crystal, Sparkling and Trout Lakes even though the three lakes differ significantly in position in the groundwater flow system and in nutrient and solute loadings. Small differences in dissolved organic carbon (dissolved color) appear to be sufficient to reduce light penetration in the lakes lower in the groundwater flow system to compensate for their higher fertility.
- An invasion of rainbow smelt in Sparkling Lake has caused the virtual extirpation of the once abundant native zooplanktivore, cisco, in the eight-year period since the invasion, apparently owing to the predation of smelt on eggs and young of the cisco.
- The experimental acidification of Little Rock Lake has demonstrated that many biological effects on the ecosystem are indirect, occur at least a year after the

decrease in pH, and are mediated through interactions in the food web.

- The position of a lake in the landscape can be used to predict the inherent variability of limnological parameters. Lakes higher in the landscape had higher inter-year variability than lakes lower in the landscape especially in edaphic properties.
- Lakes with similar exposure to climate (similar area to mean depth ratios) were more temporally coherent among years than lakes that differed the most in exposure to climate. Also, variables most closely related to climate, such as water level, were most coherent among lakes, while biological factors such as perch year class, strength and chlorophyll biomass demonstrated *no* inter-lake coherence among years. Each lake had a unique behavior for these biological variables.
- Spatial heterogeneity in littoral zone fish assemblages was essentially the same among lakes, among sites with a lake and among samples at a site. The community structure appears to be "fractal." The spatial heterogeneity in a lake was best explained by the spatial heterogeneity in the habitat rather than the species diversity in the lake.

### *Intersite Research Results*

The ease with which comparisons and common analyses can be accomplished among LTER sites which differ greatly from each other is contributing to a new synthesis and level of generalization in the LTER Network. Example results of intersite analyses with which we have been associated follow:

- Measures of temporal (among years) and spatial (among locations at an LTER site) variability in LTER sites may provide a metric for ecosystem comparisons that is not parameter or ecosystem specific. Analyses of LTER data at an intersite workshop indicated that ecosystems as diverse as deserts, forests, streams and lakes have common features in variability. For example, the biological features are more variable than are the edaphic and climatic features regardless of ecosystem type. Important differences are also apparent; deserts have greater temporal variability than lake districts but lower spatial variability.
- Landscape position was a significant predictor of temporal variability at locations within four LTER sites studied (forest stream, desert, estuary, and lake district). Specific mechanisms relating spatial position to variability differed at the four LTER sites, but at each site (1) locations differed in annual variability, (2) for at least a subset of parameters, this variability was related to position in the landscape, and (3) water movement across the landscape was the important underlying factor determining variability patterns.

## FUTURE DIRECTIONS

Research at the North Temperate Lakes LTER site is continuing on our set of primary questions, but is evolving to an increased focus on global climate change, an expanded evaluation of microbial in-lake processes, and a more detailed assessment of land-water interaction at a lake and regional scale. Specific questions related to these foci are listed below.

### *Climate Change*

One of our long-range goals is to predict changes in limnological processes due to global climate change. This involves three steps in which we (1) develop models of the influence of climate on thermal conditions within lakes, (2) predict the impacts of warming scenarios on lake conditions, and (3) examine the effects of predicted thermal conditions on internal lake processes. This work will be regionalized through cooperative research with the USGS through simulations with a regional hydrologic model. Some of the questions we will be addressing are:

- What is the relationship between climatic factors and thermal conditions in lakes?
- How will thermal structure of lakes change following global climate warming?
- How will inlake processes respond to global climate warming?
- How will climate-associated changes in water levels and thermal regimes influence patterns of colonization and extinction?
- How will global change affect water table and lake levels, lake-connectedness, and the relative percentages of land, lakes and wetlands?

### *Microbial Inlake Processes*

Our results to date indicate the influence of several factors in controlling the production of our study lakes. Evaluations of the interplay of these factors remain to be completed.

- What is the role of nutrient loading to the photic zone in controlling primary production among lakes differing in groundwater inflow?
- To what extent does the proportion of primary production processed by zooplankton and the microbial food web vary among lakes?
- What is the role of phosphorus immobilization by iron in limiting production in the NTL region?

### *Land-Water Interactions*

The NTL LTER site is a mosaic of terrestrial and aquatic ecosystems where terrestrial systems have the potential to exert major influences on lake conditions. Such terrestrial influences operate directly through the input of allochthonous materials and indirectly through an influence on hydrologic inputs. Characteristics of terrestrial ecosystems surrounding lakes, and their potential influence on lakes, vary as a function of soil substrate and natural and/or human-mediated disturbance regimes. Therefore, landscape position and disturbance regimes of terrestrial ecosystems must be considered in evaluating the factors influencing long-term patterns in aquatic ecosystems. Expanded research here will focus on more detailed measures of the interaction between aquatic and terrestrial systems.

- How does terrestrial vegetation affect the hydrologic regimes of lakes?
- What are the relative effects of allochthonous inputs of coarse woody and fine litter material on dynamics of lakes?
- How do long-term changes in terrestrial vegetation influence lakes?
- Can a regional hydrologic model be developed as a synthetic tool for understanding terrestrial/aquatic interactions? ■

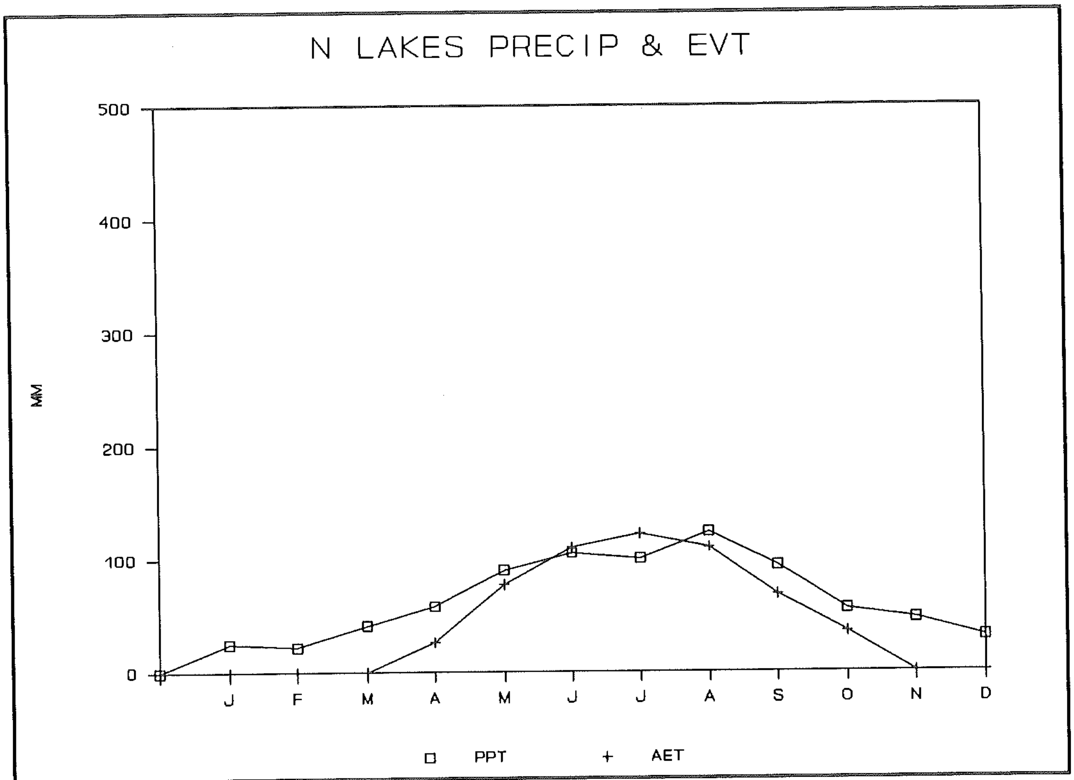



**Figure 2.** Monthly water budget values, including precipitation and actual evapotranspiration.

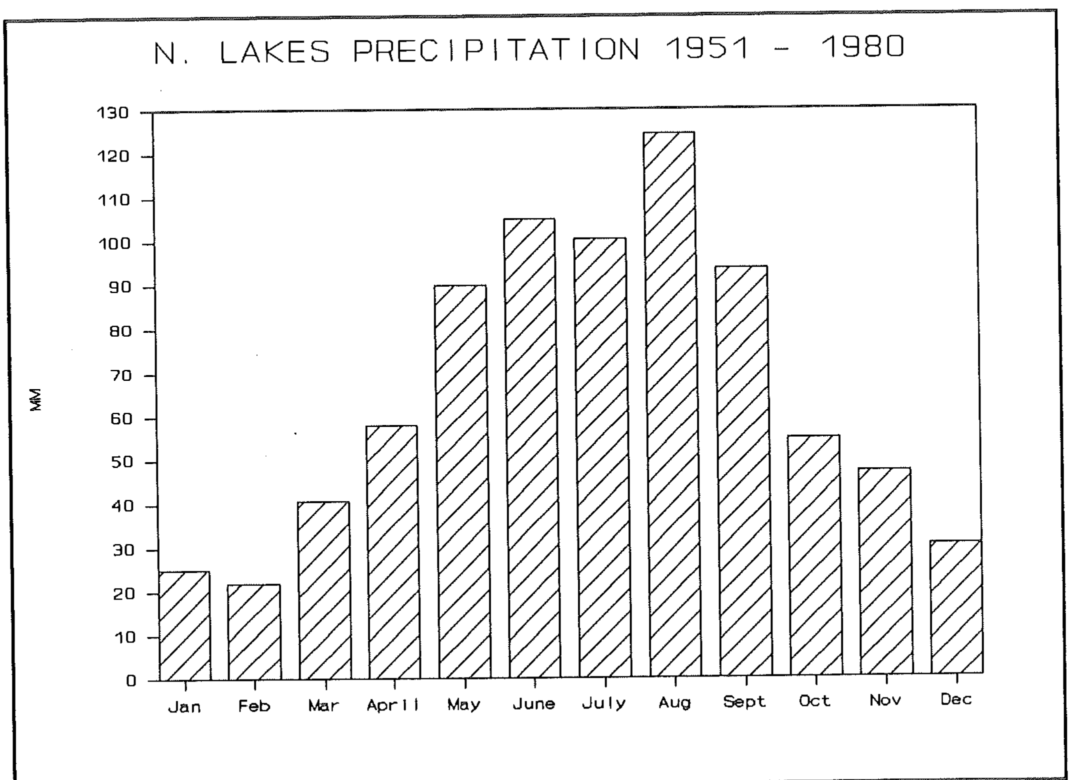



**Figure 3.** Average annual precipitation totals.

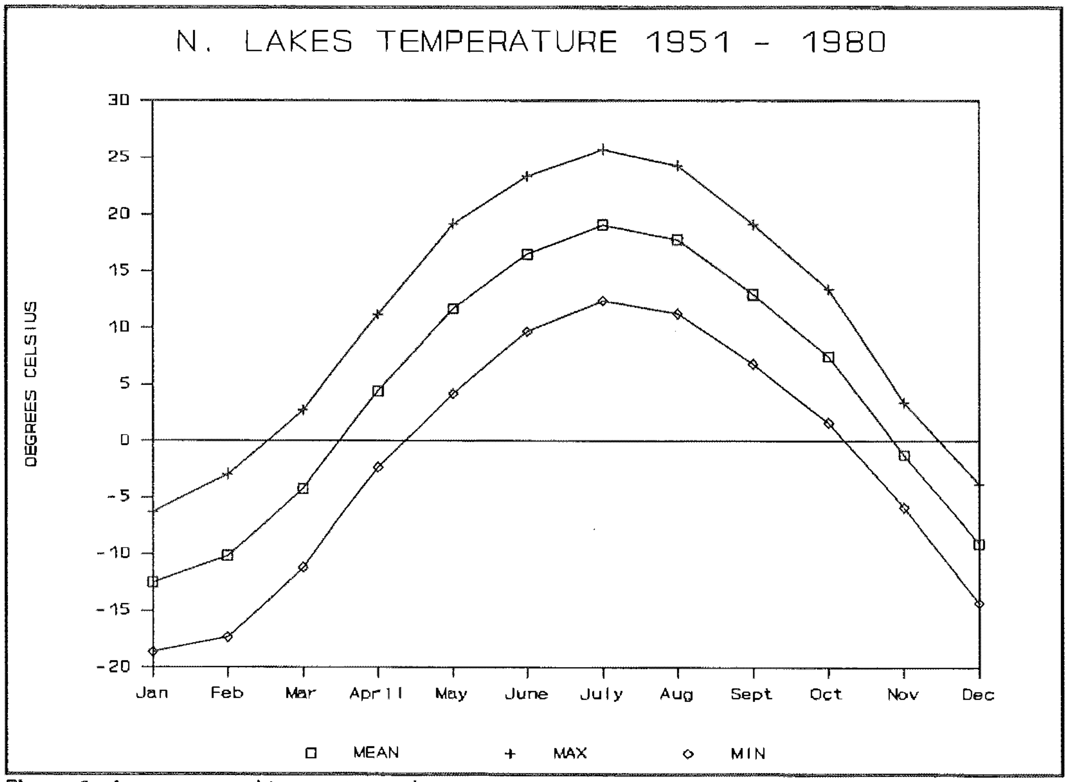
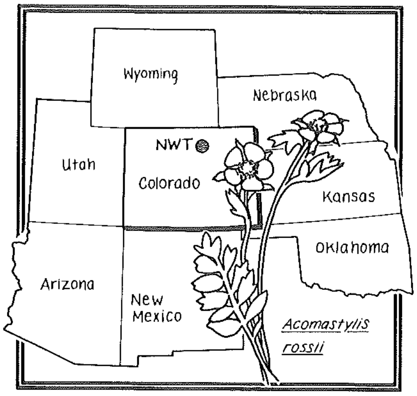



**Figure 4. Average annual temperature values.**

* Data from on-site or nearest weather station.




# Niwot Ridge/Green Lakes Valley (NWT)

## RESEARCH SETTING

Niwot Ridge/Green Lakes Valley is the only LTER site that includes a cirque glacier and extensive alpine tundra. The area also features a variety of glacial landforms, glacial lakes and moraines, cirques and talus slopes, patterned ground and permafrost, and the entire study site lies above 3,000 m elevation. When compared to nearby low elevations, it is characterized by reduced temperatures throughout the year, increased solar radiation (and consequently higher levels of ultraviolet radiation), higher wind velocities, and an abbreviated growing season. Animal and plant species inhabiting the site are adapted to this environment.

Precipitation is highly variable temporally—most occurs as snow during the winter and spring months and annual totals vary greatly from year to year. The interactions between wind, snow and high relief result in a mosaic of snow-free and snow accumulation areas with consequent wide variability in the amount and timing of meltwater release. Summer precipitation is also highly variable, both temporally and spatially, usually arriving in brief convective storms. Thus, the moisture available to the tundra plants is vary unevenly distributed.

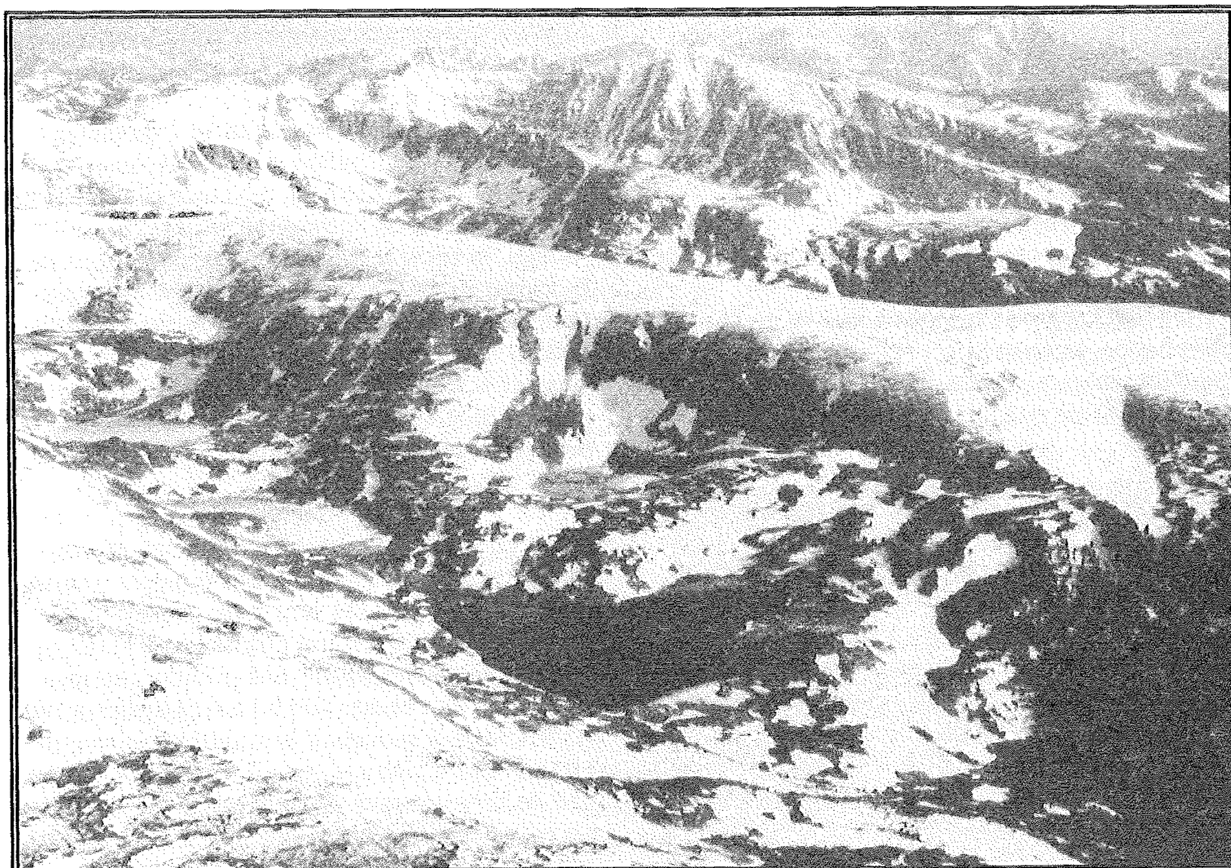
The headwaters of the the three major rivers of the southwestern United States (the Arkansas, Colorado and Rio Grande) are located in the Colorado Rockies. The mountain snowpacks provide most of the water used in human activities in the region, which could have serious ramifications if global climate change leads to altered precipitation patterns in the mountains. However, general circulation models usually have lower confidence for precipitation than for temperature prediction, and the extrapolation from low elevations to the alpine tundra adds further uncertainty. Thus, continued analysis of the long-term climate data base at the Niwot Ridge site is critical.

### *Site Characteristics*

The site is located approximately 35 km west of Boulder, Colorado and so has a mid-latitude continental climate modified by high elevation and mountainous relief. Annual mean temperature at 3,743 m is -3.7°C. The January mean temperature is -13.2°C and the July mean is 8.2°C. Mean annual precipitation is about 930 mm, of which one-third is used in evapotranspiration, the remainder leaving the system as runoff.

The alpine study area is reached by an unimproved road from the Mountain Research Station (2,895 m) which leads to within 2 km of the main tundra research site, the Saddle (3,525 m). The D-1 research site, for which climate records are continuous from 1952, lies a further 3 km from the road head. The Martinelli study area (3,380 m) is located 1 km southwest of the Saddle, in the forest-tundra ecotone. The Green Lakes Valley lies immediately south of the western half of Niwot Ridge. It includes the Arikaree Glacier at its head (3,798 m), and the Wetland, Green Lake 4, and Albion research sites. The Green Lakes Valley and Martinelli sites are all within the City of Boulder watershed which is closed to public access.

