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LONG-TERM ECOLOGICAL RESEARCH ON THE LUQUILLO EXPERIMENTAL FOREST II

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Summary

The Luquillo Experimental Forest (LEF) Long-Term Ecological Research Program began in 1988 with the goal of integrating studies of disturbance regime and forest structure and dynamics with a landscape perspective. Two central research questions addressed 1) the relative importance of different disturbance types within the four tropical rain forest life zones of the LEF and 2) the importance of the biota in restoring ecosystem productivity after disturbance.

The long-term monitoring program initiated as part of the Luquillo LTER was critical to the evaluation of immediate and subsequent effects of Hurricane Hugo, which struck Puerto Rico in 1989. The occurrence of a hurricane soon after the initiation of the LTER program provides an opportunity to study the long-term dynamics of a tropical forest as it recovers from a major disturbance.

Integration of the spatial and temporal patterns of the different disturbances affecting the LEF (tree falls, landslides, hurricanes, and human land use) indicated that even the effects of large disturbances are not homogeneous over the forest landscape. A strong gradient in damage from Hurricane Hugo occurs from northeast to southwest in the LEF, corresponding to the direction of the strongest winds. However, even in severely disturbed areas, many forest attributes were approaching their pre-hurricane values within four years of the storm. Forest response depended both on the successional status of the site at the time of disturbance and the intensity of disturbance. In many areas, the legacy of past human activities was apparent in forest composition and structure even after Hurricane Hugo.
The long-term experiments and measurements initiated in 1988 will remain the central focus of the Luquillo LTER as it moves into its second phase. Analysis of the dynamics of recovery after the hurricane and its associated landslides and synthesis of the interaction of multiple disturbances continue to be the primary goals of collaborating investigators. New initiatives will concentrate on defining the distinctive characteristics of anthropogenic disturbance and on evaluating the importance of pivotal species in shaping the path of succession. As before, a major emphasis of the Luquillo LTER will be to provide information and ideas for cross-site and network-wide syntheses.

Results from prior NSF support

LONG-TERM ECOLOGICAL RESEARCH ON THE

LUQUILLO EXPERIMENTAL FOREST
NSF GRANT BSR-8811902, Oct. 1988 to Sept. 1994, $2,700,000

The initiation of the Luquillo Long-Term Ecological Research (LTER) program in 1988 consolidated studies of populations, communities, and ecosystems of the Luquillo Experimental Forest (LEF) being conducted by the International Institute of Tropical Forestry (IITF), the University of Puerto Rico (UPR), and numerous collaborators. By focusing research on issues central to understanding tropical forest structure and function, the LTER program furnished the catalyst for studies that cut across geographical and temporal scales. The long-term nature of the program provided the means to conduct experimental studies that complement the long time series of observations already available from the LEF.

The primary goal of the Luquillo LTER project is to understand the interaction of disturbance, physical parameters, and the tropical biota from population, community, ecosystem, and landscape perspectives. The eventual objective is to broaden this understanding to regional and global scales. To address this primary goal during the first six years of the program (hereafter referred to as LTER 1), we asked the following two questions about the tabonuco forest ecosystem:

What is the distribution of different disturbance types within the landscape of the LEF, and how does the disturbance regime at a given site affect the structure and function of the ecosystem?

What is the response of the biota to disturbances differing in scale, severity, and frequency, and how does this response affect a site's recovery toward mature forest?

To address these questions, we proposed to examine:

1. Pattern, frequency, and intensity of disturbance in the LEF (e.g., treefalls, landslides, and hurricanes).

2. Environmental properties that are expected to vary with disturbance size, age, and origin (e.g., light, nutrient availability, moisture, temperature, and soil organic matter).

3. Biological properties that are expected to vary with environmental properties (e.g., species composition, growth, nutrient dynamics, reproductive success, carbon fixation, and food web structure).

4. System properties that emerge from the effects of disturbance pattern and frequency on the mutual interaction of abiotic environment and biota (e.g. nutrient cycling, phases of recovery, and rates of recovery).

Research Accomplishments

Long-Term Experiments and Measurements. Considerable long-term data existed before the establishment of the LTER project. During the last six years we have acquired, archived, and documented as many of these existing data sets as possible. We have augmented the existing long-term data by standardizing data collection in some cases (weather, streamflow, litter decomposition) and initiating monitoring of key ecosystem parameters for which long-term data were not available (plant reproductive phenology, litterfall, wood decomposition, animal populations, disturbance history).

The principal long-term experiment scheduled for the first six years of the LTER was a controlled harvest in two watersheds at Bisley (Fig. 1). As the calibration phase of the experiment(1987-89) was drawing to a close and before the harvest, Hurricane Hugo struck the LEF, causing severe damage to the Bisley watersheds. After consultation with our Advisory Committee (Wayne Swank, Hal Mooney, Paul Risser, Dick Weigert, and Howard Odum), we decided to re-orient the experiment to study the long-term effects of one of the key disturbance types in the LEF in a watershed context. Disturbance Regime - Understanding the dynamics of different types of disturbance is the first step towards discovering correlates of disturbance and evaluating the interactions among successive disturbances and the biota. At the initiation of the Luquillo LTER, large portions of the forests of the LEF were approaching a mature stage of succession after two hurricanes in the 1930s and various types of agriculture and forestry activities at lower elevations that lasted until the 1950s. With this context in mind, the following conclusions about disturbance were reached in the first LTER phase:

Analysis of historical archives dating back to the Spanish Crown and aerial photography from 1936 and 1989 established a strong relationship between the type of previous land use and present day forest composition, structure, and function (Scatena 1989, Garcia 1991, Garcia and Scatena 1994).

Treefall gaps are the most common patch-creating disturbance in tabonuco forest. Gap formation is less frequent in the LEF, however, than in mainland tropical forests and median gap size and proportion of forest in gaps are less (Brokaw ms). These differences result from the relatively small size of trees in the LEF, the strength of the interconnected (grafted) root systems of the dominant tree (tabonuco) that minimizes treefalls even after death (Basnet et al. 1993), the periodic culling of weak and susceptible trees, and the relatively young age of the forest. All of these attributes are consequences of the occurrence of hurricanes in Puerto Rico (Lugo and Scatena in review).

The proportion of area in gaps increases along an elevational gradient in the LEF from 0.4% in tabonuco forest to 8.4% in cloud forest (Brokaw and Grear 1991). This result can be attributed to both greater rates of gap formation (because of slope steepness) and slower recovery in low-productivity cloud forest.

Disturbance fosters subsequent disturbance; Hurricane Hugo triggered over 285 landslides, principally in areas receiving more than 200 mm rainfall (Scatena and Larsen 1991). Trees weakened by the hurricane or resulting environmental conditions continue to form gaps four years later. Landslide formation is highest along roads or in other areas affected by humans (Guariguata and Larsen 1989). Landslides in the LEF are more frequently associated with soils overlying granitic bedrock (Guariguata and Larsen 1989, Guariguata 1990) below 640 m; spatial distribution thus exhibits strong geomophological and topographical control (Scatena and Larsen 1991). Temporal patterning is controlled by infrequent climatic (high rainfall) or geologic (earthquake) events. Landslide patches occupy a relatively small area of the LEF compared to other kinds of disturbances.

Hurricanes can be dissected into component factors of wind intensity, wind direction, rainfall intensity, duration, and overall direction of movement, each of which can vary among hurricanes and each of which is important in the pattern of damage (Scatena and Larsen 1991, Boose et al. 1994, Foster and Boose 1994). Models of hurricane meteorology (HURRECON) and topographic exposure (EXPOS) developed in LTER 1 are being used to reconstruct regional gradients of hurricane frequency and intensity and landscape-level patterns of long-term exposure to catastrophic winds (Boose et al. 1994).

Each disturbance type has its own frequency and intensity pattern (Waide and Lugo 1992) and thus its own effect on forest structure and function. However, each individual disturbance occurs in an historical context of previous disturbances, each of which has left its effect on the ecosystem. Overlapping patterns of disturbance combine with physiography and biogeography to determine the distribution of ecosystem attributes along multiple gradients.