Niwot Ridge, including the main alpine study site, is part of the Roosevelt National Forest and has been designated a Biosphere Reserve (United Nations Educational, Scientific and Cultural Organization, UNESCO) and an Experimental Ecological Reserve (USDA Forest Service).



*View north across Niwot Ridge to Langs Peak, with the lower Green Lakes Valley in the foreground. The Saddle, the main research area on Niwot Ridge, is at the right edge of the photo.* *N. CAINE*

## RESEARCH PROGRAM STATUS

In Phase I (1980-1985), our initial hypothesis was that the present system reflects past climatic conditions and that disturbance would accelerate its adjustment to the present climate. This hypothesis introduced the importance of a truly long-term (Pleistocene-Holocene) history of the system and the paleoenvironments in which it has existed in postglacial time. A concern with paleoecology and disturbance ecology was continued into Phase II when a focus on materials budgeting and its significance in the mediation of ecosystem function was a central theme. Thus, there was development from the nature of system response (Phase I) to the reaction rates and buffering ability of the system (Phase II). Phase II (1986-1990) further emphasized two lines of research: initiation of studies at the landscape level with the introduction of Geographic Information Systems (GIS) and remote sensing capabilities, and the development of a hierarchical, conceptual framework of the alpine ecosystem focusing on the micro- to mesoscale levels as an anchor for modeling and synthesis.

This evolution of concerns has continued into Phase III (1991-1996) during which the goal of the research is to understand the influence of snowpack and summer precipitation on ecosystem processes and landscape patterns and to use this understanding to predict responses to climate change. The central hypothesis is that alteration of snowpack or rainfall regimes will cause changes in alpine ecosystem processes and patterns at site and regional scales (Figure 1). There are three broad objectives for Phase III: (1) process studies intended to improve our understanding of relationships among rainfall and snowpack patterns, biological processes, and the landscape; (2) modeling to link studies of process and pattern with remotely sensed data and to predict the effects of changed precipitation regimes; and (3) integrated long-term research to document the interrelationships between precipitation patterns and ecosystem properties at a variety of spatial and temporal scales.

### *Research Questions*

To achieve these objectives, we have identified five central questions:

- How do changes in snowpack and summer precipitation patterns affect soil water regimes, runoff and stream geochemistry?
- How do snowpack and summer precipitation affect tundra processes of nutrient cycling, production and decomposition?
- How do snowpack, summer precipitation and nutrient availability affect patterns of production and populations of plants and animals in a hierarchy of temporal and spatial scales?
- What have been the effects of past changes in snow regime on alpine ecosystems and are these appropriate analogs of predicted future changes?
- Can we simulate, then predict, tundra response to altered snowpack regimes by adaptation of models developed in other biomes?

*Niwot researcher ear tags a pika for long-term population studies.* *J.C. HALFPENNY*

Question #1. We are testing three hypotheses in order to answer Question #1: (1) At the onset of the alpine growing season, moisture conditions in the soil depend on snow distribution. Thus, changes in snow regime will produce changes in flow routing and in stream chemistry. (2) Alpine tundra systems are decoupled from the stream systems except during peak snowmelt or intense summer precipitation events. (3) Nutrient losses and leaching episodes from alpine tundra systems depend on water fluxes and antecedent moisture conditions.

Question #2. In approaching Question #2, we start from present knowledge of the influence of snow regime on alpine ecosystem processes through its effects on soil nutrient and water budgets, soil temperature and growing season length. Six hypotheses will be tested in this work: (1) The winter snowpack is a source of nitrogen input to the alpine system. (2) The ability of plants and microbes to take up nutrients released during spring snowmelt is determined by soil temperature and moisture. (3) Competition for nutrients between plants and microorganisms is also influenced by soil temperature and degree of water saturation. (4) Through its influence on plant-water relations and the mineralization of soil organics, soil water availability is a basic constraint on primary production in those alpine communities which receive little snowmelt. (5) Nitrogen availability limits photosynthesis and primary production in communities which are not subject to water stress. This limitation is influenced by atmospheric inputs of nitrogen from anthropogenic sources. (6) Plant allocation of nitrogen will be determined by its availability (as influenced by soil temperature, moisture and microbial competition), and will then influence photosynthesis, reproduction, allocation to secondary compounds and decomposition.

Question #3. There are four hypotheses linked to Question #3: (1) Regional patterns of production in the alpine are a function of accumulated snowfall and summer rainfall distributions. (2) Soil water-holding capacity, nutrients and animal disturbance are constrained by snow distribution and reflect average snow distribution patterns, whereas interannual variations in primary production are constrained by summer precipitation and temperature. (3) Reactions of species to changes in snowpack are individualistic and will shift in a manner that is predictable from their present-day distribution patterns. (4) Altered snowpack regimes will result in changes in pocket gopher (*Thomomys talpoides*) activity and consequent alteration of the distribution of plant species and communities.

Question #4. The hypothesis used to approach Question #4 is that changes in Holocene precipitation regimes have substantially affected the modern alpine ecosystem and that past ecosystem responses to such changes provide analogs for future responses.

Question #5. The objectives in answering Question #5 are: (1) to develop predictive hierarchical spatial models of the response of soil characteristics, plant populations, plant communities, and animals to alterations of precipitation regimes; and (2) to test hypotheses concerning the response times of ecosystem components to climatic excursions of varying lengths by model simulation.

## Research Results

General results pertaining to the alpine systems of the Southern Rockies derive from our previous LTER work and have been incorporated into ongoing work.

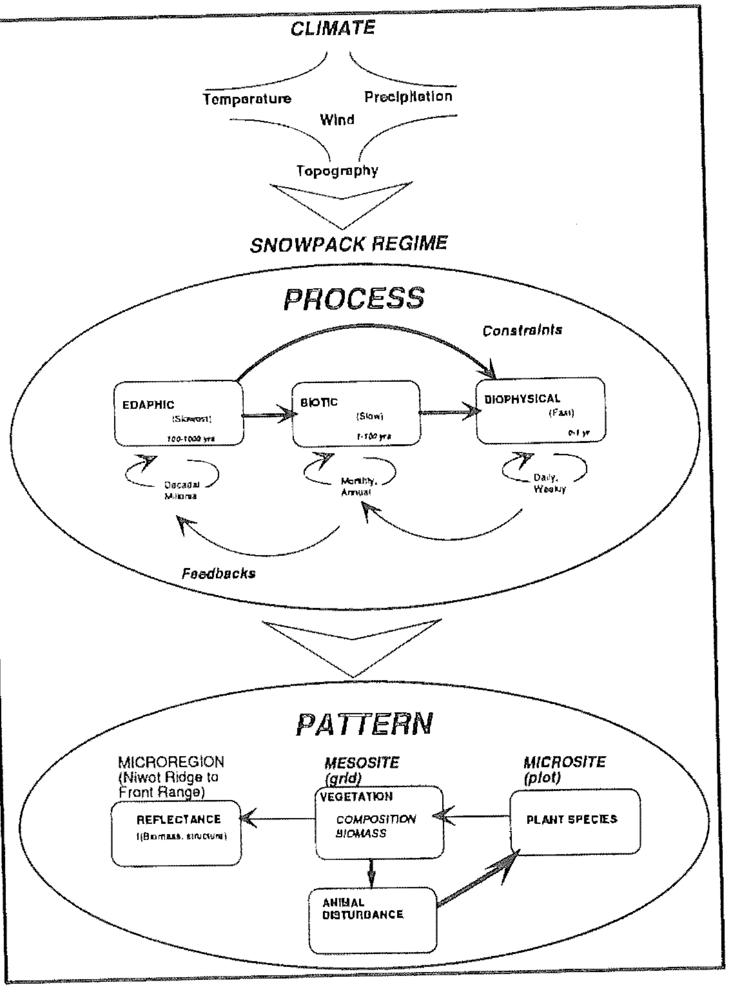



Figure 1. Interactions between climate and topography result in a pattern of snowpack distribution, which is a major constraint (symbolized by ellipses) on ecosystem patterns processes in the alpine. Processes can be divided into three major types, based on their relatlive rates: (1) Biophysical processes, for example uptake of nutrients, occur very quickly. (2) Biotic processes, such as growth and reproduction, occur on a longer time scale, and represent the integration of biophysical processes over that time period. (3) Edaphic processes, such as the conversion of litter into various soil organic matter pools, take place on a longer time scale still. In all cases, the biological system is the mechanism for integrating fast processes into slower systems. The result of these process-based responses to climate-topographic interactions are the patterns of species, communities, and standing crop biomass present on the landscape. The primary patterns being considered on Niwot Ridge are species distribution (microsite), vegetation composition and biomass (mesosite), and spectral reflectance (macrosite), which is a function of biomass and canopy structure. Animals respond to patterns of vegetation composition and biomass and subsequently change microsite patterns of species distribution.

First, there is the stability of many of these systems in the face of disturbances that have recurrence intervals of less than millenia. Events with a return period of decades have occurred during the years of LTER research but appear to have been absorbed with relatively few impacts by the alpine. Second, plant species and community structure seem to be controlled by keystone animal species such as the pocket gopher and alpine vole. These species have important influences on sediment movement, soil drainage and soil profile characteristics.

Since the Southern Rockies are basically semi-arid, it is not surprising that water and snow distributions are critical to system processes and to landscape patterns in the alpine. These influences are evident at a variety of scales up to the regional level. Finally, the significance of atmospheric inputs to the alpine is an overriding one. The input of particulates from the atmosphere has been important to soil development and sediment yields from the alpine for the duration of the Holocene. In recent decades, nitrogen loading from the atmosphere as both wet and dry deposition may have increased by an order of magnitude, with important ecological implications.

Comparisons between this site and other, especially grassland, sites within the LTER network in terms of ecosystem structure and function continues to be important to our work.

## FUTURE DIRECTIONS

Directions to be pursued in future work on Niwot Ridge are all set within the context of global change, since alpine systems are clearly defined by climatic conditions. A large part of future work is to evaluate the influence of snow regimes and rainfall patterns in Rocky Mountain alpine areas. This work will emphasize influences on system function and nutrient cycling. There is still little information about the influence on plant and animal populations of sub-nivean conditions during winter and spring (prior to melt-off). The recently constructed Tundra Laboratory on Niwot Ridge will facilitate proposed work on ecological conditions beneath snowpacks of varying depths.

These research topics are capable of being influenced by projected global changes in climate. They are, therefore, set into the context of broad environmental change, in which a high priority is to be placed on questions of spatial scale interpolation and extrapolation within and between alpine areas.

### * NWT Climate Record 1951 - 1980

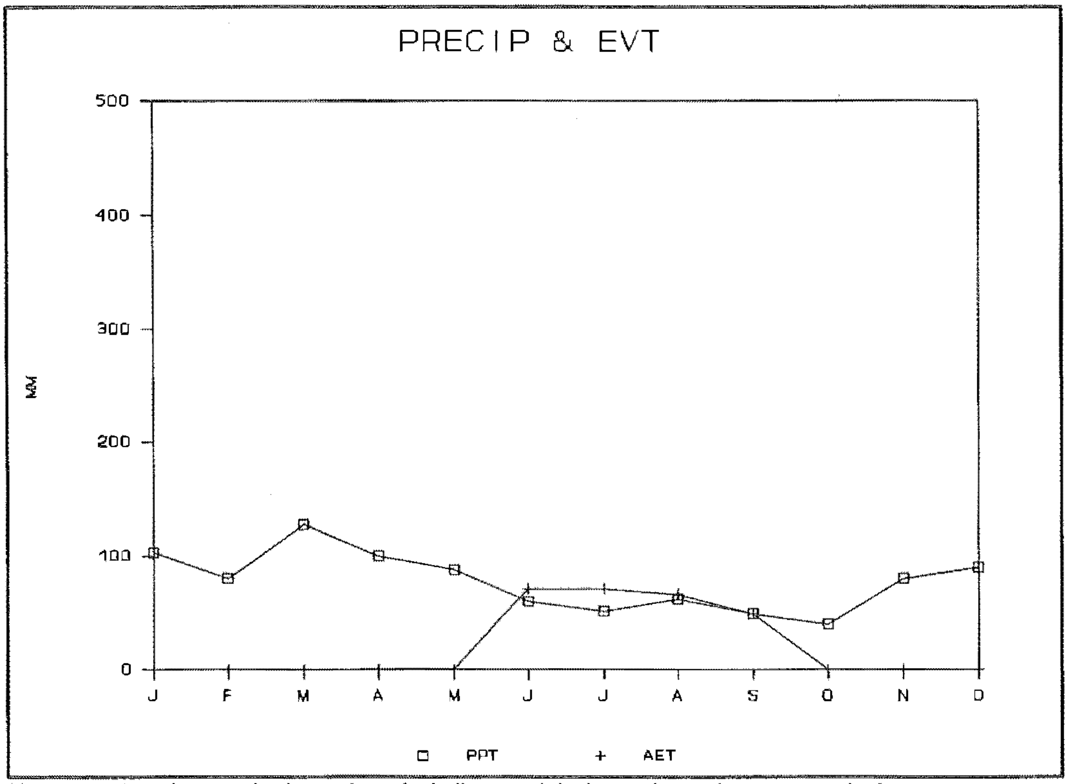



**Figure 2.** Monthly water budget values, including precipitation and actual evapotranspiration.

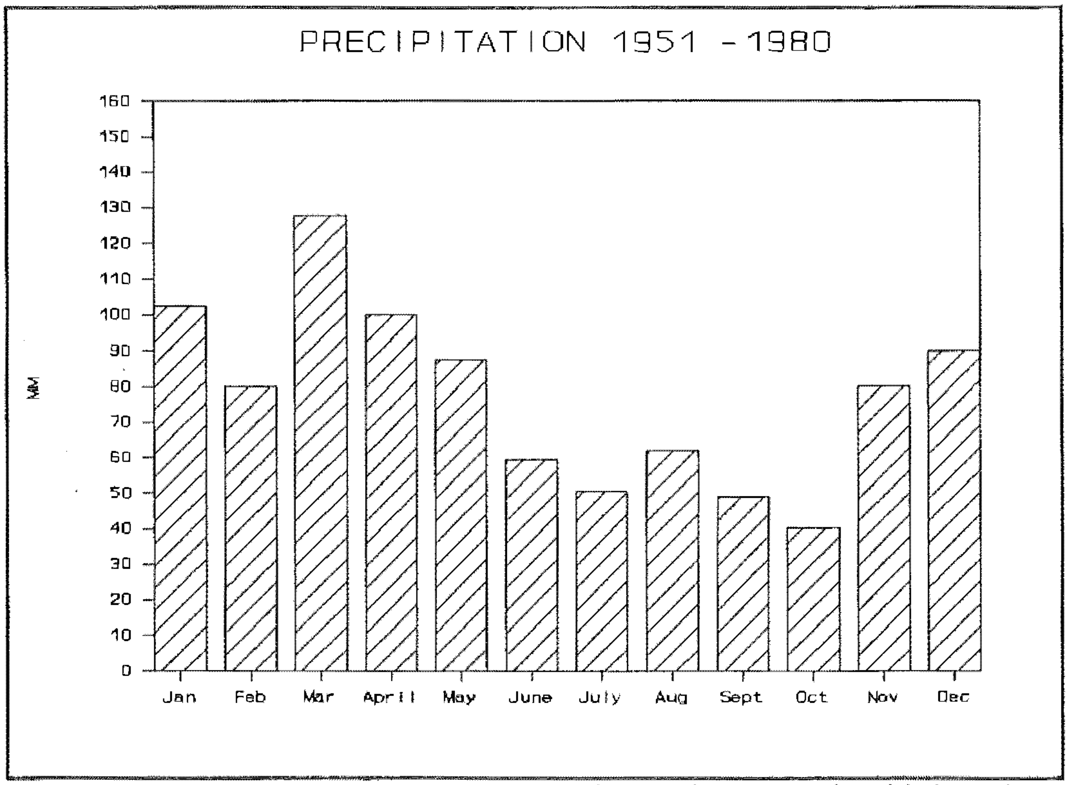



**Figure 3.** Average annual precipitation totals.

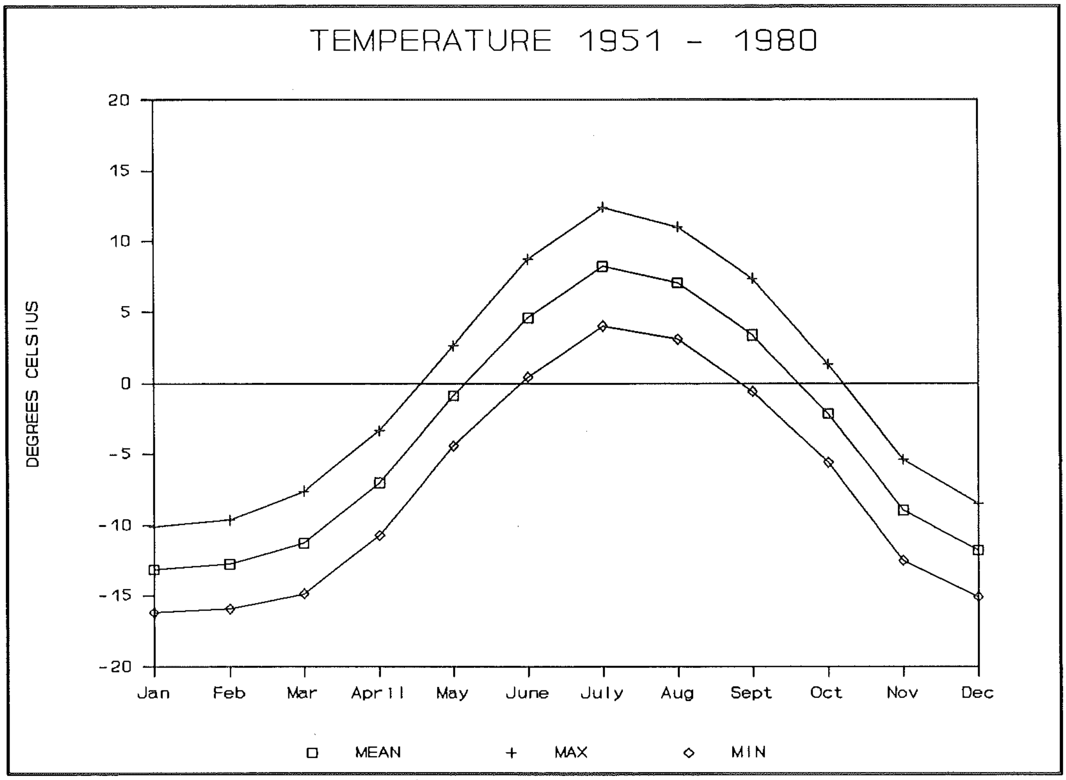
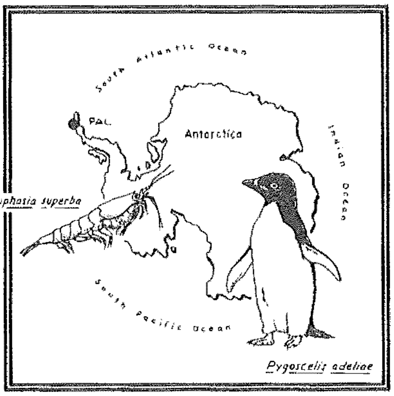



**Figure 3.** Average annual temperature values.

* Data from on-site or nearest weather station.




# Palmer Station Antarctica (PAL)

## RESEARCH SETTING

Research at the Antarctic marine LTER site, Palmer Station and surrounding waters, will focus on the pelagic marine ecosystem and the ecological processes which link the extent of annual pack ice to the biological dynamics of different trophic levels. In polar environments, the annual advance and retreat of the pack ice is an important physical feature covering vast areas of the marine environment. In the Southern Ocean this seasonal cycle of ice formation and melting affects about 50 percent of the open sea.

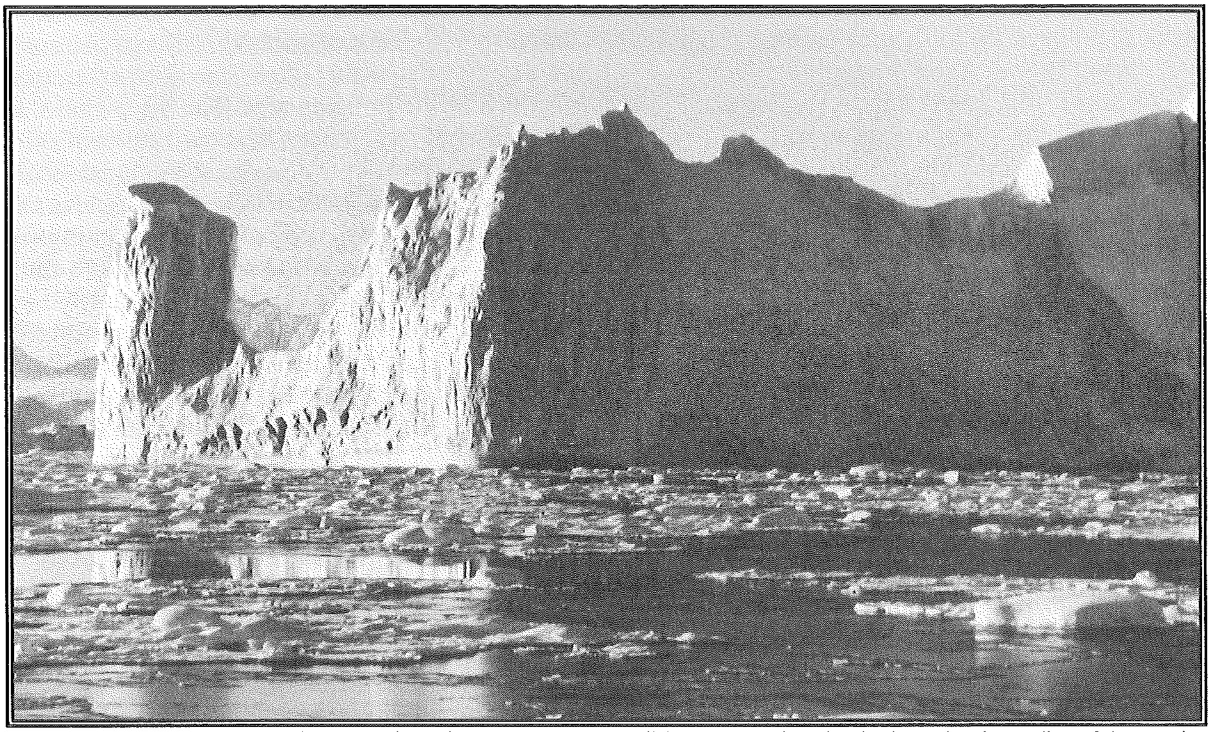
Pack ice not only provides marine habitats distinct from open-water habitats, but also may be the major physical determinant of temporal/spatial changes in the structure and function of polar biota. Thus interannual cycles and/or trends in the annual extent of pack ice are likely to have significant effects on all levels of the food web, from total annual primary production to breeding success in seabirds. The amplitude and phase of interannual variability in the regional extent of pack ice is not the same in all sectors of the Southern Ocean. In the region around Palmer Station the maximum extent of pack ice varies widely, from near zero to halfway across Drake Passage, and appears to be on a six- to eight-year cycle (Figure 1).

Although the antarctic marine food web is as complex as any other marine food web, the links between primary producers, grazers and apex predators (seabirds, seals and whales) are often short and may involve fewer than three or four species. Predators tend to concentrate on a core group of species, especially some extremely abundant euphausiids (krill) and fish close to the base of the food web. Our general approach capitalizes on this close coupling between trophic levels, the limited number of species involved, and the fact that the dominant predators are seabirds that nest on land and are efficient collectors of their prey items within the foraging area around the rookeries.

Seabirds collect prey samples for us for various physiological and biochemical analyses, and aspects of seabird foraging and reproductive biology will be used as indices of prey abundance and availability. Because these seabirds are easily accessible during the spring and summer breeding season, these indices can be evaluated with greater precision than can the biomass and distribution of their prey by classical oceanographic methods. Although aspects of the biology of dominant consumers may be good indices of prey abundance and availability, we are also examining the mechanisms behind changes in prey levels within the foraging area—such as changes in water mass distribution, variability in reproductive and recruitment success of the prey, and food availability during critical periods of the prey's life history.

### *Pack Ice / Biological Community Interactions*

In the Southern Ocean, pack ice affects primary production in three communities: open water communities, ice-edge blooms, and ice algae. The



*Zodiacs (small inflatable boats) are used as platforms for SCUBA diving near and under the ice edge in studies of the sea-ice microbial communities.* LANGDON QUETIN

stable layer created by melting pack ice and increasing incident radiation in the spring promotes ice-edge blooms that precede blooms in open water in the surrounding seas. Ice-edge blooms are a significant component of total productivity in the Southern Ocean, and variation in the timing and amount of ice-edge bloom production from variation in the extent of pack ice will affect both total primary production and the timing and extent of food availability to the grazers. Although low levels of primary production are detectable in winter, because primary production is limited by light, food availability for herbivores is intensely seasonal and spatially variable. Although macronutrients seldom limit primary production, there may be times during intense ice-edge blooms or within the sea ice when nutrients do limit production.

Growth and reproduction of the dominant herbivore, the antarctic krill (*Euphausia superba*), appear to be food-limited in most areas of the Southern Ocean. The population distributions are suggestive of a close coupling between krill populations, ice dynamics and the associated ice-edge blooms. In addition, unlike adult krill, larvae and juveniles cannot survive long periods of starvation. This inability coupled with a six-month-long winter suggests that food availability in the winter must be critical for survival of larvae and juveniles. Although questions remain about the quantitative importance of ice algae, larvae and juveniles do feed on ice algae both winter and spring; and in winters with heavy pack ice cover, larvae and juveniles are in better physiological condition than in winters with low ice cover. We would predict that better physiological condition should lead to better survival and recruitment of that year class.

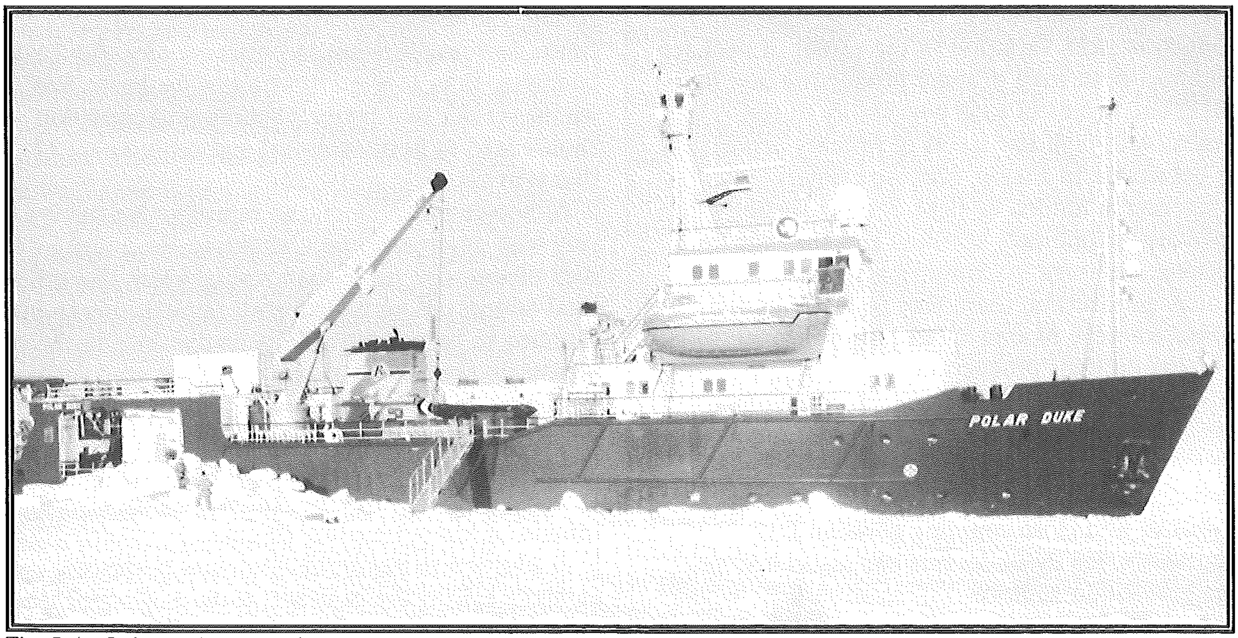
Although recruitment and reproductive success vary with environmental conditions, for animals with lifespans of more than several years like krill, total biomass in an undisturbed population can be assumed to be constant. Thus fluctuations in the mesoscale abundance of antarctic krill are usually attributed to their redistribution by physical forces, not to intrinsic features of krill biology. Abundance of adult krill west of the Antarctic Peninsula varies with year, and is greatest after winters of heavy ice cover (Figure 1).

In addition to being the dominant herbivore, antarctic krill is the principal dietary component of both Adélie and chinstrap penguins (*Pygoscelis* *adeliae* and *Pygoscelis antarctica*). Adélies are dependent on pack ice for winter survival (Figure 1) and during critical stages in the reproductive cycle. Although Adélie and chinstrap penguins depend on krill for food during summer, in some years krill are scarce within the foraging area and they must switch to prey such as the antarctic silverfish (*Pleuragramma antarcticum*), with a concomitant decrease in reproductive success.

Antarctic silverfish are one of the most abundant fish in high-antarctic marine environments, and serve as an important prey item for many consumers, including south polar skuas (*Catharacta maccormicki*). Spawning adults and the first two age classes of antarctic silverfish occur in cold shelf waters, but older juveniles and subadults move to the warmer East Wind Drift and are often found within krill swarms. Silverfish eat copepods, larval krill and other euphausiids, but rarely adult antarctic krill. Year class strength appears to be higher in years when the ice melts earlier, i.e., warmer years, and thus should be the inverse of that of antarctic krill. Although the mechanisms behind this variation are not yet clear, we believe that the abundance of copepods during the early life history may be critical to survival. The abundance of these copepods may in turn be a function of the timing of the ice-edge blooms, as has been found for shelf-dwelling copepods in the Bering Sea.

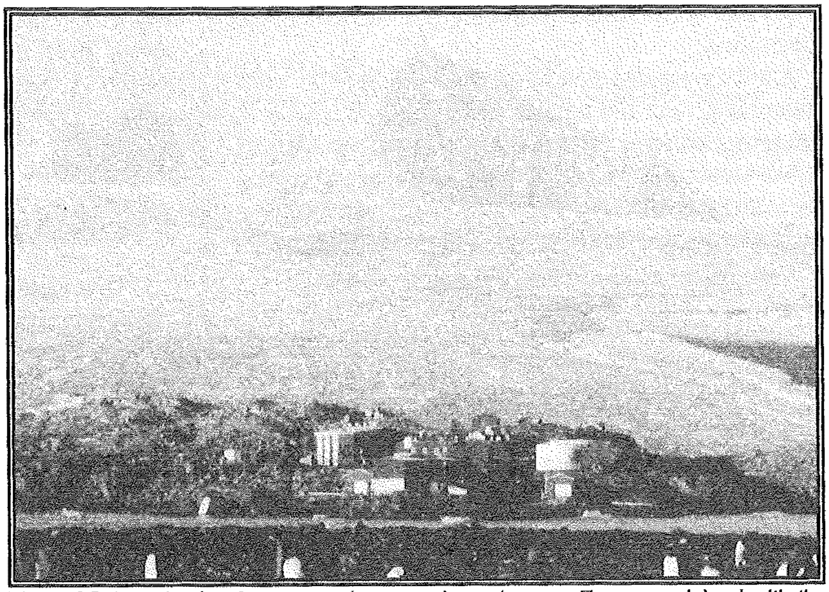
Reproductive success of south polar skuas is linked to the extent of pack ice through the abundance of subadult (Age Class 8+) antarctic silverfish in the foraging area. The lag period between high recruitment in antarctic silverfish and reproductive success in the south polar skuas is thus about eight years. Unlike the penguins that arrive at the rookery ready to lay eggs, south polar skuas depend on local food resources within the foraging range of the nesting sites to bring the female into breeding condition. If prey availability is low the female will not lay eggs, and the skuas will not attempt to breed. As a result, reproductive success (number of chicks per pair) is either zero or 1.0 to 1.5 in south polar skuas (Figure 1). In contrast, chicks are fledged per pair of Adélies, 0.67 to 1.17, with no total year class failures.

Predictions suggest that the effects of global change (climate warming, ozone depletion, and increased human pressure on resources) will be more pronounced in Antarctica than in mid-latitudes. Thus detection of these changes above the ever-present background of high natural variability will be easier in Antarctica. Monitoring the ecological effects of changes in sea-ice extent and thickness, and studying the processes underlying these effects, as recommended by the International Geosphere-Biosphere Programme (IGBP), will enable us to predict the impacts of global warming and attendant changes in the




The *Polar Duke*, an ice-strengthened research vessel, is used during time-series and process cruises. LANGDON QUETIN annual cycle of pack ice on antarctic biota. An additional concern is the seasonal thinning of the ozone layer over Antarctica which leads to increases in ultraviolet (UVB) radiation. Although research on the effects of changes in the ozone layer is not within the the core effort, we are closely connected to a separate project examining the effects of UVB on primary production.

One of our principal objectives is to separate long-term (decadal) systematic trends from large interannual variability in populations. This ability is vital if we are to measure the effects of increased human pressure on living resources. In fact, the Antarctic treaty nations signing the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) agreed not to fish any living resource (including krill) to such an extent that either the population itself or consumers depending on that food item were affected. Using the logic that consumers integrate changes over several seasons, CCAMLR is monitoring the consumers of krill rather than the krill themselves in an effort to separate interannual variability in local krill biomass from the effects of commercial fishing. With the Antarctic marine LTER we expect to understand the processes underlying interannual variability, and thus be in an excellent position to separate changes due to natural cycles from those due to commercial fishing pressure.



*View of Palmer Station from a nearby penguin rookery on Torgersen Island with the glacier and Mt. Williams in the background.* ROBIN ROSS

### Site Characteristics

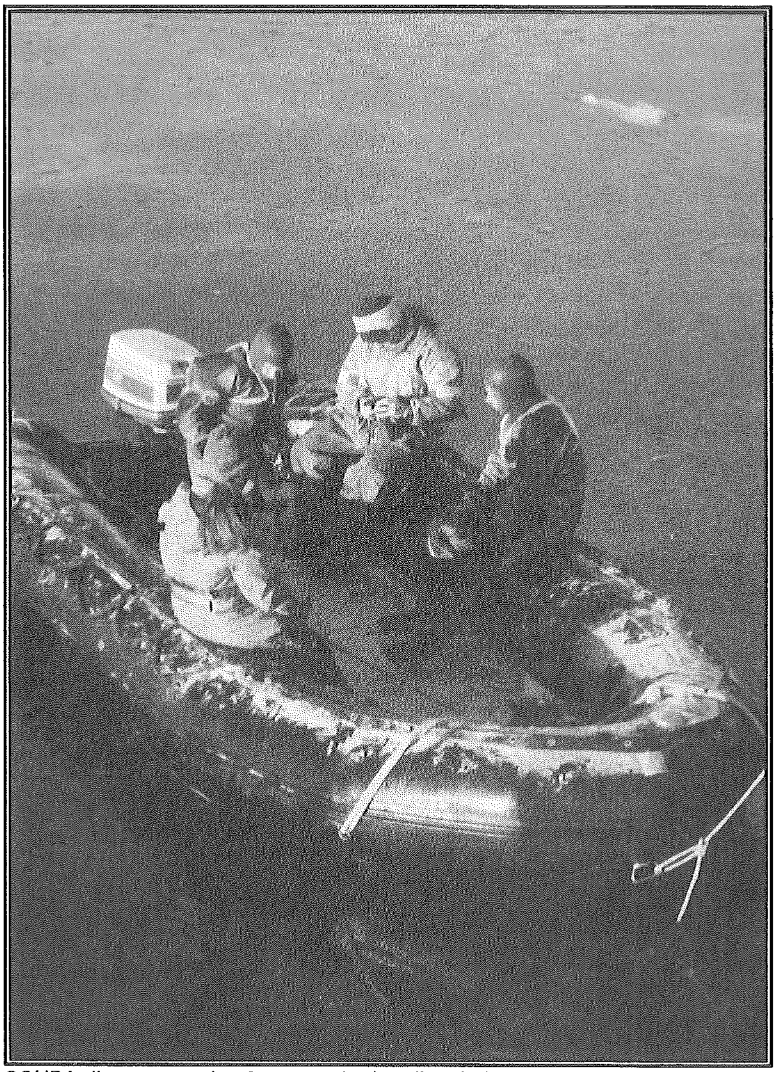
The LTER site region surrounds Palmer Station, located in a protected harbor on the southwest side of Anvers Island midway down the Antarctic Peninsula (64°40'S, 64°W). Within a 9-km radius of Palmer Station are two exposed, prominent points, and groups of islands that extend to the edge of the Bismarck Strait to the southeast. These islands have a diverse topography which extends into the intertidal and subtidal zones surrounding and linking the islands. Palmer Basin, 22 km southwest of Palmer Station, is the only deep basin in the area. The maximum depth is 1,280 m, and the basin is connected to the open ocean on the west side of Anvers Island, and to the southern end of the strait between Anvers Island and the Antarctic Peninsula to the northeast. Both channels are about 450 m deep.

The climate is typically maritime Antarctic, with snow and rain common any time of the year. The temperature at Palmer is relatively mild, averaging about -10°C in July and 2°C in January, with temperature extremes recorded at -31°C and 9°C. Annual rainfall averages about 20 inches and snowfall about 14 inches.

Mesoscale oceanic circulation patterns are reasonably well-known. A southwest setting flow (East Wind Drift, EWD) beginning around Anvers Island, feeds into a cyclonic eddy about 300 km south and seaward of the EWD. The Antarctic Circumpolar Current (ACC) flows northeast on the outside of this gyre. The extent of sea ice is highly variable in the area, with particularly severe ice conditions occurring roughly every seven to 10 years and lasting two to three years.

Palmer is especially well-situated for studies of birds, seals, and other components of the marine ecosystem, and it is equipped with a large, well-outfitted laboratory and seawater aquaria. The station consists of two major and several smaller buildings. Peak population is 43, including support personnel. Many Palmer-based research projects are undertaken in conjunction with the research ship *Polar Duke*. Small boats support research near the station.

Adélie penguins dominate the seabird assemblage, but the islands and points of land in the area also support chinstrap penguins and south polar skuas. About 12,000 pairs of Adélie penguins are distributed among five main island rookeries within two miles of the station. The Adélies from Palmer Station are believed to winter in the pack ice of the Bellingshausen Sea near Palmer. About 600 pairs of south polar skuas reside on about a dozen islands in the vicinity. During the summer breeding season, the seabirds depend on resources in the adjacent deep-water foraging area: 50-km radius for the Adélies, 160 km for the south polar skuas. Both antarctic krill and silverfish are found within Palmer Basin, within the EWD and on the eastern edge of the ACC.