Response and Regeneration - The impact of disturbance in the LEF is often mediated by the physical location of the affected site (slope, aspect, slope position) and the structure of the biota. Even a large, intense disturbance such as a hurricane can produce local effects that are highly variable in their severity. Patterns of hurricane damage become more coarse going from local to landscape scale, where exposure to direct hurricane winds is the principle factor influencing degree of damage. Regeneration depends on the abiotic and biotic conditions occurring at the onset of succession, which are influenced by the most recent and earlier disturbances. At local scales, patches dominated by the effects of recent disturbance are mixed with patches reflecting previous disturbance. At landscape scales, either recent or previous disturbance dominates over large areas. Experiments and long-term measurements in LTER 1 provided the following insights into the immediate impact of Hurricane Hugo and the dynamics of succession following the hurricane.

Through the analysis of meteorological data and post-hurricane aerial photography, Boose et al. (1994) were able to determine how hurricane winds and rain interacted with topography and forest type to produce the pattern of damage observed after Hugo (Fig. 2). In general, patterns of damage at the landscape scale reflected the degree of protection from direct hurricane winds and the distance from the eye of the storm (Boose et al. 1994, Foster and Boose 1994). Within a watershed, damage was closely related to steepness of slope, slope position (Basnet et al. 1992, Basnet et al. 1993, and the wood density of the component species, leaving a mosaic of more and less damaged patches relating to species distributions within the stand (Zimmerman et al. in review).

Biotic responses to hurricane disturbance can be positive, negative, or neutral depending on what sector of the ecosystem is influenced by the disturbance (Walker et al. 1991a). Using baseline measurements from LTER 1 and other studies in the LEF, we were able to quantify the consequences of

Hurricane Hugo for plant (Walker 1991, Brokaw and Grear 1991, You and Petty 1991, Parrotta an Lodge 1991, Frangi and Lugo 1991, Dial 1992, Reagan 1992, Basnet et al. 1992, Walker et al. 1992, Silver and Vogt 1993, Vogt et al. 1994) and animal (Woolbright 1991, Reagan 1991, Covich et al. 1991, Willig and Camilo 1991, Waide 1991, Alvarez and Willig 1993, McMahan and Blanton 1993, Gannon and Willig in press) populations (Walker et al. 1991a, Lugo and Scatena 1994).

Following total defoliation of the forest after Hurricane Hugo, cloud formation occurred at elevations higher than normal and this induced a local drought that abated after refoliation restored forest transpiration (Scatena and Larsen 1991). These results suggest that the forest feeds back strongly on local weather patterns.

Streamflow varied spatially and temporally throughout the LEF, showing extended low flow periods in the northern watersheds following Hurricane Hugo (Fig. 3). Locally, short-term droughts were found to affect both plant and animal populations.

Litterfall and decomposition emerged as key processes in the LEF. The pulse of litterfall resulting from the hurricane was followed by a dramatic decrease in annual litterfall (Fig. 4; Lodge et al. 1991). Increased forest floor mass gave anoles and adult frogs additional habitat (Woolbright 1991, Reagan 1991). Litterfall and canopy damage removed habitat for canopy specialists, temporarily displacing some of these to the forest floor. In streams, litterfall altered the available retreat sites for decapods (Covich et al. 1991).

Litterfall residence time in streams may be significantly shortened by washout events resulting in disruption of debris dams and export or turnover at shorter time scales than in terrestrial habitats (Covich and Crowl 1990).

Investigation of the rates of wood, leaf, and root litter decomposition in streams, riparian, and upslope areas at both at El Verde and Bisley (Vogt et al. 1994) indicate that fine-scale decomposition processes (i.e. individual species) reflected the spatial patterns in the landscape (e.g., streams, topographic location) and the region (Bloomfield 1993, Bloomfield et al. 1993). The chemistry and magnitude of above- and belowground litter inputs and decomposition varied spatially corresponding to plant species distribution, and temporal relationships were established between pulses of microbial activity and nutrient immobilization from decomposing litter before and after Hurricane Hugo (Vogt et al. 1994).

Turnover rates for stems dying as a result of hurricane damage is more rapid than turnover as a result of treefall gaps (Scatena and Lugo in review); background mortality leads to more rapid turnover of stems than either hurricanes or gaps (Lugo and Waide 1994).

Topography plays a predominant role in the structure and function of forest stands in the LEF. Predictable patterns of primary productivity, nutrient cycling, species composition, vegetation structure, etc. occur along the gradient of ridge, slope, and valley, and streams at a given elevation (Basnet 1992, Scatena and Lugo 1994, Bloomfield et al. 1993, Bowden et al. 1992, McDowell et al. 1992, Vogt et al. 1994).

Populations of stream invertebrates varied with elevation within a watershed, but were dramatically different between watersheds, possibly because of human intervention downstream from the LEF.

In some places, forest composition reflects previous human land use predating hurricanes that have severely affected stand structure (Fig. 5; Garcia and Scatena 1994). The legacies of different disturbances are a primary factor structuring tabonuco forest.

In addition to the results presented above, a large series of measurements and experiments addressing specific ecosystem, community, or population issues were conducted under the auspices of the Luquillo LTER or by collaborating scientists (see bibliography below).

Synthesis and Modeling Accomplishments - Results from LTER 1 have been summarized in two books, one on long-term research in the Luquillo Experimental Forest (Lugo and Lowe in press) and the other on the food web of tabonuco forest at El Verde (Reagan and Waide in review). Special issues of the journals Biotropica and the Kansas Journal of Entomology have been devoted to research from the Luquillo LTER site. A review of the state of knowledge of ecosystem properties (Lugo and Scatena in press) and a general summary of the LTER program (Waide and Lugo 1992) are also available.

Simulation modeling has been used as a tool to both integrate and guide research (Wooster 1989, Sanford et al. 1991, Everham et al. 1991, Hall et al. 1992a, Boose et al. 1994, Zimmerman et al. in review) . We have used existing models (CENTURY, PROSPER) to foster comparisons with other LTER sites. Interactions among different components of the project have led to the development of models simulating spatial mesoclimate for the LEF (TOPOCLIM), energy flow in tabonuco forest (TABONUCO), climate-sensitive forest growth (FORGROW), numbers of landslides and treefalls under different topographic conditions (DISTURB), surface wind conditions during a hurricane (HURRECON), local exposure to wind for a given hurricane (EXPOS), stream energy flow (QBRADA), stream litter retention (LITFLOW), and changes in soil and aboveground nutrient pools along a topographic gradient (CATENA). A guide to these models including copies of the software and instructions has been developed as an in-house publication (Everham 1993).

Relationship of Past Research to Proposed Research - LTER 1 was based in part on our perception that the environment of the LEF is stressful to organisms, with high rain, winds, temperature, and leaching potential as well as frequent and severe disturbances. Set against the backdrop of steep topography, these stressors produce environmental challenges that the biota must overcome to persist. Having experienced the extent of these environmental challenges in LTER 1 (Fig. 6), we conclude that the biota of the LEF has developed mechanisms to contend with even severe natural disturbances with little disruption to plant and animal communities. The nature of these mechanisms forms one area of inquiry for LTER 2. LTER 1 has also shown us that previous land use can leave a long-lasting signature on the tabonuco forest landscape that in many cases overrides natural stressors. We do not know what specific environmental changes are associated with long-lasting effects, but we do know that in the aggregate they are very important in determining ecosystem structure and function. We also know that the combination of natural and anthropogenic disturbances modifies the nature of abiotic gradients in complicated ways, leading to a redistribution of populations and communities. This fact calls into question our ability to predict the attributes of tabonuco stands without detailed knowledge of their history. Finally, it is apparent that the length of the data base on many forest processes is insufficient at present to measure temporal variability or detect long- term trends. LTER 2 will focus on the experiments and measurements necessary to address the issues raised above. As a framework for these inquiries, we establish below a series of six premises that will serve as the intellectual core of the proposed work in LTER 2 as well as subsequent funding cycles. These premises describe a consistent approach that we will use in our efforts to integrate the physico-chemical environment, the biota, and the disturbance regime of the LEF into a coherent picture of a dynamic tropical forest.

LTER PUBLICATIONS

The following list contains publications resulting directly from work performed under the Luquillo LTER or that was supported in a substantial way by the LTER. Authors who are Co-Pi's on the original LTER proposal are indicated with an amper sign (&). Authors who were not participants in LTER 1 but who are Co-Pi's on the renewal are underlined. Authors who were graduate students supported by the Luquillo LTER are indicated with an asterisk (*). The list includes 128 refereed publications, 37 submitted manuscripts, and 23 dissertations, theses, or Master's projects.