*SCUBA divers preparing for an under-ice dive during the austral winter. LANGDON QUETIN*

## RESEARCH PROGRAM STATUS

Our central hypothesis states that many significant biological processes in the antarctic marine environment are strongly affected by physical factors, particularly the annual advance and retreat of pack ice and variations in ocean currents. The overall objectives of the Antarctic marine LTER are:

- to document interannual variability in the development and extent of annual pack ice, and in life-history parameters of primary producers and populations of key species from different trophic levels;
- to quantify the processes that underlie natural variation in these representative populations;
- to construct models that link ecosystem processes to physical environmental variables, and that simulate the spatial/temporal relationships between representative populations; and
- to employ such models to predict and validate the impacts of altered periodicities in the annual extent of pack ice on ecosystem dynamics.

Each component (seabirds, prey, phytoplankton) has a series of testable working hypotheses. Our general approach capitalizes on populations of seabirds that are easily accessible near Palmer Station during a prolonged breeding season, and that sample the marine environment. We are monitoring a suite of critical biological and environmental variables continuously on a small spatial scale (Palmer Station and environs) representing the seabird summer foraging area, but on a long and recurrent temporal scale (every year, the entire breeding season). We will use satellite imagery to continuously monitor certain environmental parameters such as sea ice extent and thickness, sea surface temperature, and potentially color (fluorescence) on larger spatial scales and throughout the year. In addition, automatic weather stations at several selected positions in the regions will continuously monitor atmospheric pressure, wind speed and direction, and air temperature.

Research at Palmer Station and in the surrounding nearshore marine environment focuses on the seabirds, the prey of the seabirds, primary production and hydrographic characteristics of the water column throughout the austral spring/summer. Aspects of the foraging behavior of the penguins and south polar skuas serve as indices of the abundance of the two prey items (krill and silverfish). We are monitoring processes (reproduction, recruitment) and parameters (food availability) that are sensitive to environmental change and are important in the structure and function of the communities.

To verify that this area is representative of the entire region we are extending the spatial scale of sampling of prey distribution, abundance, and physiological condition, water column properties, primary production estimates, and hydrographic measurements during two types of research cruise. (1) Time-series cruises (two weeks) are scheduled for the same timeframe every year (late spring) to survey the foraging area of the seabirds and determine how well the continuous measurements of the nearshore marine environment represent the basin as a whole. (2) Process-oriented cruises (six to eight weeks) at critical times in biological cycles will confirm that local monitoring of critical environmental parameters will allow modeling of regional processes, particularly of primary production and oceanic circulation.

The first of these pairs of cruises is planned for the fall and spring of years representing the extremes of pack ice cover. The inherent interannual variability in the extent of pack ice allows us to "conduct" natural experiments of the effect of pack ice on the various trophic levels by monitoring parameters and processes during and after seasons of different pack ice cover.

## FUTURE DIRECTIONS

We anticipate that the core program will serve as a nucleus for satellite or collaborative proposals intended to address questions of interest not presently perceived as intrinsic to the testing of our hypotheses. For example, the initial research plan does not encompass either the antarctic terrestrial or the marine benthic ecosystems because exchanges of organic matter/nutrients appear to flow one way—from the marine to the terrestrial, and from the pelagic to the benthic realm. However, research on terrestrial and benthic ecosystems could easily be conducted from Palmer Station. Thus, this LTER site may be useful for such studies in the future.

We expect that cross-site comparisons of control mechanisms of different populations (biological versus physical) and patterns of interannual spatial and/or temporal variability in populations or parameters like nutrients or dissolved organic carbon (DOC) will prove enlightening. For example, primary production in the Southern Ocean is generally believed to be light-limited, although some nutrient limitation may occur in ice algae and at the end of ice-edge blooms. Cross-site comparisons of the pattern and control of primary production and the resulting community structure and function of nutrient-limited and light-limited ecosystems would be valuable. ▫

## * *PAL Temperature Record 1974 - 1990*

*(precipitation and evapotranspiration data not available)*

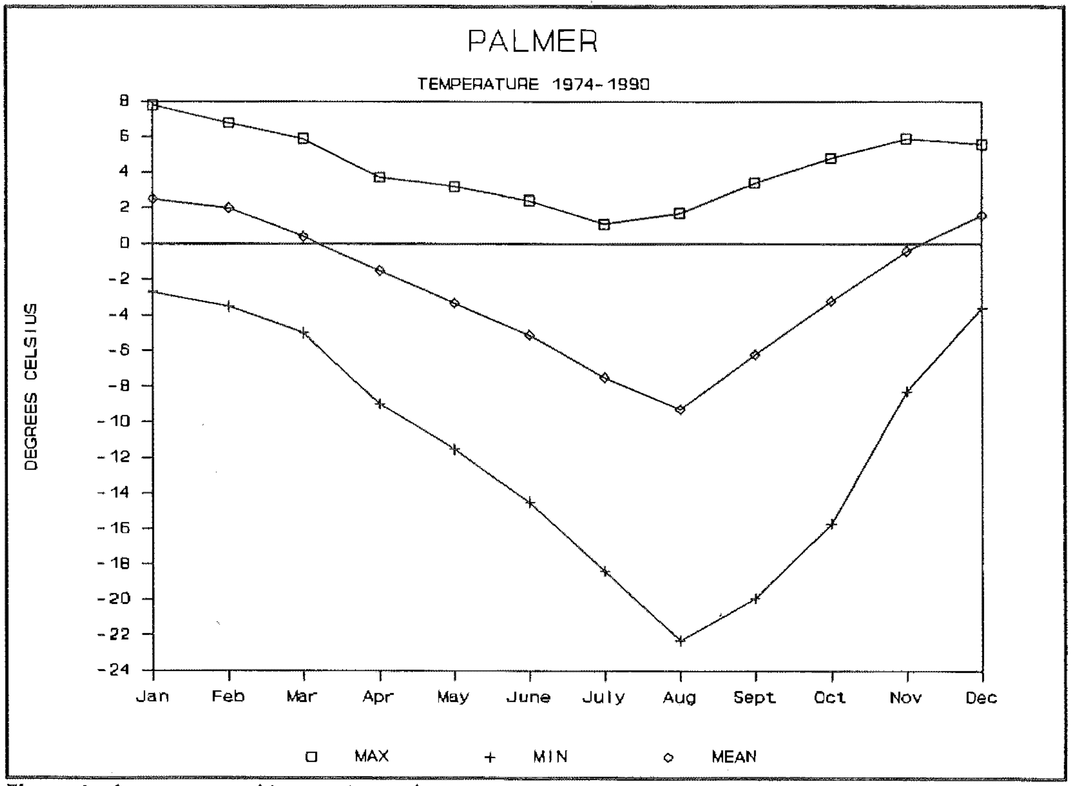
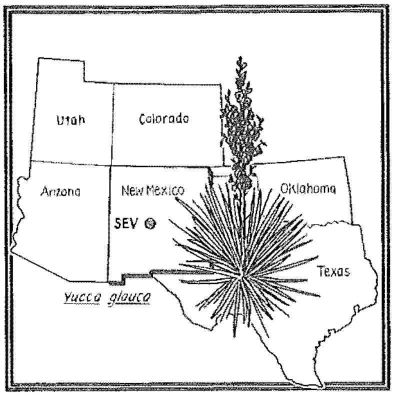



**Figure 1. Average annual temperature values.**

* Data from on-site or nearest weather station.




# Sevilleta (SEV)

## RESEARCH SETTING

The Sevilleta LTER was initiated as the Sevilleta National Wildlife Refuge, a former Spanish land grant now administered by the U.S. Fish and Wildlife Service (USFWS). The LTER program recently has been expanded to a research area of approximately 3,600 $km^2$ that ranges from Rio Grande riparian forests (*bosque*) and Chihuahuan Desert up to subalpine forests and meadows. Four dedicated research areas comprise the core sites; Sevilleta National Wildlife Refuge (100,000 ha), Bosque del Apache National Wildlife Refuge (25,300 ha), Sierra Ladrones Wilderness Study Area (28,390 ha) and the Magdalena Mountains Research Area (15,000 ha).

### Site Characteristics

The research region spans the Rio Grande River basin with elevations ranging from 1,350 m at the Rio Grande to 2,195 m in the Los Pinos Mountains in the east, to 2,797 m at Ladrone Peak in the northwest, and to 3,450 m in the Magdalena Mountains to the southwest. Climate is characterized by an intriguing combination of abundant sunshine, low humidity and high variability in most factors.

The site exists in the boundary between several major air mass zones which contributes to the dynamics of the local climate. Annual precipitation ranges from less than 100 mm to 600 mm with an average of 280 mm (100-year record). Summer precipitation occurs as intense thunderstorms often accounting for over half of the annual moisture. El Niño and La Niña events influence winter precipitation and marked variations occur on an inter-annual basis. Mean monthly temperatures range from +2.5°C to 27°C.

Topography, geology, soils and hydrology, interacting with major air mass dynamics, provide a spatial and temporal template that has resulted in the region being a transition zone for a number of biomes. The region contains communities representative of, and at the intersection of, Great Plains grassland, Great Basin shrub-steppe, Chihuahuan Desert, interior chaparral, and montane coniferous forest biomes. The elevational gradient of the Magdalena Mountains provides further transitions for interior chaparral, pinyon-juniper woodland, petran montane conifer forest, petran subalpine conifer forest, and subalpine grassland. The Sevilleta is the primary research area at this time and the research discussed below is focused on this area.

The most significant features of the Sevilleta are its very large size, its location at the transition between a number of biomes, and the high biological and environmental diversity. The transitional area that occurs between any pair of biomes occurs over a large area. The transition can express itself in a number of ways as soils, geology, topography, climate, etc., change in space and over time. The transitional area represented by the Sevilleta is superb for studying the ecological effects of climate change. The effects of climatic change will occur over a range of temporal and spatial scales and the Sevilleta represents an opportunity to examine many of them. Climate signals are comprised of a rich set of physical "behaviors." We anticipate that the Sevilleta will demonstrate a wide range of biological "behaviors" in response to the dynamics of climate. At one end of the spectrum, the entire 100,000 ha can be viewed as a single pixel and will show variations in spectral reflectance from seasonal to annual and longer. Analyzing different reflectance measurements will allow interpretations of plant biomass and productivity (greenness indices), moisture, soils, etc., at very broad scales across a range of temporal scales. At another point in the spectrum, species are subject to genetic change and demonstrate an evolutionary response to climate dynamics, at both fine and broad scales.

In between these examples is a rich diversity of other biological and ecological features that can be utilized to evaluate climate change. It is hypothesized that many of them will demonstrate relatively unique "behaviors" and thus represent a rich set of "tools" for study. The Sevilleta LTER is attempting to employ a wide diversity of biological and ecological "tools" capable of quantifying the range of responses to climate change. We have planned a balanced research approach from genes to landscapes.

## RESEARCH PROGRAM STATUS

This section identifies the multiple approaches that will take advantage of the Sevilleta site's large size and valuable characteristics as a biome transition zone for testing our hypotheses. The approaches are designed to emphasize scales and levels from landscape to phenotypic plasticity.

### *Box Transects*

The principal, large-scale environmental gradients on the Sevilleta are related to the north-south and east-west characteristics of meteorologic dynamics and topography. We have established three box transects, 3 km wide, boundary to boundary.

*The Sevilleta National Wildlife Refuge lies in the transition zones of several biomes, including the desert-grassland-woodland transition shown above.* JAMES GOSZ

Transect 1 traverses the large flat plain parallel to the Los Pinos Mountain range on the east side (26 km). This transect minimizes topographic and soil variation but maximizes seasonal temperature and precipitation variation due to north-south patterns of climatic variability or change. It spans the biotic gradient from shortgrass-shrub steppe to Chihuahuan Desert elements on fine-textured sedimentary soils.

Transect 2 parallels the topographic features on the west side (19 km). This transect shows Great Basin influence, more heterogeneity, and more soil variation than the Plains transect. Soil texture contributes significantly to the steepness of soil moisture gradients in our system. The west side transect spans the biotic gradient from Great Basin shrub-steppe to Chihuahuan Desert elements.

Transect 3 (east-west) will intersect the maximum topographic variability running from Ladrone Mountain across the Rio Grande Basin to the Los Pinos Mountain Range (50 km). Vegetation ranges from conifer woodland (*Mogollon flora*) at upper elevations on Ladrone Mountain to the Great Basin flora at its base, riparian-bosque vegetation along the Rio Grande, Great Plains shortgrass east of the river, and back to conifer woodland on the Los Pinos. This transect will incorporate climatic influences on orographic effects, precipitation-runoff relationships, and topographic modification of climatic change.

A 3-km width was chosen to provide a 1-km core transect with a 1-km buffer on each side allowing remote sensing analyses from aircraft to satellite. Remote sensing is being performed on 100 percent of the transect areas with 30 m (TM) to 1 km (AVHRR) coverage. Remote sensing, aircraft photography, balloon photography and ground truthing identify gradients in spectral reflectance, species distributions, and substrates. Within the transect, 1 $km^2$ plots were chosen to concentrate plant transect measurements. We concentrate biological research activities on the transects for short periods (two weeks) during winter (conifer greenness), spring (cool season greenness) and summer (warm season greenness).

### Watershed Studies

The justifications for including a watershed approach within the proposed Sevilleta LTER are:

- Watercourses amplify variation in precipitation, especially in arid and semiarid regions where there is a nonlinear relationship between variation in precipitation and variation in runoff. Hence, biological responses (demographic, functional, etc.) to changes in mean climate will be magnified along ephemeral watercourses;
- drainage networks have a natural, hierarchical organization and scale by both size and dynamical behavior, with the smallest watersheds flowing at high frequency and low magnitude and large watersheds at low frequency and high magnitude;
- watershed studies have as a central focus, movement of water across the landscape, the focal constraint in our proposed study, and represent especially steep, spatially predictable, gradients (e.g., from drainage channel to hillslope) in water availability; and
- watershed-based analyses will allow comparative studies with other LTER sites (e.g., Andrews, Coweeta, Hubbard Brook) with Sevilleta representing the arid end of the continental-scale gradient.

The watershed studies are based upon a conceptual view of watershed processes developed in the Negev Desert. The focus is on biotic responses to the hydrologic redistribution of water as a consequence of interaction between scale, climate, local geology, and microtopography. These interactions result in spatially predictable patterns of average runoff intensity and frequency. A diverse pattern of high and low soil moisture gradients is formed in the landscape as a consequence of the non-uniformity in runoff generation and infiltration over the heterogeneous patches of rock and soil. In turn, this unevenness in soil moisture distribution affects soil salinity gradients, and nutrient distribution, which amplify landscape heterogeneity. In this model, interactions result in spatially predictable patterns of average runoff intensity and frequency which are translated, via biotic responses, into variation in ecosystem structure (e.g., biomass) and function (e.g. rates of decomposition) across a landscape. Recent studies of El Niño/La Niña effects on the Sevilleta also identify temporal predictability at certain scales. Thus, our observational and experimental watershed studies may (1) form a model for studies of other constraints which change across scales in other landscapes, and (2) form an empirical basis in attempts to link ecological studies to regional and global biogeospheric studies.

We are studying eight ephemeral stream sites nested within the Rio Salado drainage with watershed areas spanning several orders of magnitude (four at 12 ha, two at 75 ha, one at 1,000 ha, one at 350,000 ha). At these sites we monitor precipitation, surface flow, sediment dynamics, soil moisture, primary production and litter production by riparian plants, and surface and sub-surface decomposition.

### *Common Garden Studies*

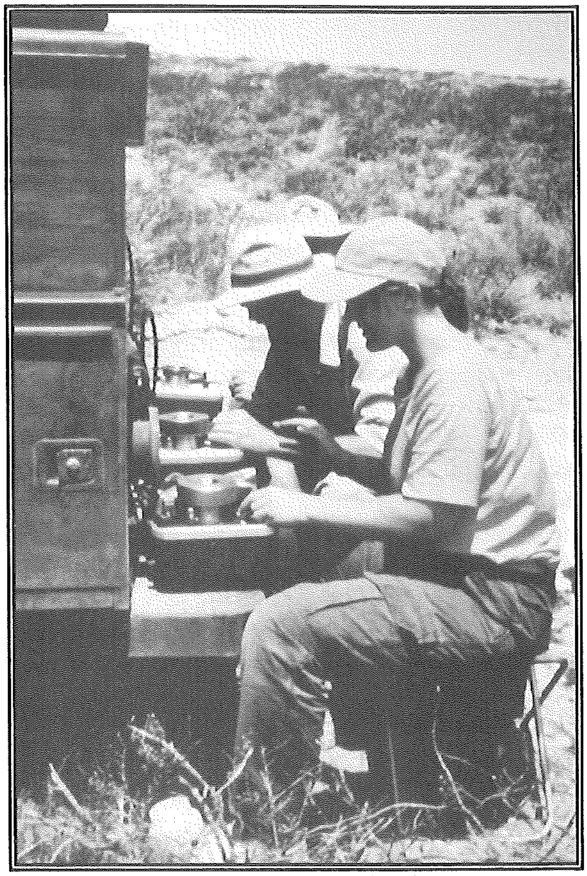
Common garden studies provide a means to identify the role of genetic variation and plasticity in species' response to environmental contraints and change. These studies are aimed at the level of the individual and will not account for competition, etc. This technique tests for the effects of climate change by bringing plants from other regions and evaluating their performance under a different climate (a form of space-for-time substitution).

Predictions suitable for experimental testing in common gardens include: (1) Genetic differentiation in species has occurred among regional LTER sites and will continue to occur over time at any given site. Changing climatic conditions will be a rapid selection force. (2) Altering the moisture regime will change the competitive balance among $C_3$ and $C_4$ plant species. The partitioning of resources between $C_3$ and $C_4$ plants is in part caused by differences in root morphology selected for by growth in warm or cool seasons. (3) Climatic change can increase the vulnerability of species to herbivores due to changes in plant secondary chemistry. (4) Climatic-caused changes in community level patterns result from differences in colonization ability of seedlings. This ability is expressed best in disturbed areas.

### *Exclosure Experiments*

The Sevilleta represents a 100,000-ha exclosure experiment relative to other lands in New Mexico because of the exclusion of cattle grazing. Fence-line contrasts are marked and a number of "inside-outside" studies have quantified the effect. Within the Sevilleta a range of experiments are being performed to isolate the effects of certain taxa. These range from litter decomposition bags (that exclude certain litter fauna) to rodent exclosures and antelope exclosures. Excluding certain fauna removes a process, often on a specific system component (e.g., forb removal by pronghorn), that can be used in conjunction with other manipulations (e.g., fire, irrigation) to control community composition and evaluate its response to climatic variations such as El Niño/La Niña events.

Exclosures or enclosures of other types of organisms such as kangaroo rats can influence soil disturbance rates and magnitudes and evaluate species response to climate dynamics on sites relatively free from competition by established



*Pressure-bomb measurements of midday plant-water status at the desert-grassland transition. R. PARMENTER*

communities. The utilization of natural agents (i.e., biological control) to design manipulative, broad-scale experiments for studying potential climate change response is an innovative and inexpensive approach. Fortunately, the Sevilleta is large enough to utilize this approach.

### *Spatial & Temporal Population Studies*

**Plant Populations:** Our ideas focus on the interaction between climatic change and evolutionary change. Climate change may both stretch the limits of response and change the process of evolution through climate-induced changes in population structure. For long-lived species it is crucial to understand the limits of phenotypic response. We are accomplishing this in two ways. For long-lived conifers, stable isotope analysis of existing tissues is used to explore the ability to respond to past changes in the environment and the limits of conditions that have been survivable. The limits of phenotypic response of grasses are explored by subjecting clonal material to a variety of conditions. For shorter-lived species, genetic change is possible. We collect seeds of several species, store them, and investigate genetic and phenotypic differences in plants grown from the seeds after they have been collected for at least five years. We also are exploring the effects of short-term climatic change on the evolutionary process by investigating the effects of La Niña and El Niño conditions on gene flow and reproduction in current populations. The measurement of vegetative density and cover (by species) provides a starting point for an interdisciplinary study of process-scale dependence and the role of population dynamics. Vegetation measurements across long time and large spatial scales yield information on how changes at the landscape level influence succession, as well as how fine-scale processes regulate community change.

In addition, changes in the interactions of plant and herbivore populations due to climatic change may occur in the LTER time scale. Climatic change may lead to changes in plant defensive chemistry that can increase or decrease plant vulnerability to herbivores. Existing spatial variation in habitats may be used to magnify these effects. There may be genetically distinct populations across habitats within the Sevilleta or across LTER sites. The effects described above are also likely to be magnified for species at the margins of their ranges. Such species, near the limits of physiological tolerance, are most likely to be affected by short time scale changes in climate. Permanent transects document population changes through space and time. Our studies document spatial and temporal patterns in species distributions, genetic plasticity, growth forms, and habitat occupation.

**Animal Populations:** We are quantifying movement of individuals, dynamics of populations, abundance and distribution of species, and trophic and taxonomic composition of assemblages of rodents, large herbivorous mammals, birds, lizards, and surface-active arthropods. In addition, rates and patterns of genetic change (in isozymes and mitochondrial DNA clones) are monitored in rodents and reptiles. These measurements are made over a sufficient range of spatial and temporal scales to: (1) document the response to heterogeneity across the entire site, and (2) assess the detailed response of individuals and local populations to both natural environmental change and to our experimental manipulations.

Animal populations and assemblages are monitored on two levels: extensively at selected sites along the permanent transects to document natural spatial and temporal variation, and more intensively in conjunction with several experiments to monitor responses to these perturbations. Along the transects, small mammal populations are sampled on replicated 3-ha plots. Birds are sampled using replicated variable circular plots. Lizards are sampled using shaded pitfall traps in combination with drift fences. Surface-active arthropods are collected in pitfall traps.

Some of the small mammals and lizards captured in this sampling regime are sacrificed and preserved as museum specimens for morphological, reproductive, parasite, and genetic data using techniques developed at the Museum of Southwestern Biology (MSB). Specimens are stored and recorded using the MSB's existing computerized information retrieval system, which is interfaced with the project's data management system. Populations of antelope, mule deer and waterfowl species are monitored by the USFWS.

**Past Human Populations:** The vital framework for interpreting patterns of human adaptations in the Sevilleta over broad stretches of time includes mapping of past human settlements in space and time, and charting of specific climatic events on the same time scale. Archeological surveys are locating, dating and estimating size and type of human residence and work sites across a specific segment of the landscape. We visualize production of a series of maps of human settlement over time within the Sevilleta, revealing the distribution of this population in sites of varying sizes and types.

From these will proceed an analysis of settlement patterns with respect to plant communities, geography, and changing climate.

### *Patterns & Frequency of Disturbance*

We are aware of the scale-dependent nature of perturbations and their incorporation by system components and hierarchical levels. Disturbance is viewed across many scales ranging from antelope hoof-marks in the soil crust between plants to individual plant mortality (gap dynamics), to mammal mound activity, to frequency and intensity of flooding/scouring in ephemeral streams, to grassland fires that are increasing in frequency and to decadal patterns of climatic change. The acquisition of Global Positioning Systems (GPS) by the LTER Network will allow detailed mapping of the varied types of disturbances to build a history of the spatial dynamics associated with these disturbances.

### *Retrospective Studies*

Packrat middens also provide a key to the past. Some date to 11,500 years ago and in general they show advances and retreats of plants and a relatively recent invasion by creosote (*Larrea tridentata*). The middens also are being analyzed for insect species changes and rodent species changes (taxonomy based on hair DNA). DNA amplification techniques may allow analyses of evolutionary change in given species.

Aerial photos from the 1930s on allow analyses of large shrub and tree dynamics, especially the widespread mortality of Juniper during the 1950s drought. We are initiating a collection of historical photos from Socorro County, New Mexico and are starting repeat photography to document community changes.

## FUTURE DIRECTIONS

### *Regional Transects*

We believe that the most successful approach to evaluating climate change is to analyze regional LTER and other sites as points along environmental gradients. No single site can verify that changes within it are solely due to climate change. Individual sites are fine-scale features relative to scales associated with climate change and many local, site-specific factors can complicate (reduce or amplify) the responses to climate change. Networks of sites will be required to represent the large spatial scales needed to recognize and document changes that occur at those scales. Such networking allows sites to work on a common time scale and synchronize efforts at quantifying responses to large scale environmental phenomena.

For example, an El Niño or La Niña ocean/climate event may cause very different responses among different ecological parameters at one site and among different sites. Each site has many interacting, site-specific factors; however, the initiation of the responses may well be caused by the El Niño/La Niña phenomena, a triggering effect which could be common to all sites. Such networks could identify the spatial scale of the phenomena, the times of initiation and conclusion, and the types of ecological responses that were similar and dissimilar. For some sites it could separate the triggering response from the subsequent chain of events (succession of events) until a new triggering event occurred. Some portions of regions may respond while others may not. This networking could help identify the significance of various types of constraints on systems, the regional extent of those constraints, and the sequence of ecological phenomena that is typical following changes in these constraints.

We believe transition zones can play a special role in studies of change detection and extrapolation across regions; however, changes in these zones must be compared with sites along gradients in several directions to fully evaluate their significance. We intend to develop cooperative agreements with the Central Plains and Jornada LTER sites, and the Los Alamos National Environmental Research Park (NERP). Each site would provide common garden space for reciprocal transplants of species which co-occur in both their area and Sevilleta. This cooperation will allow us to investigate the genetic and phenotypic basis for variation in vegetation along the north-south, east-west, and elevational gradients that cross the region. We also intend to extend the gradient analysis and comparison into central Mexico to the Mapimi Biosphere Reserve. The Mapimi represents a climate dominated by warm-season moisture and the core of the Chihuahuan Desert.

There is a continuum of studies and experiments that can be performed ranging from documenting natural change in the biome transition zone to various manipulations. Some of the studies discussed above (e.g., common garden studies) could be viewed as manipulation experiments as well as taking advantage of changes on natural gradients. Thus, the following experiments extend the research proposed above on climate change.

### *Novel Communities*

Recent developments in the study of scale and its ecological effects have implications for topics of global change, resilience, and stability. First, we now know that a "system" such as a forest or a desert is only an "entity" with respect to the spatial and temporal extent and resolution used by the observer. An individual 1-$m^2$ plot in a "boreal" forest has too few elements of the forest to actually be the forest. Rather, an arbitrarily large region with repeating elements (e.g., spruce trees, moose, and aspen trees) is required before the forest is recognized as such. Humans generate typological concepts of systems when sufficient spatial redundancy and temporal persistence is observed to warrant assigning a name to a system. Unfortunately this has led to our tendency to view systems as static, and to think that disturbances and perturbations are somehow unnatural interferences with the *status quo.*

The paleoecological record shows that the boreal forest as we know it has been assembled relatively recently from species that behave individualistically. Indeed, the individualistic responses of North American tree species indicate that, in the face of climatic change of the magnitude currently predicted, we should expect little natural integrity in the systems we recognize currently. Therefore, according to existing models, we should expect that studies focusing on existing "systems" are likely to see the systems dissolve in 15 to 20 years, as the component species go extinct or migrate to other locations, thereby forming novel systems. An important research theme should focus on how members of the biota, including humans, evolve or acclimate to accommodate new and almost certainly novel interactions among themselves and with abiotic elements. The nature of these new assemblages, their dynamics and the implications for the persistence of all species are the central issues. These novel associations currently occur in many forms on different substrates over much of the Sevilleta: various combinations of Chihuahuan, Great Basin, Great Plains and Mogollon (conifer woodland) flora. In addition, various exotic species (primarily from the steppes of Eurasia) occupy these novel assemblages of North American flora.

The order in which species are added to or removed from a community may alter the dynamics within the community as well as ecosystem processes. The timing and competitive abilities of the species may alter the future trajectory of the community. An added issue is the role of a constantly changing climate during the course of succession. Experiments can be designed to vary the order of addition and removal in a number of novel communities on the Sevilleta. A given experiment can be repeated annually to identify the role of interannual variability (El Niño/La Niña events) on the success or influence of the novel community.

### *Burning/Exclosure Experiments*

Natural fires have become more common on the Sevilleta during recent years as a result of the large "standing dead" grass component (grazing was stopped in 1973) and the natural high frequency of lightning in July. Three natural fires occurred during the summer of 1989 and five occurred in 1990. The influence of fire is very species specific as perennial grasses with large belowground root systems (e.g., blue gramma of the Great Plains flora) survive while Chihuahuan species (e.g., black grama, desert shrubs) are eliminated. Thus, in this tension zone between Chihuahuan and other biomes, fire may be a primary agent in controlling species movement due to climate change. Fire can only occur and spread where there is sufficient standing fuel; thus, its effect may only be important in areas where Chihuahuan species are becoming established in grassland communities.

In areas where the desert species have been established for a longer period of time, the grass component is greatly reduced and fires are rare or nonexistent. The natural fires allow studies of species changes and effects on subsequent ecosystem processes. Fire represents a useful tool to facilitate species removal experiments as called for in previous sections.

The movements and feeding activities of pronghorn antelope in these same grasslands also create ecosystem disturbances at a number of scales, ranging from local, physical trampling effects to widespread selective herbivory on grassland plants. Pronghorn antelope and mule deer have replaced domestic cattle as the dominant ungulate herbivores in this ecosystem. However, the magnitude of influence of pronghorn on the Sevilleta grassland ecosystem remains unknown at this time. In addition, it is unlikely that this grassland system has stablized since the removal of cattle, and that future changes in such ecosystem attributes as soil organic matter and nutrient pools, plant community structure and productivity, and nutrient cycling and energy flows, will continue to be observed as the "restored" system evolves. Throughout this recovery period, pronghorn antelope activity may prove to have an important influence on the successional trajectory of the grasslands.

Our planned research will use a replicated two-by-two factorial experimental design, in which the factors are Burn/No Burn and Pronghorn Present/ Pronghorn Absent. The four distinct treatments are replicated four times, for a total of 16 study plots. Each study plot is 300 m x 300 $m^2$ (9 ha), separated from other study plots by at least 300 m. Eight of the 16 plots are fenced to exclude pronghorn antelope; the other eight are left open. Eight plots (four open, four fenced) are subjected to controlled burns.

Generally, natural fires in desert environments occur most frequently after wet years (when fuel loads are high following increases in plant growth), and are started by summer lightning-strikes. Our purpose in this experiment is to simulate the natural sequence of wildfire occurrences. As such, controlled burns will take place during the summer (during periods of natural lightning-ignition events, i.e., May through September) of certain "burn years," years preceded by a wet, El Niño year. We anticipate that these criteria will call for burning the plots once every three to five years.

As the proposed experiment continues for many years into the future, we will be able to correlate observed trends in biotic responses to the treatments with numerous wet and dry precipitation cycles. These analyses should provide significant insights into the role of climatic fluctuations and long-term global climate warming on ecological processes in the grassland ecosystem. Increased fire frequencies may be one of the results of climate change (e.g., more dry lightning storms in early July). Annual experimental burns can provide a spatial template on which natural variations in El Niño or La Niña events can be evaluated as well as the interaction between fire and moisture regimes.

### *Watershed Manipulations*

In addition to monitoring natural watersheds at different scales, entire watershed manipulations are possible, aiding in the interpretation of climate change scenarios. The fortuituous position of some watersheds allow significant increases in stream flow without irrigating. In one situation, the stream of a large, upper watershed passes within several meters of the upper boundary of a lower watershed. A simple pipe diversion can add significant quantities of water to the stream bed of the lower watershed and simulate the effects of increased winter precipitation (spring discharge) on the riparian communities of the lower watershed stream. The predictions would be that species would migrate up in elevation dependent on their life-history strategies and dispersal mechanisms. We hypothesize that long-lived species are present in the lower reaches of a given basin streambed since those areas receive infrequent, but large flow events. The long-lived nature of the plants allows persistance between the infrequent events. These species are prevented from moving up the stream bed because although the frequency of discharge events increases at higher elevations in the watershed, the volume of water is too small to be effective. If the volume of water throughout the watershed stream system is increased, they should migrate up the stream bed providing seed sources for the adjacent watershed area.

Concurrent with the stream diversion from the upper watershed, downstream areas on that watershed should demonstrate the inverse pattern; an increasing mortality that progresses from higher to lower reaches of the stream channel. The long-lived nature of those species may cause a significant lag in their mortality response; however, short-lived organs (leaves, flowers, fruits) may demonstrate the response. This experiment would provide a valuable test of the hypothesis that stream systems and their riparian communities will magnify the effects of climate change. ▧

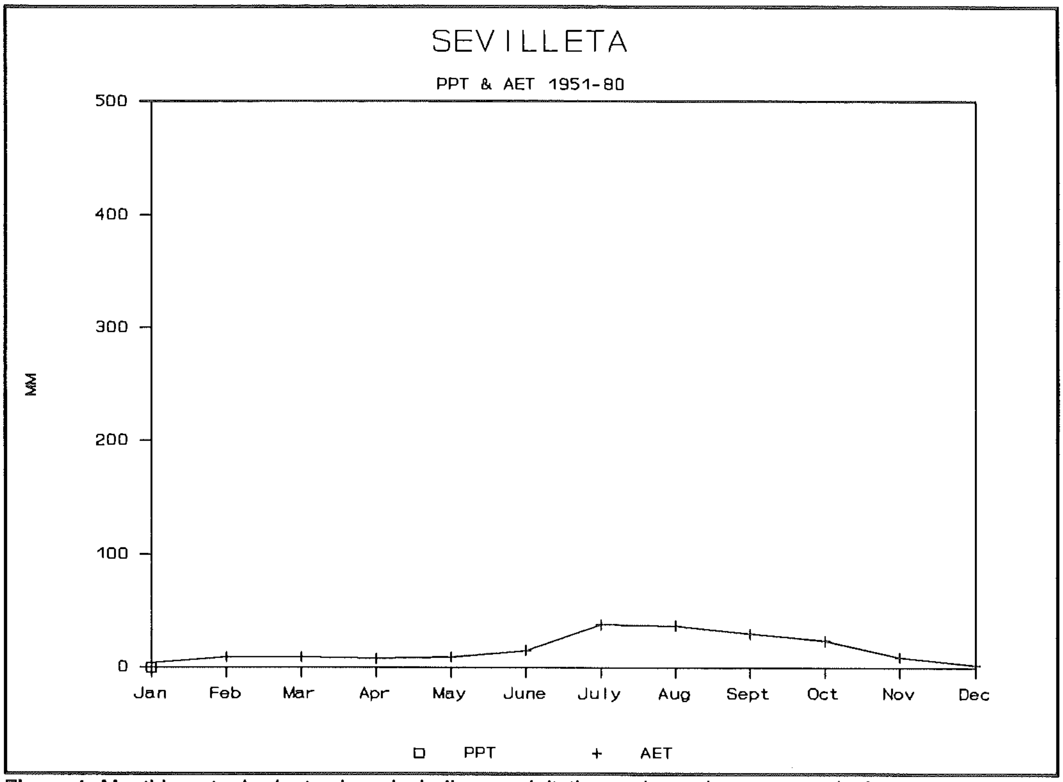



**Figure 1.** Monthly water budget values, including precipitation and actual evapotranspiration.

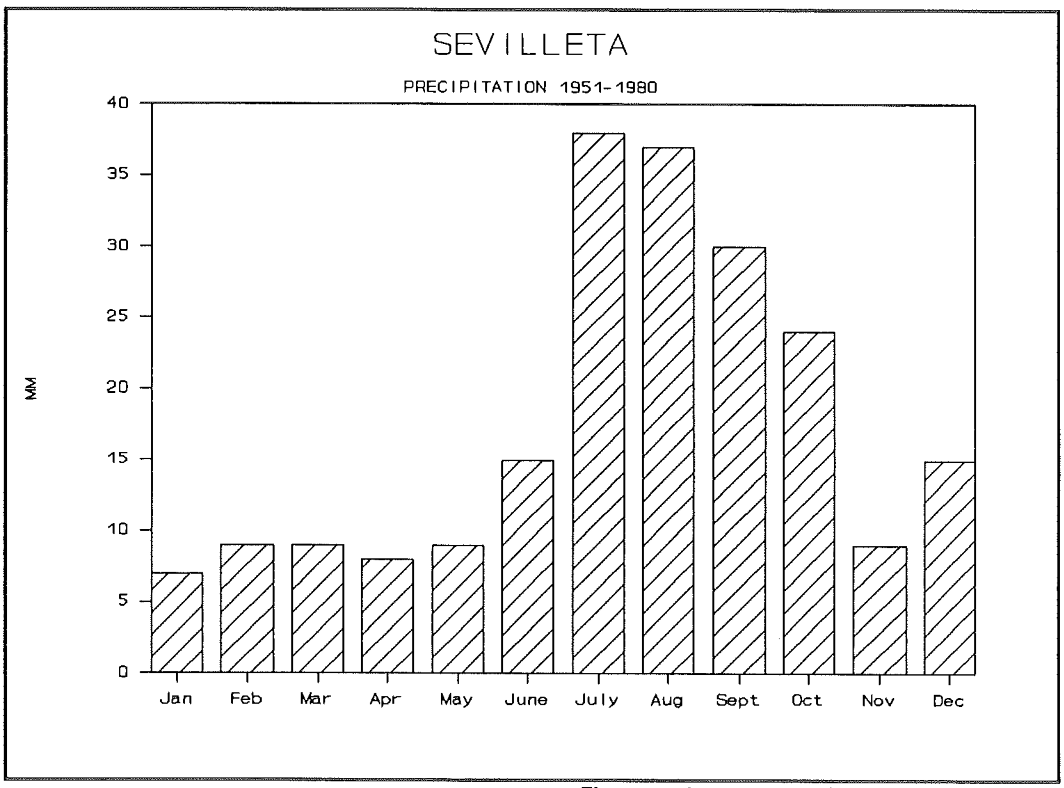



**Figure 2.** Average annual temperature values.

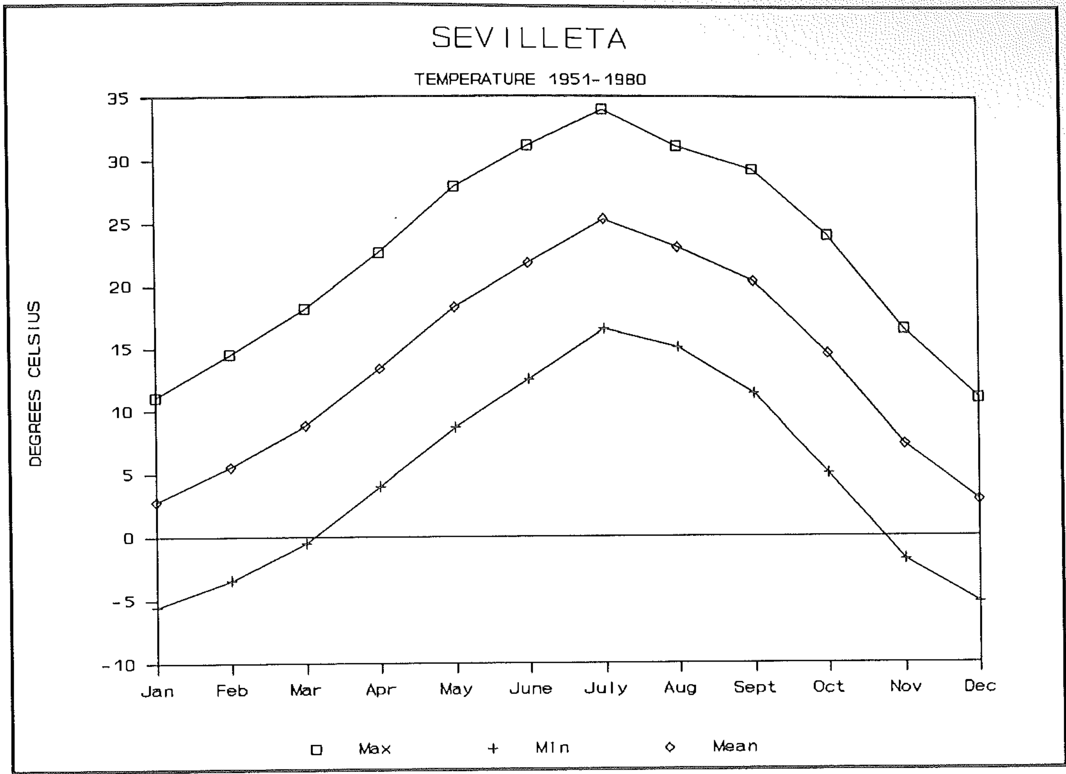
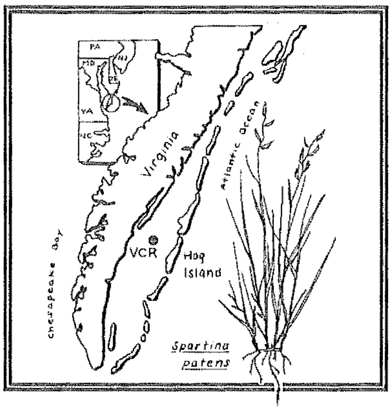



**Figure 3.** Average annual precipitation totals.

* Data from on-site or nearest weather station.