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INTRODUCTION

When we became part of the Long-Term Ecological Research (LTER) network six years ago, we proposed to examine the roles of disturbance and the biota's response to disturbance as primary factors determining the structure and function of tabonuco (Dacryodes excelsa) forest in Puerto Rico (Waide and Lugo 1992). These twin concepts of disturbance and response will continue to provide the unifying theme for the second phase of our LTER. Our work since 1988 has confirmed the overriding importance of these factors in tabonuco forest and has revealed differences in biotic response to specific disturbance types and combinations of disturbance. We will focus on these differences in the next six years.

We have shown that the ecosystems of the Luquillo Experimental Forest (LEF) are dominated by recurrent episodic disturbances such as hurricanes (and isolated high wind and rain events; Walker et al. 1991a, 1992, Zimmerman et al. 1994), landslides (Scatena and Larsen 1991), and also by events of longer duration such as agricultural activities (Fig. 7; Garcia and Scatena 1994). These disturbances have different frequencies and severities and result in different pathways of ecosystem response. Because ecosystems in the LEF are so dynamic, physical location alone is an unreliable predictor of ecosystem state. Each point in the landscape incorporates the previous history of natural and anthropogenic disturbances (Hubbell 1979) as one of the factors that influence community composition and ecosystem attributes.

Thus, a key issue that arises from the first LTER phase is the importance of residual effects from previous disturbances on present forest community composition. We can see clearly the legacy of previous landslides and hurricanes in our study plots (Lugo and Battle 1987). However, in many places the dominant signature comes from previous human land use (agriculture, timber extraction, and charcoal production) that took place as long as 100 years ago. Areas used by humans have regenerated into forests with community organization and functional characteristics similar to those not influenced by humans, but with a different species composition. In parts of the forest, this legacy of human activities has survived three hurricanes during the last 60 years. The persistent nature of human activities suggests that they lead to unique environmental conditions inhospitable to some species involved in secondary succession after natural disturbance. Clearly, a full explanation of the functioning and present state of tabonuco forest requires understanding of historical patterns of all kinds of disturbance, the environmental conditions resulting from disturbance, and the ecological characteristics of the species making up the successional community.

THEORETICAL FOUNDATIONS FOR LTER 2

The first phase of the Luquillo LTER focused on defining various disturbances interms of their severity, scale, and frequency (Figs. 8 and 9) and in examining the systemsproperties arising from the effects of disturbance on the mutual interaction of abioticenvironment and the biota. Evidence obtained in this effort suggests that the present state ofboth the abiotic environment and the biota are in part functions of previous disturbances;hence, understanding of the effects of present-day disturbance may require a historicalcontext. The challenge of LTER 2 is to determine the extent to which previous eventsdictate forest structure and function. In order to address this issue, we need to understandthe suite of mechanisms by which individual species adapt to different disturbance types andthe properties of individual species that feed back on the process of succession. We furtherrequire a better understanding of the factors determining the direction and speed ofsuccession. Finally we need to distinguish clearly between the attributes of natural andanthropogenic disturbance and to evaluate our ability to predict responses to disturbance atvarying temporal and spatial scales. To integrate the concepts of disturbance regime and the biota's role in recovery, weare attempting to quantify the impacts of disturbance on the patterns of resource gradientsover the landscape (Keddy 1991, Hall et al. 1992b, Gosz 1992). The central premises to thisapproach are as follows:

1) The distribution of organisms and associated rates of ecosystem processes arecorrelated to several gradients of environmental factors over the LEF landscape. Wecategorize these gradients as either primary or secondary. Primary gradients directly impactphysiological processes. These gradients are limited in number and have consistent impactacross temporal and spatial scales. In the LEF we believe these to be: temperature, sunlight,soil moisture, and soil nutrient levels. Secondary gradients (e.g., elevation, slope, rainfall,historical land use, and disturbance intensity) correlate to these primary gradients. Theimpact of these secondary gradients on primary gradients, and therefore ecosystem structureand function, may change with changing temporal or spatial scales. Although speciesdistributions or rates of ecosystem processes may closely correlate to secondary gradients,describing these distributions or rates based on their positions along primary gradients leadsto process-based hypotheses and models.

2) Each position on the landscape (i.e., geographical space) exists as a position in n-dimensional gradient space (or ecological space). The position in ecological space isdetermined by the actual physical condition of the site which in turn is determined byinteractions of geographical space, climate, disturbance history, and the biota, whichcollectively determine position along each primary gradient.

3) Disturbance can be viewed as a displacement in gradient space. Disturbancemodifies the

position along many or all gradients, (Fig. 10A), resulting in a new position inecological space. Describing this displacement in primary gradient space potentially allowsfor explanations rather than just predictions in changes of distributions and rates ofprocesses.

4) The gradient approach allows us to integrate different disturbance regimes. Different disturbance types have characteristic directions of displacement in ecological space. Size and especially intensity of disturbance influence the magnitude of the displacement inthat characteristic direction. The vector of recovery is controlled by the new position inecological space. Frequency of disturbance, in conjunction with recovery time, influencesthe impact of subsequent disturbance; i.e., if the return time for a given disturbance, or anew disturbance, results in a further displacement before recovery is complete, new andunique positions in ecological space may result (Fig. 10B).

5) System resistance and resilience to disturbance can be quantified in this conceptualframework. Resistance is a measure of the displacement in ecological space for a givendisturbance. Resilience of a system is the time required to return to the original position fora given displacement.

6) The role of the biota in this conceptual framework is threefold. The biota: 1)modifies the landscape gradients of abiotic factors and therefore influences the local positionin ecological space; 2) influences the resistance of the site to a given disturbance; and 3)influences the resilience of the site by controlling the direction and speed of the vector ofrecovery. In general, the greater the intensity of the disturbance the less the role of the biotain influencing resistance. With greater displacement in ecological space, the influence of thebiota on the initial recovery is decreased. As the vector of recovery returns towards theoriginal position in gradient space, the influence of the biota in controlling the recovery andultimate position increases. We feel this approach promises to integrate the relationship between disturbanceregimes and landscape patterns and processes in a quantifiable framework. Once we canidentify the shifts in gradient space for a given disturbance and the resulting impact on thevector of recovery, we can compare disturbances of different types, sizes, frequencies andintensities, and project the possible impacts of disturbance regimes not yet felt by the LEF. Such an approach integrates studies at various levels of biotic organization and provides amechanism for synthesis and modeling that is extremely powerful because of its quantitativenature. Understanding gained from this approach is directly applicable to evaluation oftechniques for ecological management of tropical forests under different disturbance regimes. The Luquillo site has a long tradition of managerial manipulations by the USDA ForestService that provide a network of managed stands in which the ecological insights of ourLTER research can be verified and tested (Brown et al. 1983).

PROPOSED RESEARCH

Many of the experiments and measurements initiated in LTER 1 were designed formore than six years. These studies will continue in LTER 2 and will be augmented by thejudicious addition of new experiments. Our research plan for LTER 2 comprises thecontinuation of monitoring directed toward understanding long-term disturbance and climaticphenomena as well as five working hypotheses addressing issues arising from the theoreticalfoundation presented above (Table 1). These hypotheses focus our attention on key points ofecosystem structure and function that limit our understanding of the response of tabonucoforest to different kinds of disturbance. The first of our five working hypotheses is designed to evaluate and extend theconceptual and simulation models of forest structure developed in LTER 1 by validation overthe range of conditions extant in tabonuco forest. The second working hypothesis continuesthe examination of the dynamics of successional pathways initiated in LTER 1. The otherthree working hypotheses represent an expansion into areas that were not addressed in depthin LTER 1. Each working hypothesis discussed below is followed by material describing theconceptual background and the general approach we will take in each area. Sub-hypothesesunder each working hypothesis describe the specific issues to be addressed, and the rationalefor and approach to each experiment is given under the sub-hypothesis. More detailedmethods are contained in Appendix A. After each sub-hypothesis in the text is a list ofpeople involved, with the lead scientist given first. Tables 2 and 3 provide information onthe affiliations of scientists involved in LTER 2.