# Virginia Coast Reserve (VCR)

## RESEARCH SETTING

The Virginia Coast Reserve of The Nature Conservancy is a complex assemblage of 14 major barrier islands, associated inlets and beaches, extensive back barrier islands, shallow bays and deeper channels, mud flats, expansive salt marshes and contiguous mainland ecosystems. From a research perspective the site possesses exceptional qualities. The low-lying landscape (mean elevation of less than two meters) provides an unusually sensitive location for the study of the ecological effects of climatic variability on time scales ranging from daily tidal variations and individual storms through longer term changes in precipitation and, ultimately, eustatic sea-level rise.

For example, variation in daily tidal range controls marsh zonation patterns. Individual storms can cause extensive changes in dune plant communities and also contaminate shallow aquifers with enough salt water so that effects on plants can be detected for years. Storm flooding causes extinction of some small mammal species from low-lying islands and may shift community composition for decades or centuries. Drought can lower barrier island water tables to the point that both shrubs and trees are affected or excluded.

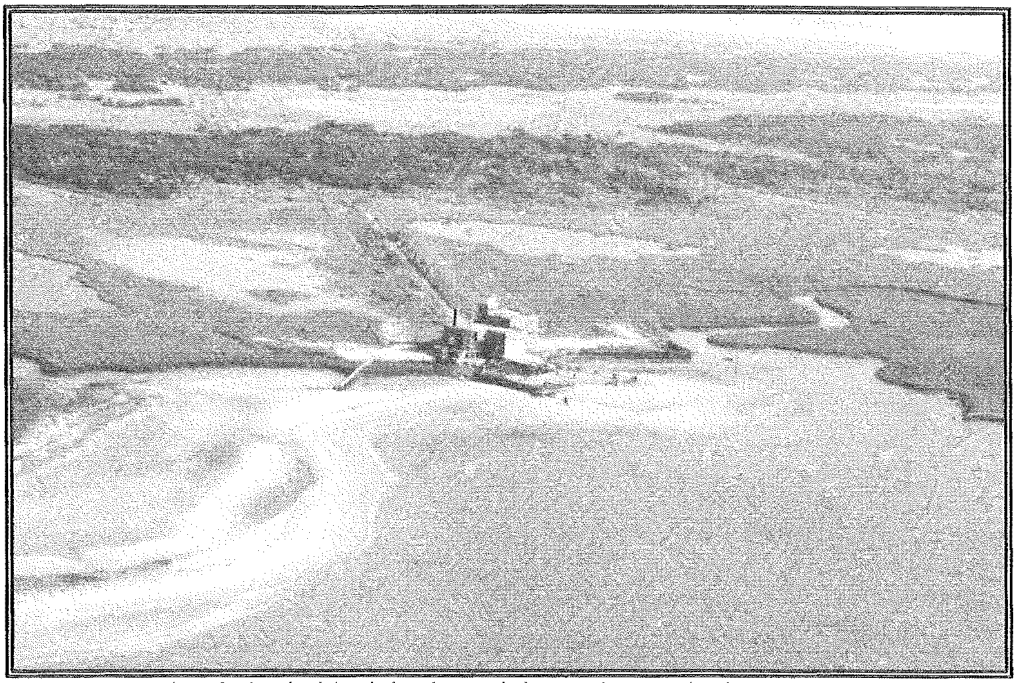
On longer time scales, even tiny fluctuations in sea level between years can have major effects on coastal marsh productivity. Sea-level change of a few centimeters over several years can alter tree species dominance in the estuarine/upland ecotone. Ultimately, long-term changes in eustatic sea-level control landscape dynamics as evidenced by rapid changes in island, inlet and marsh morphology have been documented even in historical times.

Often, the result of these geophysical perturbations is a major system state change in which an ecosystem undergoes a transformation to a new type of ecosystem. For example, rising sea level can cause a transition from low-lying forests to salt marsh in a few decades or salt marsh to sub-tidal mud flats in a few years; a major storm can convert vegetated dunes to unvegetated open beach in a single night. The VCR LTER is a special site in that major system changes are unusually common and can be monitored effectively.

The dynamic nature of the Virginia Coast Reserve is further enhanced by its permanent ownership and protection by The Nature Conservancy and its existence as a Man and the Biosphere (MAB) site. This status guarantees protection, continuity, and research opportunities into the foreseeable future and strongly supports the concept of a long-term research program.

### Site Description

The Virginia Coast Reserve (VCR) extends approximately 100 km along the seaward margin of the Delmarva Peninsula from Assawoman Inlet southward to the mouth of the Chesapeake Bay. Included are over 14,000 ha of principal barrier islands and the associated ecosystems of intervening lagoons, back islands, and marshes. Fringing mainland areas are composed of forest, freshwater marshes, agricultural fields and fishing villages. Most LTER research projects are concentrated upon a belt transect stretching from Hog Island on the seaward edge of the VCR to the Brownsville plantation on the mainland. A few projects, particularly those dealing with processes at the landscape level of organization, include the entire VCR plus contiguous areas such as Assateague, Chincoteague and Wallops Islands and the eastern portion of Chesapeake Bay.



*Accretionary portion of a barrier island showing evolutionary phases of landscape from open water to salt marsh and vegetated dunes.* TERRY COOK

The contemporary barrier island-lagoon-mainland complex took its present form during the late Holocene rise in sea level, although the underlying framework can be traced back to earlier high stands of sea level during the Pleistocene. Rapid change has taken place during the last few thousand years with the island complex migrating westward across the continental slope at a rate as great as a kilometer per thousand years. As a result the modern islands typically exhibit dynamic shoreline change characterized by local deposition and erosion rates as high as 13 m per year and major changes in island morphology on a decadal scale.

The climate of the VCR is dominated by extratropical storms (i.e., northeasters) and by tropical storms and hurricanes. Each year an average of 38 extratropical storms occurs with magnitude sufficient to rework beach sands and to elevate tides above astronomical norms. These storms are largely responsible for changes in the morphology of the islands, the associated vegetative cover and, ultimately, in combination with sea-level rise, for the landward migration of the islands across the lagoonal marshes. In effect, this site is a perpetual experiment in ecosystem disturbance and plant succession.

The vegetation of the islands, marshes and nearshore sections of the mainland is conspicuously patchy, with distinct zonation and sharp transition between patches. High and low salt marshes, unvegetated sand and mud flats, grasslands, shrub savannas and maritime forests occur in close proximity, with sharp ecotones. Vegetation heterogeneity is futher accentuated by interannual climatic variation. Precipitation records indicate a range of variation between 85 to 140 cm a year. This arises primarily from variation in summer rainfall, with thunderstorm frequency influencing local land/sea temperatures. In addition, 45 percent of late summer and autumn rainfall comes from tropical storms.

While the barrier islands have been inhabited sporadically since the landing of Captain John Smith in 1608, they are currently isolated, uninhabited and relatively little changed from the natural state. The adjacent Delmarva Peninsula supports a rural population dependent primarily upon agriculture and fisheries for subsistence. Land use is 29 percent agriculture, 29 percent woodland, 32 percent tidal marsh, 2 percent beach and 8 percent miscellaneous. Currently, anthropogenic effects are largely restricted to sediments and agricultural chemicals washing into VCR watersheds. In the future, there will undoubtedly be a major shift in land-use patterns since this section of the coast is one of the least settled and developed coastal areas in the United States.

## RESEARCH PROGRAM STATUS

The VCR LTER project focuses upon understanding changes of system states or, more simply phrased, transitions from one type of ecosystem to a totally new ecosystem at the same geographical location. These transitions may span short, intermediate or long time scales. Typically, they occur in response to geophysical processes (storms, long-term sea-level changes, climate change, etc.) although they may result from biological processes associated with ecological succession or human-induced alterations (Table 1.)

Certain fundamental research questions can be addressed in all of these cases:

- What is the basic cause of the state transition? Is it due to biological or geophysical processes? Did it occur in a stochastic or deterministic manner? Was it a short-term or long-term process?
- Are there differences in state transitions caused by geophysical versus biological processes? For example, is organic carbon lost during geophysically driven transitions in contrast to carbon/nitrogen accumulation in biologically driven transitions?
- What is the frequency of state transitions in the past? What factors affect this periodicity?
- What processes act to keep an ecosystem in the same state for extended periods of time? Under what conditions do "internal" ecological processes resist "external" geophysical forces of change?
- How are ecological processes affected by state transition? For example, what are the patterns of primary production, decomposition, nutrient cycling, population dynamics, etc., during and after a transition event?
- Are state transitions linear or are there multiple alternate system states in the future? Under what circumstances do transitions occur in reverse to an earlier state?
- How does a state transition event affect nearby, contiguous ecosystems? Since there are usually extensive connections between adjacent ecosystems, alterations to one can have cascading effects across the landscape. Introduction of agriculture during the 17th century on the eastern shore of Virginia profoundly affected the sediment and nutrient movements into adjacent marshlands and shallow lagoons which, in turn, altered the mean elevation relative to sea level.
- How can research on ecosystems state transitions be utilized for management purposes? This is particularly critical for The Nature Conservancy in its effort to manage the populations and ecosystems of the Reserve. As an example, the management of endangered populations such as certain shore birds, requires a thorough understanding of habitat nesting requirements; in many cases, a key limiting factor is the shortage of recently altered beach overwash areas, a relatively uncommon and short-lived system state.

*Dynamic boundary between salt marsh and mainland forest.* *LUIS LAGERA*

### *Research Plan*

Our research plan, as outlined in the following sections, is designed to understand state transitions at the Virginia Coast Reserve by combining information from the paleontological record with contemporary studies of the interplay between ecological and geophysical processes. The research effort is built on a combination of stratigraphic studies, long-term field monitoring, field experimentation, remote sensing and the hybridization of Geographic Information Systems (GIS) techniques with simulation modeling.

Terrestrial. Because the VCR is a large and complex region and because system state transition events are frequent and widespread, we have chosen to focus most of our field monitoring and experimentation upon several state transition sites. To accomplish this effectively and maximize inter-action between researchers, the LTER effort is divided into three fundamental work-ing groups. The first is the terres-trial team who are concerned with sites which lie above mean high tide. They have chosen to study transects which cross a major barrier island, Hog Island, along with several locations on the mainland. Included in these transects are ecosystems which have recently passed through or are poised to pass through a major transition. Particular emphasis has been placed on recently overwashed and flattened dunes and on vegetated dunes which have not been flooded for decades. The role of the island's subsurface water table aquifer has emerged as a key research question both because it influences the composition, distribution and productivity of the patchy terrestrial vegetation and because it provides an important link to subtidal processes studied by the second group.

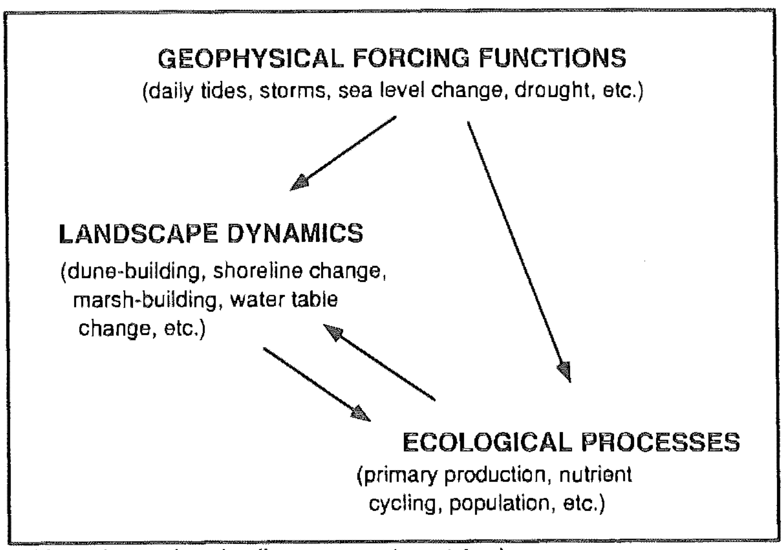



*Table 1. Interactions leading to ecosystem state changes.*

Aquatic. The water team focuses upon several transects on the island and mainland which cut across the "dynamic edge" spanning the land-sea ecotone from subtidal mud flats and marshes to adjacent salt-stressed wetland and low-lying terrestrial ecosystems. This group is investigating the changes in surface elevation, porewater chemistry, nutrient cycling, vascular plant composition, decomposition and other parameters which accompany both short and long-term changes in sea level. Sediment porewater, its movement, chemistry and connectivity to the shallow terrestrial aquifer, has emerged as a key focus.

Large-Scale Monitoring & System State Changes. The final group, the GIS and modeling team, is responsible for monitoring and studying system state changes on a much larger scale, including all of the VCR and, even in some cases, selected island-lagoon systems along the U.S. Atlantic Coast. Emphasis is placed upon the temporal and spatial character-istics of system state changes which can be identified from remotely sensed data, and analyzed with GIS techniques and simulation models. Examples include changes in distribution and size of terrestrial vegetation patches, marshes, beaches, dune fields, overwash fans, inlets, mudflats, etc., from the mid-19th century (maps) to the present (aerial color/InfraRed photography, multiple-band imagery, etc.).

Long-term monitoring activities form the core of the VCR LTER research effort and, at the same time, generate a number of exciting research questions. The terrestrial team monitors changes in vegetation including species composition, productivity, patch dynamics, root dynamics, and decomposition rates above- and belowground.

Table 2. System state changes at Virginia Coast Reserve LTER site.

| State Change | Cause |
|---|---|
| lagoonal seagrass beds to muddy bottoms | seagrass wasting disease |
| sea-side agricultural fields to salt marsh | sea-level rise |
| upland forest to salt marsh | sea-level rise |
| freshwater marsh to salt marsh | sea-level rise |
| salt marsh to sub-tidal mudflat | sea-level rise |
| maritime forest to grass-covered dunes | island erosion pattern change |
| grass-covered dunes to shrub-covered dunes | ecological succession |
| grass-covered dunes to open beach | major storm |
| forests to agricultural fields | human alteration |
| shrub forest to grass-covered dunes | saltwater contamination of acquifer, salt spray |

Small mammal and shore bird populations are followed annually. Geophysical data includes changes in meterology, topography and water table height and geochemistry. The water team monitors changes in mudflat and marsh surface topography, porewater chemistry, marshgrass dynamics, belowground decompostition and carbon accumulation rates, and marsh surface fish and invertebrate populations. Paleontological data is monitored from analyses of cores including sediment type, CS-137 and Pb-210 dating, forams and other characteristics. Finally, the GIS data is obtained from maps, historical and current National Aeronautic and Space Administration flights and other imagery.

The Reserve's research plan should lead to a better understanding of the details of major state changes caused by climate change, sea-level rise, storms, ecological succession and human activities. As an example, how does the frequency and duration of salt water innundation affect wetland and terrestrial processes such as primary production, nutrient cycling, gas exchange to the atmosphere, carbon accumulation in soils, and animal population fluctuations? Given certain state changes in the future, how can we manage a barrier island system such as the VCR for optimal conservation goals? These are among the objectives for the project and our host, The Nature Conservancy.

## FUTURE DIRECTIONS

It appears that modern landforms within the coastal barrier system are strongly influenced by earlier Pleistocene landforms. For example, the present location of inlets between barrier islands probably reflects small river valleys during lower stands of sea level. This helps to explain the apparent compartmentalization of the coast into repeating landscape units which cut across the entire system from mainland to inner continental shelf waters. The concept of repeating landscape units, possibly on several spatial scales, has significant implications for understanding ecological processes and state changes at the landscape level of organization.

About 1870 a major shift occurred in the dynamics of the islands of the VCR. As a result, islands such as Hog Island, in the middle of the LTER intensive box transect, experienced dramatic changes in patterns of erosion and deposition. This led to widespread system changes including inundation of grasslands, forests and human settlements over the next century as the shoreline receded in some areas over one kilometer. Future research will explore the long-term ecological effects related to this key event.

The unconfined water table aquifer apparently plays a major role in influencing plant distribution on barrier islands. Contamination of this aquifer by overwashing seawater or a drop in the piezometric head due to drought can influence germination, growth and even presence or absence of shrub and tree species. In future research, the connection between water table morphology and the patchy distribution of VCR plant communities will be investigated.

Seasonal changes in sea level, due to shifts in prevailing winds, can alter the tidal marsh water budget sufficiently to raise porewater salinities in the higher sections of the intertidal zone and suppress net primary production dramatically and even create totally unvegetated zones near mean high tide. Longer-term sea-level change permanently influences the marsh/upland ecotone. Future research is aimed at monitoring and predicting the effects of sea-level change on upland plant communities.

In biogographical studies of small mammal species, mitochondrial DNA analysis has been proven to be an effective index of species mobility. For example, this technique allows investigation of population phenomenon over short periods of time (e.g., differences in genetic composition of populations on the mainland and islands at varying distances and of different size, elevation and flooding frequency). Ultimately, this should allow the successful integration of genetics, population and community ecology in answering questions related to island biogeography.

### *Cooperative Projects*

In terms of LTER intersite research, scientists from the VCR are involved primarily in three areas: comparative decomposition studies, data management, and simulation modeling. The data management program has emphasized intersite projects within the LTER Network. Simulation modeling has been designed to facilitate interaction with both LTER and MAB sites. Comparison of decompositon progress is also coordinated with other sites.

An important cooperative program at the VCR LTER is with the National Park Service (NPS). The southeast region of the NPS has contracted with the University of Virginia to be responsible for both remote sensing and GIS activities associated with southeastern National Seashores. This involves considerable overlap with VCR LTER projects. For example, both groups utilize the imagery produced by NASA's high altitude photography program. Both utilize ERDAS and ARC/INFO software to create and analyze GIS files. Finally, both partners are interested in the landscape dynamics of barrier island systems. A proposed NPS program would establish a barrier island simulation modeling group at the University of Virginia with modeling objectives very similar to present LTER programs. This is a good example of how two organizations, the National Science Foundation and NPS, with compatible research needs, have combined their funding and scientific abilities to tackle research problems of common interest.

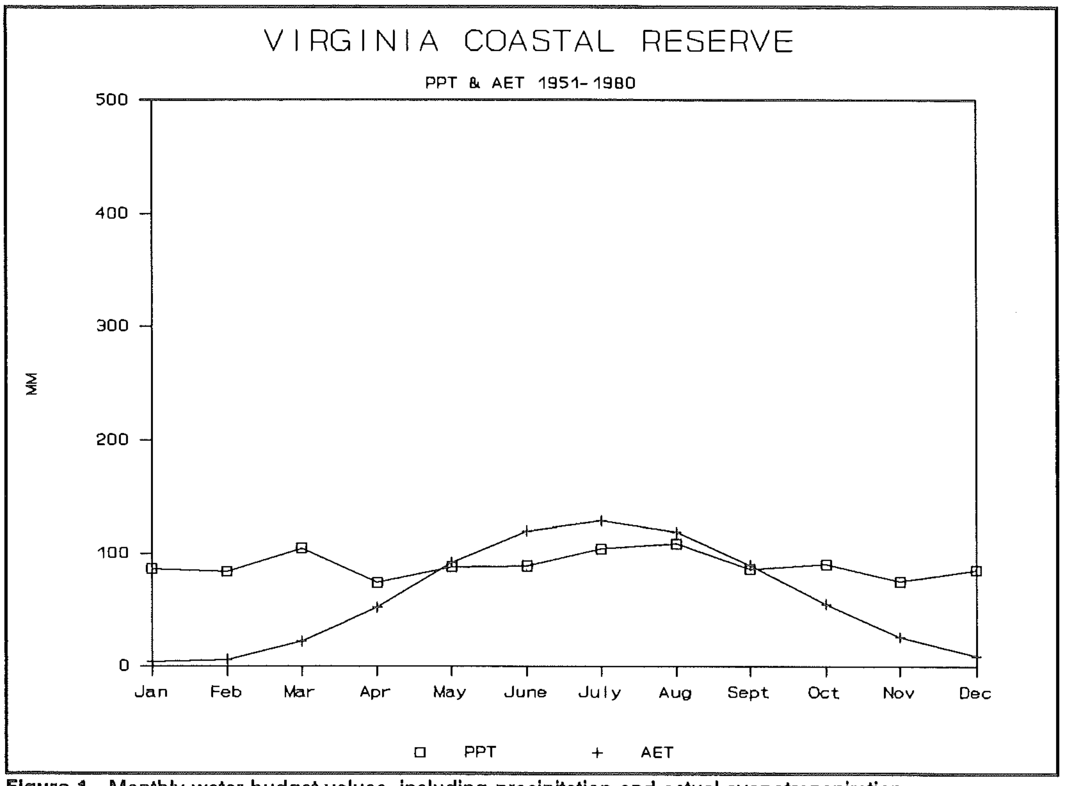



**Figure 1.** Monthly water budget values, including precipitation and actual evapotranspiration.

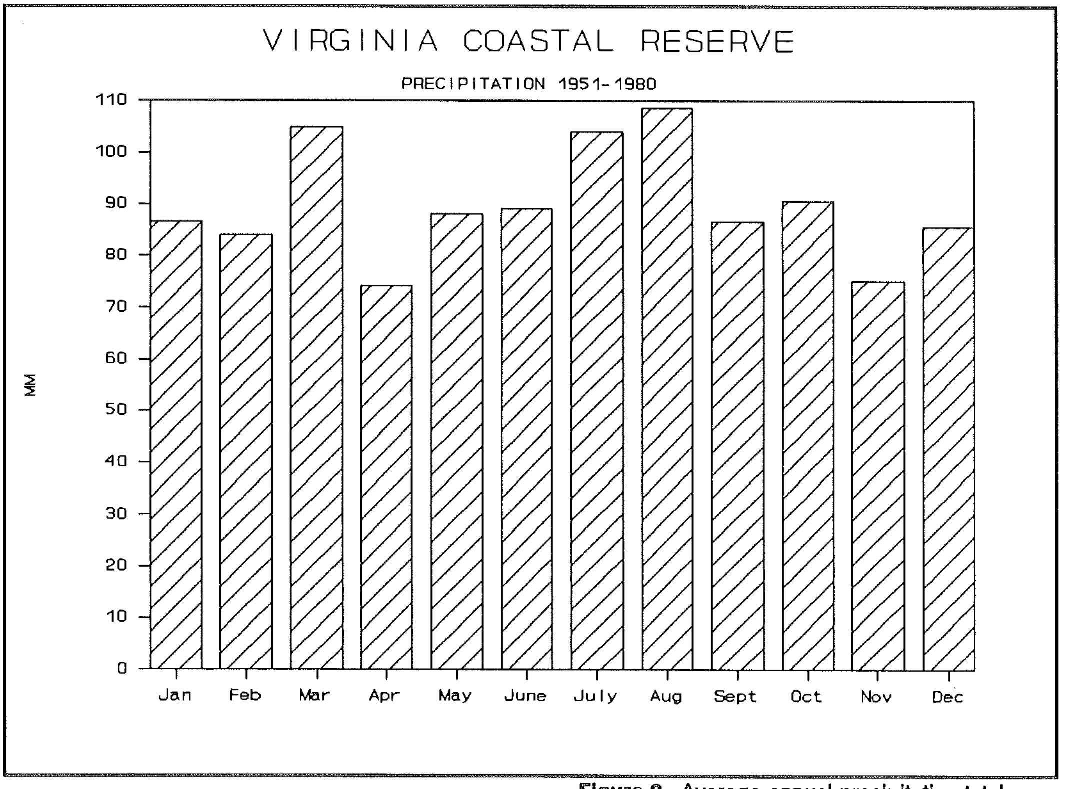



**Figure 2.** Average annual precipitation totals.

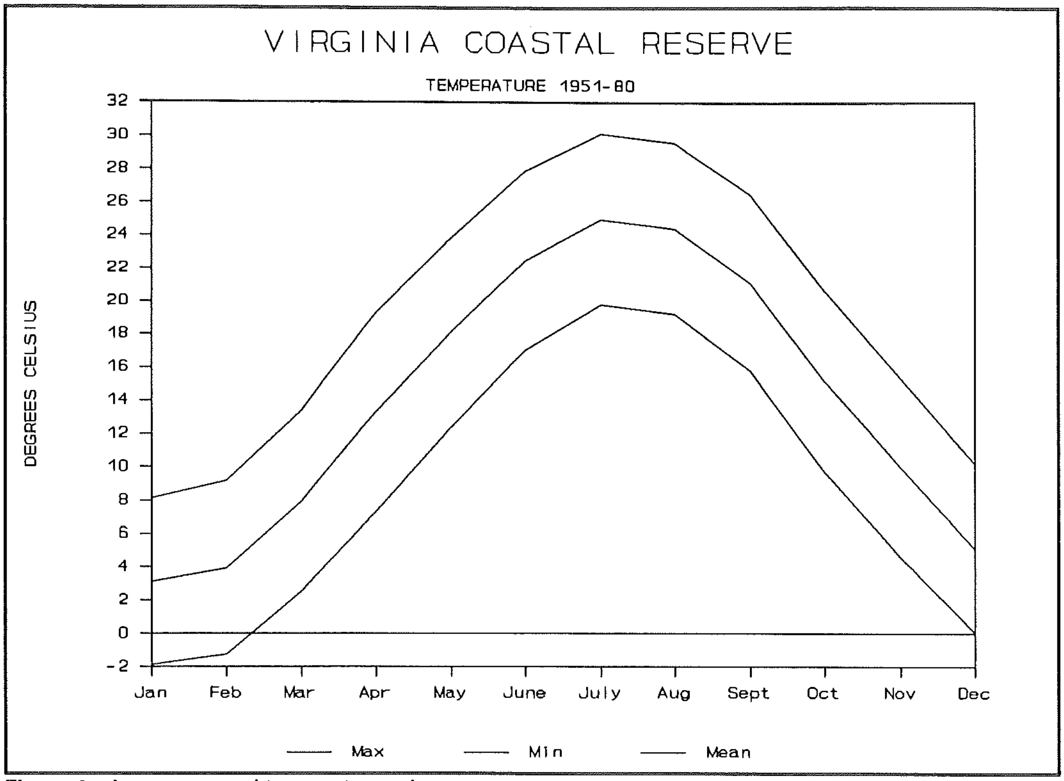



**Figure 3.** Average annual temperature values.

* Data from on-site or nearest weather station.

## *Table I.* Characteristics of the Long-Term Ecological Research Sites

| Site Abbrev/Name/Location | Institutional Affiliations | Principal Biome/Main Communities | Research Topics |
|---|---|---|---|
| **AND** H.J. Andrews Experimental Forest, Blue River, Oregon | Oregon State University; USDA Forest Service, Pacific Northwest Research Station | Temperate coniferous forests. Douglas-fir—western hemlock—western red cedar; true fir and mountain hemlock; streams | Successional changes in ecosystems; forest-stream interactions; population dynamics of forest stands; patterns and rates of log decomposition; disturbance regimes in forest landscapes |
| **ARC** Arctic Tundra, Toolik Lake, Brooks Range, Alaska | The Ecosystem Center, Marine Biological Laboratory; Universities of Alaska, Massachusetts, Minnesota, Cincinnati, and Kansas; Clarkson University | Arctic tundra, lakes, streams. Tussock tundra; heath tundra; riverine willows; oligotrophic lakes; headwater streams | Movement of nutrients from land to stream to lake; changes due to anthropogenic influences; controls of ecological processes by nutrients and by predation |
| **BNZ** Bonanza Creek Experimental Forest, Fairbanks, Alaska | University of Alaska; Institute of Northern Foresry, USDA Forest Service, Pacific Northwest Research Station | Taiga. Areas of boreal forest including permafrost-free uplands and permafrost-dominated north slopes and lowlands; flood-plain seres | Successional processes associated with wildfire and floodplains; facilitative and competitive interactions among plant species throughout succession; plant-mediated changes in resource and energy availability for decomposers; herbivorous control of plant species composition |
| **CDR** Cedar Creek Natural History Area, Minneapolis, Minnesota | University of Minnesota | Eastern deciduous forest and tallgrass prairie. Old fields; oak savanna and forest, conifer bog; lakes; pine forest; wetland marsh and carr | Successional dynamics; primary productivity and disturbance patterns; nutrient budgets and cycles; climatic variation and the wetland/upland boundary; plant-herbivore dynamics |
| **CPR** Central Plains Experimental Range, Nunn, Colorado | Colorado State University; USDA, Agricultural Research Service | Shortgrass prairie. Shortgrass steppe; flood-plain; shrubland; saltmeadow | Hydrologic cycle and primary production; community and population dynamics; organic matter aggregation or degradation; influence of erosion on redistribution of matter, nutrients, and pedogenic process; influence of atmospheric gases, aerosols, and particulates on primary production and nutrient cycles |
| **CWT** Coweeta Hydrologic Laboratory, Otto, North Carolina | University of Georgia; USDA Forest Service, Southeastern Forest Experiment Station | Eastern deciduous forest. Hardwood forests and white pine plantations | Long-term dynamics of forest ecosystems including response to perturbation; input-output elemental dynamics in forested ecosystems; land-stream interactions; consumer regulation of ecosystem processes; atmospheric deposition |
| **HBR** Hubbard Brook Experimental Forest, West Thornton, Hampshire | Yale, Cornell, and Syracuse Universities; Institute of Ecosystem Studies; U.S. Forest Service, Northeastern Forest Experiment Station | Eastern deciduous forest. Northern hardwood forests in various developmental stages, spruce-fir forests; streams and lakes | Vegetation structure and production; dynamics of detritus in terrestrial and ecosystems; atmosphere-terrestrial-aquatic ecosystem linkages; heterotroph population dynamics; effects of human activities on ecosystems |
| **HFR** Harvard Forest, Petersham, Massachusetts | Harvard University; Universities of New Hampshire and Massachusetts; The Ecosystem Center, Marine Biological Laboratory | Eastern deciduous forest. Hardwood-white pine-hemlock forest; spruce swamp forest; conifer plantations | Long-term climate change, disturbance history and vegetation dynamics; comparison of community, population, and plant architectural responses to human and natural disturbance; forest-atmosphere trace gas fluxes; organic matter accumulation, decomposition and mineralization; element cycling, fine root dynamics and forest microbiology |
| **JRN** Jornada, Las Cruces, New Mexico | New Mexico and San Diego, California State Universities; USDA, Agricultural Research Service; Duke University; Oregon Graduate Institute | Hot desert. Playa, piedmont, and swale; bajada, basin, mountain and swale shrubland; mesquite dunes | Desertification; factors affecting primary production; nitrogen cycling; animal-induced soil disturbances; direct and indirect consumer effects; organic matter transport and processing; vertebrate and invertebrate population dynamics |

| Site Abbrev/Name/Location | Institutional Affiliations | Principal Biome/Main Communities | Research Topics |
|---|---|---|---|
| **KBS** Kellogg Biological Station, Hickory Corners, Michigan | Michigan State University | Row-crop agriculture. Conventional corn/soybean cultivation; low-input corn/legume cultivation; perennial biomass cultivation; native successional communities | Agricultural productivity; nutrient availability and organic matter dynamics; herbivory and microbial pathogens; plant competition and C, N allocation; gene transfer |
| **KNZ** Konza Prairie, Manhattan, Kansas | Kansas State University | Tallgrass prairie. Tallgrass prairie; gallery forest; prairie stream | Role of fire, grazing and climate influencing ecosystem process in a tallgrass prairie system |
| **LUQ** Luquillo Experimental Forest, near San Juan, Puerto Rico | Center for Energy and Environment Research, University of Puerto Rico; Institute of Tropical Forestry, USDA Forest Service, Southern Experiment Station | Tropical rainforest. Tabonuco forest; palo Colorado forest; palm brake; dwarf forest and montane streams | Patterns of disturbance in space and time; ecosystem response to different patterns of disturbance; land-stream interactions; effect of management on ecosystem properties; integration of ecosystem models and geographic information systems (GIS) |
| **NIN** North Inlet Marsh-Estuarine System, Georgetown, South Carolina | Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina | Coastal estuary. Salt marsh; estuarine benthic; intertidal; barrier island; open beach; inshore oceanic | Patterns and control of primary production; dynamics of selected populations; organic accumulation; patterns of inorganic contributions; patterns of site disturbances, including hurricane effects |
| **NTL** North Temperate Lakes, near Boulder Junction, Wisconsin | Center for Limnology, University of Wisconsin, Madison | Northern temperate lakes; eastern deciduous forests. Oligotrophic, dystrophic and eutrophic lakes; temporary forest ponds; warm and cold streams; sphagnum-leatherleaf bog; conifer swamp; mixed deciduous and coniferous forests | Physical, chemical and biological limnology; hydrology and geochemistry; climate forcing; producer and consumer ecology; ecology of invasions; ecosystem variability; lakescape and landscape ecology |
| **NWT** Niwot Ridge/Green Lakes Valley, near Boulder, Colorado | Institute of Arctic and Alpine Research, University of Colorado | Alpine tundra. Fellfield; meadow; herbaceous and shrub tundras; cliffs and talus; glacial lakes; streams and wetlands | Geomorphology, paleoecology; plant communities, disturbance and recovery; root and soil interactions, vertebrate populations, aquatic invertebrates; decomposition and nutrient cycling |
| **PAL** Palmer Station, Antarctic marine ecosystem near Palmer Station, Antarctica | University of California, Santa Barbara; Old Dominion University | Polar marine. Coastal and open ocean pelagic communities; seabird nesting areas | Oceanic-ice circulation and models; sea-ice dynamics; biological/physical interactions; effect of sea ice on primary production, consumer populations and apex predators; bio-optical models of primary production; spatial distribution and recruitment in consumer populations; seabird population dynamics and reproductive ecology |
| **SEV** Sevilleta National Wildlife Refuge, near Albuquerque, New Mexico | University of New Mexico; USDI Fish and Wildlife Service | Multiple—Intersection of subalpine mixed-conifer forest/meadow, riparian cottonwood forest, dry mountainland, grassland, cold desert, hot desert. Conifer woodland/savanna; creosote bush; desert grassland; mesquite and sand dunes; Great Basin shrub and shortgrass steppes; tallgrass swales; riparian communities | Landscape and organism population dynamics in a biome tension zone; semiarid watershed ecology; climate change detection in a sensitive landscape; biospheric/atmospheric interations; paleobotany/archaeology; microbial role in gas flux; and control of landscape heterogeneity; scale effects on spatial and temporal variability |
| **VCR** Virginia Coast Reserve, near Oyster, Virginia | University of Virginia | Coastal barrier islands. Sandy intertidal; open beach; shrubthicket; mature pine forest; salt marsh; estuary | Holocene barrier island geology; salt marsh ecology, geology, and hydrology; ecology/evolution of insular vertebrates; primary/secondary succession; life-form modeling of succession |

## *Table II.* LTER SITES: Key Contacts, Investigators, Research Areas

***Note:*** *Most investigators below may be contacted via the LTERnet Electronic Mail Forwarding System. For a guide, send any message to: ForQuick@LTERnet.washington.edu (Internet); ForQuick@LTERnet (Bitnet); or LTERNET:X400 (US Forest Service). For other systems, contact Rudolf Nottrott, LTER Network Office, below.*

### (AND) H.J. ANDREWS EXPERIMENTAL FOREST

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**Site Director**
Arthur McKee
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Corvallis, OR 97331
503-750-7350

| Investigators | Research Interests |
|---|---|
| Kermit Cromack | Decomposition |
| Jerry Franklin | Succession, decomposition patterns |
| Gordon Grant | Fluvial geomorphology |
| Stan Gregory | Forest-stream interactions, decomposition |
| Bob Griffiths | Decomposition |
| James Hall | Fish population biology |
| Mark Harmon | Decomposition, tree mortality |
| Dave Hibbs | Plant competition, succession |
| Elaine Ingham | Decomposition |
| Gary Lamberti | Forest-stream interactions |
| Jack Lattin | Succession, entomology |
| George Lienkaemper | GIS, geomorphology |
| Arthur McKee | Succession, forest-stream interactions |
| Andrew Moldenke | Succession of soil invertebrates |
| Dave Perry | Population dynamics of stands, site productivity |
| William Ripple | GIS, remote sensing |
| Tim Schowalter | Succession, entomology |
| Jim Sedell | Forest-stream interactions |
| Phil Sollins | Dynamics of soil carbon and nitrogen |
| Tom Spies | Forest gap dynamics, succession, remote sensing |
| Susan Stafford | Information management and analysis |
| Fred Swanson | Geomorphology, forest-stream interactions, disturbance |
| Richard Waring | Succession, physiology |

### (ARC) ARCTIC TUNDRA

**Principal Investigators**
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Institute of Arctic Biology-Logistics
University of Alaska-Fairbanks
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| Investigators | Research Interests |
|---|---|
| Linda Deegan | Fish production |
| Brian Fry | Stable isotopes |
| Anne Giblin | Biogeochemical processing |
| Anne Hershey | Biotic interactions |
| John Hobbie | Microbial processing |
| George Kipphut | Biogeochemistry |
| Arthur Linkins | Soil enzymes, microbial processing |
| Michael McDonald | Lake trout, fisheries |
| Michael Miller | Nutrients, primary production |

**Table II. ARC, continued**

| | |
|---|---|
| Bernie Moller | Research coordinator, algae, water chemistry |
| Knute Nadelhoffer | Nitrogen cycling, decomposition, plant chemistry |
| John O'Brien | Zooplankton communities, predator foraging models |
| Bruce Peterson | Ecosystem analysis |
| Ed Rastetter | Ecosystem modeling |
| Donald Schell | Ecosystem analysis |
| Gaius Shaver | Plant nutrition |