Monitoring of Spatio-Temporal Patterns

The foundation of any long-term study of ecological processes is a program of monitoring populations and key ecosystem parameters that allows short-term measurements and experiments to be put into a spatio-temporal context. As data accumulate through monitoring, the value of the exercise increases and the scope of the questions that can be addressed broadens. Given sufficiently long records, ecological patterns manifesting themselves at different temporal scales can be disentangled and their relative importance evaluated (Magnuson 1990). Monitoring in the LTER program (Table 4) complements long- term studies initiated in the LEF over 50 years ago (Lugo and Lowe 1994) as well as more recent efforts by the USDA Forest Service and the U.S. Fish and Wildlife Service (e.g., for the Puerto Rican Parrot, Amazona vittata). The monitoring activities initiated in 1988 as part of the LTER program provided an immediate return when Hurricane Hugo struck the forest in 1989. Combined with existing long-term records from other sources (USDA Forest Service, U.S. Geological Survey), data from our monitoring program provided a means to evaluate short-term effects of the disturbance (Walker et al. 1991a) and to follow long-term forest response. The occurrence of Hurricane Hugo pointed out important parameters that needed to be monitored, some of which (e.g., flowering phenology, canopy openness, seedling dynamics) have been added in LTER 2. Because of the opportunity to study the effects of a hurricane from time zero, the monitoring program established in LTER 1 assumes even more importance and will be continued and expanded in LTER 2. Long-term data on biogeochemical processes are collected principally at the primary sites of Bisley and El Verde under LTER funding, but other data are available from independently funded grants and the Water, Energy, and Biogeochemical Budget (WEBB) Program of the U.S. Geological Survey. The small watershed approach common at other LTER sites (e.g., Hubbard Brook, Coweeta) is used to monitor three streams at Bisley and two at El Verde. Continuously-monitored parameters (e.g., rainfall, streamflow, litterfall; see Table 4) and short-term or seasonal process studies (e.g., decomposition) funded by LTER are supplemented with less frequent measurements of spatial variation in pools (e.g., soil nutrients), some of which have benefited from external support (USDA Soil Conservation Service, Mellon Foundation).

In our original LTER proposal, we identified a list of 23 focal species of trees, shrubs, herbivores and higher order consumers for intensive population studies. Focal species were chosen on the basis of their numerical dominance in their particular trophic guild. Existing long-term population data on some of these species (frogs, trees) and baseline data collected in 1988 under LTER funding allowed us to quickly gauge the impact of Hurricane Hugo in 1989, resulting in at least nine timely publications (Walker et al. 1991a). Of the 15 animal species on the original list, one mammal (Rattus rattus) was discontinued because of poor trapping success. The remaining 14 animal species plus five additions to the list will continue to be the subject of more intensive population studies in LTER 2 (Table 5). Long-term population studies of other species (Puerto Rican Parrot (Amazona vittata), Pearly-eyed Thrasher (Margarops fuscatus), Black-throated Blue Warbler (Dendroica caerulescens), Elfin Woods Warbler (Dendroica angelae), and invertebrate members of the stream community) are being carried out in the LEF by the International Institute of Tropical Forestry (IITF), the USDA Forest Service, and the U.S. Fish and Wildlife Service. In addition to our original list of eight focal tree and shrub species, we are collecting population data on over 120 species of woody plants in permanent plots at El Verde and Bisley. Monitoring of populations of trees, shrubs, and selected animal species is presently accomplished through repeated surveys of permanent plots at Bisley and the Hurricane Recovery Plot (HRP), a 16 ha, intensively studied plot at El Verde. We established the HRP in 1990 in the first year after Hurricane Hugo in order to study forest regeneration (Fig. 11). A large plot size was chosen to provide the large sample sizes and spatial data base required to evaluate the population biology of rare tropical trees and to parallel similar studies in other tropical sites (Hubbell 1979). The HRP is partly covered with older growth tabonuco forest that has been culled but never cleared as well as a section that was cleared in the early part of this century. All trees > 1 cm dbh are tagged, identified, measured for diameter, and mapped, totaling 88,000 stems of 120 species. Locations of second-order streams are mapped on the HRP, facilitating linkages between terrestrial and aquatic studies. A detailed soil map was developed for the HRP in 1993, and soil nutrient analyses are in progress. We plan successive inventories of the plot at five year intervals, giving us a large database on the populations of trees in a forest recovering from a massive disturbance. The inventories of trees and shrubs will be complemented by annual or more frequent surveys of animal populations at 40 points regularly spaced throughout the grid. We will measure a suite of environmental features on the grid, including soil moisture, soil nutrients, canopy structure, canopy openness (hemispherical photographs), slope, rock cover, and other parameters. The large sample of common trees on the HRP enable us to evaluate population patterns as a function of environment and disturbance history, including natural and human disturbance. Descriptions of previous disturbances at the site exist in USDA Forest Service records and documentation of land transactions under the Spanish Crown. The HRP and long-term growth plots monitored by the USDA Forest Service since 1943 are especially valuable for studies of populations during the early stages of recovery from a hurricane. Crow (1980) evaluated stand dynamics in 0.4 ha of tabonuco forest over several decades following hurricanes in the early 1930s. He showed changes in community diversity, population size, and size class structures of some tree species. His study, while instructive, missed the critical early years when rapid change takes place and later patterns are established. Our larger sample area permits a better understanding of the variation within and among species and the dynamics of rare species. Knowledge of the biology of such rare species is critical for a detailed understanding of the generation and maintenance of biodiversity in the tropics. Based on analyses of spatial patterns in LTER 1, we believe that work at El Verde and Bisley captures much of the range of spatial variability within tabonuco forest (Table 6) and that the conceptual models of forest dynamics we have developed at these sites are based on a clear understanding of ecosystem processes. In LTER 2, we plan to test this understanding by comparing predictions from our models with data on selected parameters from major topographic and land use types determined using the geographic information system (GIS) developed for the Luquillo LTER.

Working Hypotheses

H1: The ecosystem patterns and processes that are active at El Verde and Bisley are continuous over increasing spatial scales, so that understanding of system attributes gained at these two points can lead to accurate predictions at other sites within tabonuco forest.

Background - Implicit in most ecological studies is the idea that phenomena occurring or measured at the plot scale contribute to understanding ecological processes at larger scales. However, plots may encompass only a portion of the gradients that make up ecological space over a landscape, and therefore may provide only limited insight to system behavior outside of the plots. Even relatively large study sites (whole watersheds) are unlikely to contain all combinations of conditions, especially when disturbance is an important factor in the ecosystem. If organisms and ecological processes respond continuously to changes along gradients, extrapolation from small to large scale may be possible. If response is not continuous over the range of gradient values, plot data are of limited value in understanding ecosystem structure and function. Results from LTER 1 indicate that certain ecosystem attributes (e.g., the effect of physiography on hurricane wind damage; Boose et al. 1994) can be scale-dependent. The severity of hurricane damage can be predicted within reasonable bounds at the landscape level based on slope, aspect, and elevation, but these same parameters had little predictive power at the scale of the HRP (Zimmerman et al. in press). To increase the degree of confidence in generalizations from our work at Bisley and El Verde, we must evaluate the degree to which these sites encompass the ecological space characteristic of tabonuco forest. We must also determine how well our conceptual models of tabonuco forest work in areas other than El Verde and Bisley. If key causative factors have a discontinuous distribution in tabonuco forest, then our predictive ability will be compromised and we will have to seek ways of transferring our knowledge across scales of ecological organization.
General Approach - We will develop mechanistic explanations for the distribution of plant and animal populations, community composition, and selected aspects of ecosystem structure (biomass, leaf area index, stem density, canopy cover, dominance-diversity relationships, nutrient storage, soil organic matter, phenology, litter fall) based on work at El Verde and Bisley. These explanations will be used to calibrate simulation models to predict values for other sites. Model predictions will be validated with field surveys.

H1A: The factors that predict the distribution of populations, communities, and ecosystem attributes at El Verde and Bisley also predict their distribution throughout tabonuco forest (Waide, Brokaw, Camilo, Covich, Crowl, Everham, Hall, Parton, Pulliam, Thomlinson, Waide, Walker, Willig, Woolbright, Zimmerman, Zou).

Rationale - Within- and between-site variability at El Verde and Bisley encompass the greater part of the primary gradients that we hypothesize to directly affect the distribution of organisms and the rate of ecosystem processes in tabonuco forest (temperature, sunlight, soil moisture, and soil nutrient levels). The location of Bisley on the windward and El Verde on the leeward slopes of the LEF results in differences in insolation and temperature. Differences in rainfall and runoff result in higher soil moisture at Bisley. Comparisons of soil nutrients also suggest differences between the two sites. Finally, Bisley is in the area of the LEF most affected by Hurricane Hugo while El Verde was relatively protected. Hence, the differences in primary gradients that we find between El Verde and Bisley approach the range of differences throughout tabonuco forest. If we can explain the distribution of populations and ecosystem attributes based on differences in primary gradients within and between our sites, our explanations should have validity throughout tabonuco forest.

Workplan - After consolidating our knowledge of patterns and processes at our two study sites during the first three years of LTER 2, we will use correlative approaches and simulation models (see Synthesis and Modeling below for model descriptions) to predict ecosystem attributes (such as biomass, soil carbon, soil solution chemistry, frog densities) at other points in tabonuco forest. Sites will be selected randomly within categories of physiography and history developed using GIS. In order to examine the idea that primary gradients are the major forces affecting ecosystem attributes, we will make nested sets of predictions using 1) only field data on light, temperature, soil moisture, and soil nutrients, 2) the preceding information plus data on plant species composition of the site, and 3) the preceding information plus data on the disturbance history of the site. The CENTURY model will be used to predict soil organic matter (SOM) and soil solution chemistry, which are known to vary across catenas in the LEF (Sanford et al. 1991, McDowell et al. 1992). Biomass will be predicted with FORGROW and forest stand dynamics with ZELIG (Urban and Shugart 1992). Field surveys of sites will be conducted during intensive summer campaigns with the help of undergraduate research interns. This approach was very successful in the first survey of the HRP.

H1B: Water and chemical fluxes at different spatial scales in the LEF are controlled by different subsets of the same abiotic and biotic factors. At larger spatial scales, fewer abiotic and biotic factors will be required to predict those fluxes (Schaefer, Lugo, McDowell, Scatena, K. Vogt, D. Vogt).

Rationale - Current understanding of watershed-level biogeochemistry in the LEF is based on work in watersheds of 10 to 100 hectares (McDowell and Asbury 1994). We propose to increase the range of spatial scales at which these biogeochemical fluxes are measured. This involves both assessment of input and output fluxes, and the identification of minimum sets of abiotic and biotic factors that can predict those fluxes at different spatial scales. At larger scales we anticipate that reduced spatial and temporal variability will decrease the number of abiotic and biotic factors required to predict those fluxes.

Workplan - We will focus on a series of nested and adjacent watersheds (7 to 3800 ha) containing most of the tabonuco forest of the LEF (methods in Appendix A). Abiotic and biotic factors coded as GIS overlays will enable us to express predicted biogeochemical fluxes in a spatially-explicit manner. We will use multivariate techniques to uncover the smallest subset of abiotic and biotic factors that successfully predicts biogeochemical inputs and outputs at different scales. One major challenge for biogeochemical budgets in complex terrain is the measurement of dry deposition. Commonly-applied experimental and modeling strategies require flat terrain with homogenous vegetation (Hicks et al. 1986). We suggest that throughfall (TF) fluxes of Cl- will represent the sum of wet and dry deposition to the forest. This has been shown to be a reasonable approximation for sulfur in high-deposition environments (Lindberg 1992). Our goal is to estimate dry deposition on the landscape scale based on GIS representations of topographic and vegetation "roughness". A second major challenge is that watershed nutrient budgets involve the rarely-tested assumption of "hydrologic tightness". The assumption is that all waterborne chemicals leave the watershed in stream channels and not by deep subsurface flow. Lesack (1993), for example, showed that only a modest fraction of total export was lost as deep seepage in a small Amazon basin with deep clayey soils. As annual water fluxes through LEF watersheds are the largest of the LTER network and depth to bedrock can be unusually large here, the significance of this assumption can readily be seen. We will test the assumption of hydrologic tightness in LEF watersheds with chloride ion (Cl-) as a tracer. The LEF is particularly well-situated for such a test, as it receives unusually large inputs of Cl- (from 100 - 300 kg ha-1 yr-1, varying with elevation (McDowell et al. 1990, McDowell and Asbury 1994, Asbury et al. in press). There is no geological evidence for Cl-bearing rock in the LEF. In addition, the biological inertness of Cl has favorable implications for this test: 1) storage of Cl within the system should not change substantially through time (Cl- dissolved in soil water, anticipated to be the largest intra-system pool, is estimated to turn over at least 10 times per year, and accumulation in the biota is minor), and 2) TF samples can be collected at long intervals because microbial alteration of Cl- concentrations in samples in the field will be minor (in contrast to N and P). We already have several years of data on wet deposition inputs and stream water outputs of Cl- for Bisley and El Verde (McDowell et al. 1990, McDowell and Asbury 1994, Scatena et al. unpublished). Assessing hydrological tightness will require estimation of dry deposition inputs with TF and additional measurements to clarify relationships between wet deposition and topographic factors at the larger spatial scales.

H2: At any point in geographical space, the short-term response to disturbance and the subsequent trajectories of recovery are determined by 1) the location of the point along abiotic gradients (physical), 2) the abiotic and biotic conditions at the time of disturbance (historical), and 3) biotic conditions subsequent/consequent to disturbance (successional). The relative importance of these three factors will vary with the severity of the disturbance.

Background - Results from LTER 1 demonstrate that understanding of ecosystem recovery after disturbance in the LEF requires knowledge of 1) the spatial distribution of resources needed for growth (e.g., water, light, and nutrients distributed along gradients of slope, aspect, elevation, geology), 2) legacies of natural and anthropogenic disturbances varying in scale, frequency, and intensity, and 3) the properties of nutrient storage and cycling, reproduction, dispersal, establishment, growth, and survival inherent in the biota. Because many of these elements are dynamic in time and space, the relative importance of each in determining trajectories of recovery during secondary succession varies in geographical space. This results in complex distributions of species and ecosystem properties in space and time. Prior to Hurricane Hugo, we envisioned tabonuco forest as a matrix punctuated by disturbances such as tree falls (more frequent) and landslides (less frequent; Fig. 12A). Over ecological time, disturbed sites would recover toward conditions represented by the forest matrix, and sites within the forest matrix would experience disturbances, resulting in a dynamic equilibrium. The relative rarity of disturbed sites within the forest matrix undoubtedly had a profound impact on the mode and tempo of recovery because it strongly affected the identity and sequence of colonizing species.

Consequently, trajectories of recovery from disturbance should have been relatively invariant for particular disturbance events occurring in similar physiographic locations. After Hurricane Hugo, a few protected sites retained characteristics of the pre-hurricane matrix, but the majority of sites was moderately to severely disturbed (Figure 12B). The forest became a sea of disturbance with occasional islands of relatively unaltered matrix dispersed throughout. This transposition likely altered the mode and tempo of recovery, primarily by altering the abundance and distribution of colonizers for the disturbed sites. The trajectories of recovery after a widespread disturbance such as Hurricane Hugo may be innately different than the trajectories of recovery when the disturbance event is less extensive. The long-term data sets being collected in the LEF for populations, community composition, and ecosystem processes afford an opportunity to provide mechanistic explanations for spatial and temporal variability in ecosystem attributes. This opportunity is enhanced because of the differences between sites in the severity of damage caused by Hurricane Hugo. Within the constraints of current forest condition, we ask what biotic or abiotic factors affect trajectories of recovery and spatial distribution of organisms and processes most strongly. The trajectories of interest include 1) flux rates or storages for various nutrients, 2) measurements of production by various trophic groups, 3) plant species composition, 4) animal species composition, or 5) attributes of food web organization (e.g., connectivity, trophic levels, number of food loops). The generality of our approach allows us to analyze any suite of biological attributes that can be measured on a site-specific basis.