## (BNZ) BONANZA CREEK EXPERIMENTAL FOREST

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| Investigators | Research Interests |
|---|---|
| John Bryant | Plant-animal interactions, influence on succession |
| Rex Cates | Successional relations, plant secondary chemistry |
| Glenn Juday | Long-term forest structure and stand dynamics |
| Mark Oswood | Soil invertebrate animal ecology |
| Bill Reeburgh | Trace gas dynamics |
| Paul Reichardt | Secondary plant chemistry |
| Roger Ruess | Plant physiological ecology, root dynamics |
| Josh Schimel | Microbial ecology, nutrient cycling |
| Keith Van Cleve | Soil-plant relations, nutrient cycling, succession |
| Les Viereck | Plant ecology, succession |
| John Yarie | Soil-plant relations, plant resource availability |

## (CDR) CEDAR CREEK NATURAL HISTORY AREA

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| Investigators | Research Interests |
|---|---|
| Mark Davis | Plant spatial dynamics |
| Don Faber-Langendoen | Community ecology, oak savannah succession, fire management |
| Eville Gorham | Ecosystem ecology of wetlands |
| David Grigal | Soil science, ecosystem ecology |
| Nancy Huntly | Plant-herbivore interaction, small-mammal dynamics |
| Richard Inouye | Evolution, plant ecology, grasshopper ecology |
| Mark McGinley | Plant colonization dynamics |
| John Pastor | Soil nitrogen dynamics |
| Mark Ritchie | Mechanisms of plant-herbivore interactions |
| John Tester | Ecology, behavior |
| David Tilman | Experimental ecology, theory |
| David Wedin | Nitrogen dynamics in grasslands |
| Scott Wilson | Disturbance, productivity, and ecosystem structure |
| Don Zak | Soil science, microbial ecology |

## (CPR) CENTRAL PLAINS EXPERIMENTAL RANGE

**Principal Investigator**
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| Investigators | Research Interests |
|---|---|
| Ingrid Burke | Biogeochemistry, ecosystem ecology, plant ecology |
| Debra Coffin | Plant ecology, modeling |
| Donn Decoursey | Hydrology, modeling |
| James Detling | Primary production, plant-animal interactions |
| Donald Doehring | Geomorphic processes |
| Jim Forwood | Consumer dynamics |
| Jon Hanson | Plant physiology, modeling |
| Roger Hoffer | GIS |
| Donald Hazlett | Plant ecology, taxonomy |
| E.F. Kelly | Plant ecology, geomorphology/hydrology |
| Thomas Kirchner | Systems ecology, modeling, data management |
| Timothy Kittel | Climatology, remote sensing, modeling |
| William Lauenroth | Plant ecology, modeling, root productivity |
| Daniel Milchunas | Grazing ecology |
| William Parton | Meteorology, nutrient cycles, modeling |
| Osvaldo Sala | Plant ecology, climatology |
| David Schimel | Soil organic matter, element cycling |
| Marvin Shoop | Range management |
| B. VanHorne | Consumer dynamics |
| John Wiens | Animal movements in landscapes, landscape ecology, scaling |
| Robert Woodmansee | Landscape ecology, biogeochemistry |
| C.M. Yonker | Geomorphology/hydrology |

## (CWT) COWEETA HYDROLOGIC LABORATORY

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| Investigators | Research Interests |
|---|---|
| Ernest Benfield | Stream processes |
| Lindsay Boring | Forest succession and nutrient dynamics |
| Gil Calabria | Data management, Athens lab |
| Jim Clark | Forest succession |
| David Coleman | Microbial ecology |
| D.A. Crossley, Jr. | Consumers, decomposition |
| Katherine Elliott | Forest succession |
| John Fitzgerald | Sulfur dynamics |
| Gary Grossman | Trophic structure |
| Bruce Haines | Nutrient cycling in plants |
| Michael Huston | Modeling |
| Jennifer Knoepp | Soil processes |
| Steve McNulty | Nutrient dynamics |
| Judy Meyer | Stream processes |

**Table II. CWT, continued**

| | |
|---|---|
| Curt Saari | Data management, Coweeta lab |
| Wayne Swank | Hydrology, input-output dynamics |
| Lloyd Swift | Climatology, hydrology, forest practices |
| James Vose | Forest processes |
| Bruce Wallace | Stream processes |
| Jackson Webster | Stream processes |

## (HFR) HARVARD FOREST

**Principal Investigator**

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| Investigators | Research Interests |
|---|---|
| John Aber | Modeling, primary production, remote sensing |
| Robert Antibus | Organic matter processes |
| Fakhri Bazzaz | Disturbance, inorganic fluxes, plant ecophysiology |
| Emery Boose | Data management, GIS |
| Richard Forman | Landscape ecology |
| David Foster | Forest and wetland response to hurricanes, paleoecology |
| Arthur Linkins | Soil enzymes, microbial processing |
| Charles McClaugherty | Decomposition, fine root turnover |
| Michael McElroy | Atmosphere/biosphere interactions |
| Jerry Melillo | Element cycling |
| Knute Nadelhoffer | Decomposition, nutrient cycling, trace gases |
| William Patterson | Fire ecology, paleoecology |
| Paul Steudler | Sulfur cycling, inorganic fluxes |
| C. Dana Tomlin | GIS |
| P. Barry Tomlinson | Plant architecture |
| John Torrey | Microbes and soils, inorganic fluxes, microbial biology |
| Steven Wofsy | Atmospheric chemistry, gas fluxes |

## (HBR) HUBBARD BROOK EXPERIMENTAL FOREST

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| Investigators | Research Interests |
|---|---|
| Herbert Bormann | Ecosystem ecology and biogeochemistry |
| Breck Bowden | Forest hydrology and microbiology |
| Jon Cole | Aquatic ecology |
| Steve DeGloria | Remote sensing, GIS, modeling |
| Charles Driscoll | Environmental chemistry and modeling |
| Timothy Fahey | Forest succession and detritus |
| Tony Federer | Forest hydrology and modeling |
| Stewart Findlay | Stream ecology |
| Richard Holmes | Animal ecology |
| Jeffrey Hughes | Population ecology |
| Arthur Johnson | Soil chemistry |
| Gene Likens | Aquatic ecology and biogeochemistry |

Table II. HBR, continued

| | |
|---|---|
| Gary Lovett | Dry deposition |
| Wayne Martin | Forest ecology |
| David Peart | Plant ecology |
| Robert Pierce | Forest hydrology and soils |
| William Rieners | Terrestrial ecology |
| Thomas Sherry | Animal ecology |
| Thomas Siccama | Terrestrial ecology |
| William Smith | Forest pathology |
| Louise Tritton | Coarse woody debris |

## (JRN) JORNADA

**Principal Investigator**

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| Investigators | Research Interests |
|---|---|
| Allen Hope | Remote sensing, GIS |
| Laura Hueneke | Plant community ecology, primary production |
| Wesley Jarrell | Soil physics/chemistry, plant-soil relationships, large-scale field experiments |
| James Reynolds | Simulation modeling, GIS-modeling interface |
| William Schlesinger | Biogeochemistry, soil processes, transport studies |
| Douglas Stow | Remote sensing, GIS |
| Ross Virginia | Nutrient cycling, plant physiological ecology, large-scale field experiments |
| Tim Ward | Hydrology |
| Walter Whitford | Consumer studies, decomposition and organic matter cycling |

## (KBS) KELLOGG BIOLOGICAL STATION

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| Investigators | Research Interests |
|---|---|
| James Crum | Soil geomorphology |
| Boyd Ellis | Soil chemistry |
| Stuart Gage | Insect ecology |
| John Gorenta | Data management |
| Katherine Gross | Plant ecology |
| Patrick Hart | Plant pathology |
| Richard Harwood | Low-input agronomy |
| Lars Hedin | Biogeochemistry |
| Michael Klug | Microbial ecology |
| Bernard Knezek | Soil chemistry |
| Daniel Lawson | Soil invertebrates |
| Eldor Paul | Soil microbiology |
| Keith Paustian | Ecosystem modeling |
| Kurt Pregitzer | Forest ecology |
| Karen Renner | Weed ecology |
| Philip Robertson | Nutrient cycling |
| Mark Scriber | Insect ecology |

Table II. KBS, continued

| | |
|---|---|
| Alvin Smucker | Soil/plant biophysics |
| James Tiedje | Microbial ecology |
| Patrick Webber | Plant ecology |

(KNZ) KONZA PRAIRIE


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| Investigators | Research Interests |
|---|---|
| John Briggs | Data management, remote sensing |
| Scott Collins | Plant community ecology |
| Walter Dodds | Aquatic ecology |
| Edward Evans | Invertebrate ecology |
| David Gibson | Plant community ecology |
| Larry Gray | Stream ecology |
| Dave Hartnett | Plant population ecology |
| Geoff Henebry | Modeling |
| Barb Hetrick | Mycorrhizal fungi |
| Don Kaufman | Mammalian ecology |
| Alan Knapp | Plant physiological ecology |
| Jim Koelliker | Hydrology |
| Wendy Macpherson | Inorganic chemistry |
| Duane Nellis | Remote sensing |
| Jack Oviatt | Geomorphology |
| Charles Rice | Microbial ecology |
| Paul Schwab | Soil chemistry |
| Tim Seastedt | Nutrient dynamics, soil invertebrates |
| Haiping Su | Remote Sensing |
| Tim Todd | Soil nematodes |
| John Zimmerman | Avian ecology |

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| Investigators | Research Interests |
|---|---|
| Nicholas Brokaw | Plant ecology |
| Alan Covich | Stream ecology |
| Thomas Doyle | Forest modeling |
| Ned Fetcher | Plant physiology |
| David Foster | Ecosystem disturbance |
| Bruce Haines | Nutrient cycling |
| Charles Hall | Ecosystem modeling |
| William Lawrence | Plant physiology |
| Deborah Jean Lodge | Microbial ecology |
| Ariel Lugo | Primary production, nutrient cycling |

Table II. LUQ, continued

| | |
|---|---|
| J. Frank McCormick | Plant ecology |
| Eda Melendez | Data management |
| Randall Myster | Community ecology |
| William Parton, Jr. | Nutrient cycling, modeling |
| Douglas Reagan | Lizard ecology |
| Robert Sanford | Nutrient cycling, modeling |
| Frederick Scatena | Forest hydrology, nutrient cycling |
| Frederick Swanson | Geomorphology |
| Kristiina Vogt | Belowground processes |
| Robert Waide | Avian ecology |
| Lawrence Walker | Plant ecology |
| Michael Willig | Insect ecology |
| Lawrence Woolbright | Amphibian ecology |
| Jess Zimmerman | Plant reproductive biology |

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| Investigators | Research Interests |
|---|---|
| Bill Bowman | Biological processes |
| Nelson Caine | Hydrology, geocohemistry, time/space variability, material flows |
| Tom Davis | Lacustrine sedimentology, palynology, Quaternary stratigraphy, climate change |
| Scott Elias | Paleoecology, paleoclimatology, Quaternary insect fossils, zoogeography |
| David Greenland | Energy budget climatology, climate-plant relationships, air quality |
| James Halfpenny | Landscape dynamics, mammals, GIS, data management, phenology |
| Elizabeth Holland | Simulation of biological sources/sinks of trace gases, plant-microbial processes |
| M. Iggy Litaor | Environmental geochemistry, acid deposition, soil weathering, stable isotopes |
| Russell Monson | Plant physiological ecology/C & N allocation patterns, photosynthesis |
| Timothy Seastedt | Nutrient dynamics, soil invertebrates |
| Susan Short | Paleoecology, paleoclimatology, atmospheric/pollen deposition |

**Table II. NWT, continued**

| | |
|---|---|
| Herman Sievering | Aerosol physics, dry deposition of atmospheric chemical constituents to land/water surfaces |
| Dale Toetz | Limnology, nutrient balances, aquatic productivity |
| Donald Walker | GIS, landscape mapping, vegetation analysis |
| Marilyn Walker | Plant communities, floristics, computer-aided analyses |
| Carol Wessman | Global ecology, remote sensing, GIS, biogeochemical cycling |
| Kerstin Williams | Diatom population dynamics/ecology: past and present |

## (NIN) NORTH INLET MARSH

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| Investigators | Research Interests |
|---|---|
| Dennis Allen | Ivertebrates, migration, recruitment, predation |
| Keith Bildstein | Avian dynamics |
| Elizabeth Blood | Site coordinator, nutrient dynamics |
| Bruce Coull | Meiofauna, population dynamics |
| John Dean | Physiological ecology |
| Donald Edwards | Statistics, experimental design |
| Robert Feller | Population dynamics, secondary production |
| Leonard Gardner | Geomorphology, geochemistry |
| Bjorn Kjerfve | Physical oceanography |
| Henry McKeller | Nutrients, modeling, organic matter |
| William Michener | Data management, population dynamics, GIS |
| James Morris | Primary production, photosynthesis, respiration |
| Fred Sklar | Landscape ecology, modeling |
| Stephen Stancyk | Zooplankton |
| F. John Vernberg | Physiological ecology |
| Tom Williams | Groundwater hydrology, nutrient cycling |
| Richard Zingmark | Primary production, photosynthesis, respiration |

## (NTL) NORTH TEMPERATE LAKES

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| Investigators | Research Interests |
|---|---|
| Michael Adams | Primary production, macrophyte ecology |
| Timothy Allen | Ecological theory |
| Mary Anderson | Groundwater modeling |
| David Armstrong | Chemical limnology |
| Tim Asplund | Aquatic ecology, climate change |
| Barbara Benson | Data management, landscape ecology |
| Carl Bowser | Groundwater geology, geochemistry |
| Xiangxue Cheng | Groundwater modeling |
| John Elder | Hydrology, geochemical cycling |
| Thomas Frost | Zooplankton ecology |

Table II. NTL, continued

| | |
|---|---|
| Joel Gat | Isotopic geochemistry |
| Tom Gower | Forest ecology |
| David Hill | Physical limnology and meteorology |
| Timothy Kratz | Wetland ecology |
| Thomas Lillesand | Remote sensing |
| Mark MacKenzie | GIS |
| John Magnuson | Terrestrial ecology, consumer ecology |
| Ann McLain | Invasion ecology |
| Marketta Sagova | Macrophyte/benthos interaction |
| Randy Wynne | Remote sensing/ice cover, water quality |

## (PAL) PALMER STATION, ANTARCTICA

**Principal Investigators**

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| Investigators | Research Interests |
|---|---|
| William Fraser | Seabird ecology |
| Eileen Hofmann | Modeling, biological-physical processes |
| John Klinck | Modeling, oceanic-ice circulation |
| Simon Levin | Modeling, swarm behavior |
| Akira Okubo | Modeling, swarm behavior |
| Tom Powell | Biological-physical processes |
| Barbara Prézelin | Plant physiology, bio-optical models of primary production |
| Langdon Quetin | Ecological physiology of animals (zooplankton and nekton) |
| Robin Ross | Ecological physiology of animals (zooplankton and nekton) |
| Ray Smith | Remote sensing, environmental optics, hydrography, bio-optical models |
| Wayne Trivelpiece | Seabird ecology |

## (SEV) SEVILLETA NATIONAL WILDLIFE REFUGE

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| Investigators | Research Interests |
|---|---|
| James Brown | Community ecology, biogeography |
| James Brunt | Research information management, computer networking |
| Clifford Crawford | Invertebrate ecology, decomposition |
| Clifford Dahm | Ecology of surfaces |
| Donald Duszynski | Parasitology |
| James Findley | Mammalian community ecology, Peromyscus |
| James Gosz | Nutrient dynamics, trace gas flux |
| Herb Grover | Remote sensing, ecosystem ecology |
| Gordon Johnson | Plant physiology, nitrogen fixation |
| Tom Kieft | Soil microbe respiration |
| Diane Marshall | Plant population biology |
| Bruce Milne | Landscape ecology, fractals, scale |
| Manuel Molles | Stream and riparian ecology, climatology |

Table II. SEV, continued

| | |
|---|---|
| Brad Musick | Remote sensing, plant ecology |
| Robert O'Neill | Ecosystem modeling and theory |
| Robert Parmenter | Project coordinator, plant-animal interactions |
| Paul Risser | Landscape ecology |
| Howard Snell | Reptile physiological ecology, evolutionary ecology |
| Molly Toll | Paleobotany, archaeology |
| Carl White | Nutrient cycling, ecosystem biology, fire ecology |
| Charles Wisdom | Plant physiological ecology |
| Terry Yates | Evolutionary genetics, systematics, mammalogy |

## (VCR) VIRGINIA COAST RESERVE

**Principal Investigators**

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| Investigators | Research Interests |
|---|---|
| Ruth Beck | Ornithology |
| Linda Blum | Microbial ecology, plant-microbe interactions |
| Mark Brinson | Wetlands ecology, hydrology |
| Robert Christian | Microbial ecology, nutrient transformations |
| Frank Day | Belowground ecology, nutrient cycling |
| Tanya Furman | Mineralogy, petrology |
| Bruce Hayden | Environmental climatology |
| Craig Kochel | Coastal geomorphology |
| Aaron Mills | Microbial ecology, biogeochemistry |
| George Oertel | Coastal geology |
| John Porter | Data management, GIS |
| Hank Shugart | Landscape ecology, ecosystems modeling |
| Richard Wetzel | Nutrient cycling |
| Patricia Wiberg | Sediment transport |
| Donald Young | Physiological plant ecology |
| Jay Zieman | Aquatic ecology |

# LTER NETWORK OFFICE PUBLICATIONS

No. 1: Long-Term Ecological Research. *BioScience*, 1984

No. 2: The Climates of the Long-Term Ecological Research sites. University of Colorado, Institute of Arctic and Alpine Research (INSTAAR), Occasional Paper 44, 1987

No. 3: Standardized Meterological Measurements for Long-Term Ecological Research Sites. Bulletin of the Ecological Society of America, 1987

No. 4: 1990s Global Change Action Plan. Network Office, 1990

No. 5: Long-Term Ecological Research Network Core Data Set Catalog. LTER Network Office and Belle W. Baruch Institute, 1990

No. 6: Climate Variability and Ecosystem Response. Network Office and UDSA Forest Service SE Experiment Station, 1990

No. 7: Internet Connectivity in the Long-Term Ecological Research Network. LTER Network Office, 1990

No. 8: Contributions of the Long-Term Ecological Research Network. *BioScience*, July/August 1990 (single article)

No. 9: Long-Term Ecological Research and the Invisible Present, *BioScience*, July/August 1990; Long-Term Ecological Research and the Invisible Place. *BioScience*, July/August 1990 (three articles, including LTER Publication No. 8)

No. 10: Proceedings of the 1990 LTER Data Management Workshop, Snowbird, Utah; Network Office, 1990

No. 11: Long-Term Ecological Research in the United States: A Network of Research Sites 1991 (6th edition, revised), LTER Network Office, 1991

No. 12: Status Report on Technology Development in the Long-Term Ecological Research Network: Current Status of Geographic Information Systems, Remote Sensing, Internet Connectivity, Archival Storage and Global Positioning Systems. Network Office, available January 1991

***Planned Publications:***

LTER Atmospheric Chemistry Workshop Proceedings
LTER Stream Research Catalog

***Other Publications:***

*LTER Network News* (biannual newsletter; back issues available)

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*In most cases, the above publications are available in limited quantities at no cost. For information on their current availability and/or status, please contact:*

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**Cover image:** *NOAA-AVHRR satellite data depicting vegetation patterns. The area includes 17 of the 18 LTER sites, excluding Palmer Station, Antarctica.* JOHN VANDE CASTLE