General Approach - Each kind of disturbance alters values of ecological space in measurable ways. The LTER data base allows us to measure displacement in ecological space and track subsequent recovery. Measurements of physical characteristics (e.g light, humidity, nutrient availability, temperature), structural attributes (e.g., leaf area index, canopy cover, stem density, biomass, basal area), community composition, and ecosystem processes (e.g., deposition, mineralization, export, nutrient cycling efficiency) have been made since the beginning of LTER 1. Displacement of these attributes by Hurricane Hugo (and other disturbances) and subsequent trajectories through ecological space will continue to be measured in LTER 2. We illustrate the approach with reference to snail community organization (Fig. 12). We are interested in determining whether trajectories of the change (arrows in Fig. 12A-D) in the local composition of snail communities at each site are related to physiographic attributes (shading in Fig. 12), current community composition of snails (location in 3-dimensional space in Fig. 12), or chance. Site-specific abundances of each species of snail are subjected to a multivariate data reduction methodology such as principal components analysis (PCA) or multidimensional scaling. In addition, each site is categorized by physiographic condition (e.g., valley, ridge, slope) and disturbance history. If trajectories of recovery are determined primarily by current snail species composition, then sites with similar faunas after disturbance should proceed along parallel pathways in PCA space and share similar species compositions during recovery (Fig. 12C). In contrast, if trajectories of recovery are determined by physiographic attributes or history, then regardless of current snail composition, sites sharing similar physiographic or historical characteristics should converge and trajectories in PCA space should not be parallel (Fig. 12D). If no factor dominates, or if stochastic or chaotic processes control recovery, then trajectories should not converge, and community composition during recovery should be unrelated to physiography or initial species composition. Finally, if biotic processes subsequent to disturbance dominate recovery (e.g., establishment of a new competitor or disease), a new community may arise.

H2A: Recovery after a hurricane is more strongly affected by previous human disturbance than either by physiography or post-disturbance biotic factors (Willig, Brokaw, Camilo, Everham, Haines, Scatena, Thomlinson, Waide, Woolbright, Zimmerman, Zou).

Rationale - The distribution of tree species in a 16 ha plot (HRP) before Hurricane Hugo was more closely correlated with previous land use determined from aerial photography than with physiography. The legacy of previous land use was strong despite the fact that the area had been disturbed by two hurricanes subsequent to the discontinuation of human use. Damage from a third hurricane (Hugo) showed no significant relationship with slope, aspect, soil type, or any other physiographic character measured, but was instead most closely associated with the tree species and hence with the pre-hurricane distribution of vegetation (Fig. 13; Zimmerman et al. in press).

Workplan - Information on the location of individual plants by species, soil type, historical land use, known canopy gaps, hurricane damage, elevation, aspect, slope, and other physiographic features have been entered into a GIS for the HRP. Woody plants will be remeasured on the HRP in 1995 and 2000 and in permanent plots at Bisley on an annual basis. Herbaceous plants, snails, insects, frogs, lizards, and birds will be surveyed annually (more frequently for some groups) at 40 points in the HRP. Measurements of physical environment and vegetation structure will also be taken at these points. Trajectories of recovery will be determined as indicated above and compared with patterns predicted from the alternative hypotheses that 1) previous land use, 2) physiography, 3) biotic factors occurring after disturbance, or 4) chance determines successional pathways.

H2B: Recovery after a landslide is more affected by initial composition of the vegetation and abiotic factors than by either previous land use or biotic factors occurring subsequent to disturbance (Myster, Walker, Fetcher, Zou).

Rationale - Landslides are more severe disturbances than either hurricanes or treefalls. For example, landslides remove biomass and soil layers and so eliminate the biological legacy of previous disturbances and smooth out physiographic differences (Guariguata 1990, Myster and Camilo in review, Fernandez and Myster in review, Myster in press). Landslides are also different in that they show strong spatial heterogeneity in vegetative recovery (Myster and Fernandez in review). This is true for the recovery mechanisms of seed rain (Walker and Neris in press), seed predation and germination (Myster in review) as well. These responses after landslides can be investigated (and compared to other disturbances) by examining ecosystem recovery through successional pathways sampled in permanent plots (Myster and Walker in review).

Workplan - Intensive measurements of succession were initiated on three landslides during LTER 1 and less intensive measurements were conducted on an additional 17 slides. On the intensively-studied slides, permanent plots in vertical and horizontal transects on each slide were surveyed every 4-6 months for all plants, and trajectories of recovery for each plot have been developed (Fig. 14). We propose to continue measurements on both intensive and extensive slides during LTER 2.

H2C: Regeneration in experimentally-cleared patches where all the above-ground biomass was removed will take longer to recover than adjacent hurricane-damaged areas where the above-ground biomass remained on the site. (Silver, Scatena).

Rationale - It has often been suggested that the primary difference between anthropogenic and natural disturbances is the off-site removal of biomass and nutrients that are associated with human-induced disturbances (Bormann and Likens 1979). This removal of biomass displaces a site to a different position in ecological space than would a treefall or hurricane blowdown. The existence of paired experimental clearings that were created at Bisley as part of a series of studies on biomass (Scatena et al. 1993) and below-ground disturbance (Silver 1992, Silver and Vogt 1994) during LTER 1 create a unique opportunity to test this hypothesis and the applicability of using life-history characteristics to predict the pathways of anthropogenically induced succession.

Workplan - Intensive sampling of the soils, vegetation composition, and above- and below-ground biomass of these clearings and adjacent forests have been done on an annual basis since 1989. This sampling will be continued: 1) to quantify the rate of recovery of above- and below-ground biomass and nutrient content, and 2) to establish the successional trajectories of areas with and without biomass removal. These successional histories will then be compared to succession following other disturbances.

H2D: Recovery of biomass and soil nutrient capital on landslide scars occurs within 60 years for elements which have primarily metabolic functions (e.g., N, P, K, Mg) because of (a) the input of organic matter from adjacent intact forest and early successional vegetation with relatively high nutrient concentrations, (b) N-fixation by associative and free-living bacteria and blue-green algae, (c) retention by soil organic matter of nutrients from atmospheric deposition or weathering of residual minerals in newly-exposed subsoil (Johnson, Lugo, Scatena, Schaefer, Zou).

Rationale - Studies of nutrient recovery after clearcutting (Silver 1992) and landslides (Zarin 1993) carried out over the past five years have suggested that in the LEF, vegetation exerts strong control over the amount of nutrient capital contained in soil of the rooting zone (defined here to include forest floor and mineral horizons to a depth of 60 cm). In the colorado forest zone in the LEF (600-800 m elevation), plant-available nutrients in the subsoil exposed by recent landslides are a small fraction of the nutrient supply required by the vegetation that subsequently develops (Zarin and Johnson in review a,b,c). In spite of the oligotrophic conditions, nutrient availability does not limit the rate of recovery because of the effectiveness of biological controls on nutrient accumulation (Zarin 1993). During primary succession, nutrient accrual is correlated with soil organic matter accumulation, which adds nutrients directly and retains nutrients deposited atmospherically and weathered from soil minerals (Zarin 1993). In the colorado forest, inputs from atmospheric precipitation exceed annual nutrient requirements during primary succession for Ca and Mg but not for N, P or K (Zarin 1993, McDowell and Asbury 1994), suggesting that the ocean may be the source of much of the biomass Ca and Mg, while N accrual rates probably require significant N-fixation, and P and K are likely derived primarily from in situ weathering. Mineralization of allocthonous litter inputs from the periphery of landslide scars may also be a significant source of macronutrients. Continuing studies are proposed to refine our understanding of nutrient sources during primary succession, and the extent to which the biota control the nutritional characteristics of the rooting environment.

Workplan - We will measure litter input and mineralization rates at a chronosequence of approximately 12 landslides and adjacent older sites located in the tabonuco zone in order to determine the importance of detrital inputs to the nutrient budgets of these sites. N-fixation will be measured at the same sites in order to determine the contribution of microbial N- fixers to ecosystem N. Analyses of 87Sr/86Sr ratios in ecosystem compartments, atmospheric input, bedrock and streamwater will be initiated in order to assess the relative importance of mineral nutrient sources to the aggrading ecosystems.

H3: Anthropogenic disturbances (e.g., agriculture, charcoal production, timber harvesting, etc.) have different spatial patterns, intensities, and recovery trajectories than individual natural disturbances (hurricanes, landslides, treefall gaps).

Background - Although the first phase of the LTER focused on natural disturbances, our investigations indicated the importance of previous land use on the structure and composition of present day mature stands in the LEF (Scatena 1989, Garcia and Scatena 1993, Zimmerman et al. 1994). Analyses of historic land use at El Verde and Bisley indicated that anthropogenic disturbance had a long-lasting effect on the composition of both canopy and understory vegetation and animal populations. We hypothesize that anthropogenic disturbance is persistent because it causes changes in the gradients making up ecological space that are large relative to those caused by natural disturbances. The precise natures of these changes are unknown and will be the focus of work under this hypothesis. Given the importance of anthropogenic disturbances at lower elevations in the LEF (Fig. 15) and to tropical forests in general, we propose a special focus on human disturbances in LTER 2. The goal of this effort will be to document the occurrence and impacts of various anthropogenic disturbances in the LEF and to understand the factors that lead to their persistence. By identifying the characteristics of widespread human uses of tropical forests, we will address a problem common to many tropical areas. This effort will increase our understanding of the relationships between anthropogenic and natural disturbances and will contribute to the scientific base needed to address current issues in resource management and conservation biology of tropical forests.

General Approach - We will document the historic occurrence and distribution of major human disturbances by compiling and digitizing all available information on land use and forest conditions to produce detailed vegetation maps for the LEF for the years covering the last inter-hurricane period (1932 to 1989). Initial vegetation maps for 1936 and 1989 (Fig. 16), and similar studies at the Harvard Forest LTER site indicate the applicability of this approach. Models of hurricane meteorology and topographic exposure will be used to reconstruct damage from historical storms and to prepare a map of hurricane susceptibility for the forest (Boose et al. 1994). Empirical and retrospective studies of landslides will provide similar information for this disturbance type. Using GIS, we will develop a classification of disturbance regime for the LEF. This classification will be used to compare ecosystem attributes under different disturbance regimes.

H3A: Anthropogenically-disturbed areas occupy unique positions in ecological space. The legacies of anthropogenic disturbance remain on the landscape for long periods because the biota is poorly adapted to the conditions existing after these disturbances (Scatena, Aide, Boose, Everham, Foster, Lugo, Walker, Zimmerman, Zou).

Rationale - Observations made during LTER 1 suggest that sites of anthropogenic disturbance develop characteristic assemblages of plant and animal species (Garcia and Scatena 1994). There are also indications that anthropogenic changes alter nutrient pools and cycling. These points, plus the observed longevity of the effects of anthropogenic disturbance, suggest that recovery after anthropogenic disturbance may follow successional pathways different than those found in areas of natural disturbance. For example, Cecropia schreberiana, the dominant successional species after natural disturbance (Fig. 17), is completely absent from abandoned pastures on the edges of the LEF (Aide and Zimmerman unpublished). Thus anthropogenic disturbance may modify ecological space in ways incompatible with the life- history strategies of certain plants of tabonuco forest (see H5 below), resulting in different recovery vectors and end points than natural disturbance (see H2).

Workplan - Site-specific studies on vegetation composition and successional pathways will be conducted in areas of abandoned roads, coffee plantations, and pastures in land recently acquired by the LEF. Soil properties, plant species composition, biomass, and nutrient content will be compared in these areas and adjacent undisturbed areas to determine which attributes are likely to serve as a long-term record of anthropogenic disturbances. Animal populations will also be surveyed in certain areas to determine if feedback mechanisms exist between anthropogenic disturbances and the dynamics of populations. This work will be done in areas of known past land use determined from the disturbance classification discussed above and will be compared to ongoing studies of recovery and composition of hurricane, treefall gap, and landslide disturbances at El Verde and Bisley .

H4: Tabonuco forest contains plant and animal species (or groups of species) that alter critical ecosystem processes and successional pathways by modifying the attributes of ecological space in their vicinity.

Background - In the tabonuco ecosystem, a few plants and animals stand out as "pivotal" species. When one of these pivotal species is removed by natural disturbance or management practices, rates of ecosystem processes are altered because redundancy of function is low. No other species substitutes completely for the lost pivotal species, and dynamics change as a consequence of the missing relationships based on this single species. Examples of pivotal species include Cecropia schreberiana, a pioneer tree of disturbed sites, Prestoea montana, a palm abundant in the riparian zone, and Lamponius portoricensis, an abundant insect herbivore that is thought to influence the plant species composition of gaps (Willig et al. 1986). Pivotal species may exert their influence through a variety of processes including facilitation (Connell and Slatyer 1977), competition, or predation. The central premises adopted in this proposal (p. 2) emphasize processes that act on plant population dynamics, or from the bottom up. Top-down control of populations and hence successional pathways can also be brought about by pivotal species. The controversy between top-down (Andrewartha and Birch 1954, Strong 1984) and bottom-up (MacArthur 1958, Lack 1971) regulation of populations led to the conciliatory point of view that trophic levels in the food chain are alternately predator- and resource-limited (Hairston et al. 1960). Extensions of this theory (Fretwell 1977, 1987) and the development of trophic cascade models (Paine 1980, Carpenter et al. 1985) suggested that plant standing crop was controlled by factors acting from the top of the food chain. Recent syntheses of top-down and bottom-up approaches suggest that both act to regulate populations, but their relative strengths are determined by the abiotic and biotic characteristics of the ecosystem being considered (Power 1992, Hunter and Price 1992, Karr et al. 1992).

General Approach - The general approach will involve the removal of plants and animals. Because pivotal species are thought to perform unique roles, the effects of their loss are measurable. If the working hypothesis does not hold and functional redundancy exists in the ecosystem, removal should have little effect on ongoing ecosystem processes (e.g., succession). If the species removed have no functional equivalents, deviations in ecosystem processes compared to controls should be observed. Selected ecosystem processes will be monitored in plots where species are removed. If changes can be induced in these ecosystem processes through the removal of single species, redundancy is low and the presence or absence of single species can determine ecosystem state.

H4A: The presence of a facilitating species (Connell and Slatyer 1977) is necessary to initiate succession after disturbance in tabonuco forest. In the absence of the required facilitating species, succession may be slowed or arrested or may proceed along alternate pathways (Zimmerman, Aide, Brokaw, Myster, Scatena, Schowalter, Walker).

Rationale - Connell and Slatyer (1977) suggested three mechanisms by which species replace one another during succession. Under the "facilitation" model, specialized early colonists must be present for succession to proceed. Under the "tolerance" and "inhibition" models, late successional species can become established even in the absence of early colonizers. Tropical forests generally have one or more pioneer species whose widespread dispersal and rapid growth distinguish them from other local tree species (Swaine and Whitmore 1988). These pioneers may facilitate the progression from herbaceous to woody vegetation after disturbance by establishing shaded patches for regeneration of other tree species. In tabonuco forest, Cecropia schreberiana, Schefflera morototoni, and Miconia tetandra are the initial colonizers after disturbance (Crow 1980, Zimmerman et al. 1994). Cecropia is the most abundant and light-tolerant of these pioneer species, and pure stands of Cecropia have become common after Hurricane Hugo (> 16,000 individuals/ha). However, establishment and growth of Cecropia are limited by dispersal, light, and nutrient conditions, and where Cecropia does not become established after disturbance, a thick tangle of herbaceous vegetation and woody vines often results. The existence of this herbaceous layer close to the ground can temporarily inhibit further successional development.

Workplan - We will manipulate Cecropia density under a variety of natural and experimental conditions and monitor microenvironment, succession, and soil conditions through the next two LTER cycles (12 years). Since much of the important dynamics of succession occurs during the first decade after disturbance, any differences resulting from the manipulation should be apparent by the end of the experiment. We will perform the following manipulations of Cecropia density: 1) reduction of sapling density by 50, 90, and 100% in 10x10 m plots in existing gaps formed by Hurricane Hugo, 2) continual removal of seedlings established in new treefall gaps occurring during the first three years of the study, 3) replication of 2 in landslides, 4) continual removal of seedlings from 5x5 m experimental plots in a garden established for this purpose, and 5) transplanting of Cecropia saplings to abandoned pasture in early stages of succession. In experiments 3, 4, and 5, some plots where Cecropia are removed will be shaded artificially to mimic this effect of Cecropia establishment. In experiment 5, perches for avian dispersers (McDonnell and Stiles 1983) will be added to some plots instead of transplanting Cecropia to mimic the addition of habitat structure. Parrotta (1993) demonstrated that trees planted on degraded land acted as roosts for dispersers and increased both the rate of natural succession and species richness. We predict that plant succession will be slower in plots where Cecropia is removed, and that neither Schefflera nor Miconia will replace Cecropia. Species successfully colonizing the experimental plots will be those with resource requirements (see H5 below) most closely matching resource availability in the modified ecological space. Changes in Cecropia density and subsequent plant successional pathways will drive parallel changes in the trajectory of the recovery of animal communities. In experiments 3-5, addition of artificial shade and perches will help to focus on those characteristics of Cecropia that are most important in affecting succession. Initial and periodic measurements of soil moisture, nutrients, temperature, light, fractionated soil carbon, and infiltration rates will be performed to examine the effects of removal of Cecropia on the modification of soil characteristics during succession and hence the displacement of plots along ecological gradients.

H4B: Increases in Cecropia after disturbance in riparian areas affect stream community dynamics through changes in leaf litter dynamics and through changes in nutrient inputs (Covich, Crowl).

Rationale - Certain species such as Cecropia grow quickly and contribute a disproportional input of leaf litter into riparian areas where stream channels are disturbed. The pattern, quantity, and quality of leaf inputs shift following removal of Cecropia. Storage and retention of leaves generally are altered once Cecropia litter is removed. Pulses of large Cecropia leaves readily form debris dams in association with woody debris such as branches and stems that fall into the stream channel. These structures enhance the retention process by accumulating large amounts of other leaf litter from non-Cecropia trees. Debris dams are an integral source of energy to the aquatic food web via the detrital pathway (Covich et al. 1991). They also contribute nutrients through leaching that then may enter the primary productivity pathway.

Workplan - Leaf inputs of single species (Cecropia only) will be compared with mixed species (Cecropia plus other early successional species) to determine retention of leaf litter in streams and their effects of the aquatic community. Based on existing maps of tree species distributions along riparian corridors, we will select several species of tree (such as Prestoea montana) for leaf litter manipulations. We will monitor changes in detritivore populations (e.g., shrimp, crabs, aquatic insects) associated with different quantities and types of leaf litter as well as structural complexity provided by the litter during the processing stages.

H4C: Herbivory acts to accelerate succession by increasing stress on early successional plant species. Herbivores also tend to regulate long-term nutrient cycling by influencing the competitive relationships among successional species of different nutrient and light requirements (Willig, Aide, Camilo, Schaefer, Schowalter, Vogt, Zou).

Rationale - Schowalter (1981) hypothesized that insect herbivores promoted succession by preferentially feeding on abundant, nutrient-rich early successional plant species. As plant density and biomass increase during succession, competition for light and nutrients causes early successional plant species to approach their physiological limits more quickly than later successional species that are more tolerant to low nutrient and light conditions (Bormann and Likens 1979, Gorham et al. 1979). This physiological stress combines with large individual size and abundance to make early successional species more susceptible to insect herbivores. Selective herbivory tilts the competitive balance in favor of late-successional species, thus promoting species replacement (Connell and Slatyer 1977, Schowalter et al. 1981a). Carbon allocation strategies with regard to growth and plant compounds (see H5) determine the place of each species along the successional pathway (Coley et al. 1985). Herbivory influences long-term nutrient cycling both through its effect on succession and by mediation of the rate and direction of transfer of nutrients between live vegetation and litter (Schowalter et al. 1981b). Herbivory has been shown to increase nutrient uptake and primary productivity, translocation of nutrients within plants, nutrient concentration in litterfall, leaching of foliar nutrients, and nitrification, nitrogen-fixation, and decomposition in the litter (Schowalter 1981, Willig et al. 1986, Schowalter et al. 1991). The cumulative effect of these transformations on nutrient cycling is poorly understood.

Workplan - We will manipulate the density of the walking stick Lamponius portoricensis on 10x10 m experimental plots in the regenerating understory of tabonuco forest. Lamponius was selected for this study because it is an easily-observed, sedentary herbivore that is abundant in light gaps and whose population dynamics (Willig et al. 1986), food preferences (Sandlin and Willig 1993), habitat requirements (Willig et al. 1993), and response to disturbance (Willig and Camilo 1991) are well-known. In addition, Willig et al. (1986) suggested that Lamponius influenced the path of succession in light gaps by preferential herbivory leading to increased nutrient availability for later successional plant species. Individuals of Lamponius removed by hand will be transferred to matched plots to create high- and low-density manipulations. We will measure density of walking sticks, degree of herbivory, changes in plant species composition and biomass, rates of leaf production, litter decomposition rates, nutrient uptake, and concentration of nutrients in live and fallen leaves and throughfall for a period of five years. The amount of herbivory and densities of walking sticks will be correlated with plant ecological characteristics determined under H5 (see below). Experimental plots with reduced numbers of Lamponius should have lower aboveground primary productivity, concentrations of secondary defensive compounds, nutrient uptake, herbivory, decomposition rate, and species turnover than unmanipulated plots.

H4D: Consumer populations in tabonuco forest are limited by predation. Removal of top predators will affect lower trophic levels and through them plant species composition and productivity (Waide, Aide, Bishop, Camilo, Reagan, Schowalter, Willig, Woolbright).

Rationale - Strong (1992) suggested that top-down control is less important in species-rich communities where the effects of consumption are spread over many prey species. However, in tabonuco forest, where vertebrate and invertebrate species richness is more similar to temperate than mainland tropical forests, evidence for both top-down and bottom-up regulation of populations exists. Dial (1992) removed Anolis lizards from isolated tree branches and found a subsequent increase in insect populations that influenced the rate of herbivory. Fertilization of

20x20 m plots at El Verde led to increases in litterfall, leaf area index, seedling growth, and abundance of ants, termites, flying insects, and spiders (Waide et al. in prep.). Frogs, whose populations are limited by retreat sites (Stewart and Pough 1983), increased in mean size but not in abundance with increasing primary productivity. We propose a complementary experiment to determine the effect of predation on consumer and producer populations.

Workplan - The food web in tabonuco forest has four trophic levels and is characterized by the absence of large consumers and predators (Reagan and Waide in review). The top predators are birds (Puerto Rican Screech Owl [Otus nudipes] and Puerto Rican Lizard Cuckoo [Saurothera vielloti]), which consume lizards and frogs. Large, nested exclosures of different mesh sizes will be constructed to exclude birds and lizards and frogs. If top-down control operates, lizards and frogs should increase in the absence of their avian predators in the outermost exclosure, and the effect may cascade to lower trophic levels. Where all vertebrates are excluded, insects should increase and leaf area decrease. Exclosures will be maintained for at least five years to examine the effect of predator manipulation on plant species composition.

H4E: The decapod community is characterized by different functional feeding groups that increase the retention of the different carbon sources that are available depending on disturbance regime in the riparian zone (Covich, Crowl).

Rationale - The decapod community found in these streams is dominated by two species of atyid shrimp, one that functions primarily as a filter feeder and/or grazer (Atya lanipes) and another that functions as a shredder/detritivore (Xiphocarus elongata; Fig. 18). Xiphocarus processes leaf material, making it available to the filter-feeding shrimp and other aquatic invertebrates. By decreasing the size fraction of leaf material, this species could be significantly increasing the retentiveness of the carbon and nutrients available from detritus. When tree fall gaps occur in the riparian corridor, resulting in a decrease in leaf litter and an increase in light, algal production in the stream can increase. Grazing Atya utilize this food source resulting in tight, rapid cycling of nutrients otherwise tied up by the algae. In addition, when riparian disturbances result in high silt loads, Atya makes food sources more available by acting as a bioturbator, removing silt from feeding surfaces (Pringle et al. 1993). Because both species are very abundant in Luquillo streams, all types of food sources resulting from the riparian vegetation dynamics are quickly processed, resulting in high retention and rapid turn-over.

Workplan - We will remove Atya only, Xiphocarus only and both Atya and Xiphocarus from small reaches of stream (40-100 m in length) on a weekly basis. Small headwater streams with steep gradients and relatively small pools will be used to minimize re-colonization dynamics. Leaf litter inputs and outputs (both amounts and the size fraction) as well as algal production will be measured from these areas four times per year. Cecropia leaves will be added to other experimental pools and the changes in size distributions of leaf fragments will be sampled on a weekly basis. In addition, aquatic insects will be sampled for changes in community structure.

H4F: Terrestrial carbon and nutrient levels vary on a micro-scale in tabonuco forests because individual plant species of different successional status produce varying quantities and chemical qualities of litter that result in chemical imprints in the soil or the presence of past structures (e.g., coarse wood) that modulate how the plant and animals respond to and recover after a disturbance. (K. Vogt, D. Vogt, Lugo, Scatena, Schaefer)

Rationale - In terrestrial ecosystems, individual plant species contribute to small-scale variation in resource availability by differentially modifying either soil organic matter or nutrient accumulation/depletion over successional time scales (Lugo et al. 1990 a,b, Wedin and Tilman 1990, Wang et al. 1991). These ecosystem-modifying processes occur at the scale of the individual plant or by topographic zone if there is a clumped distribution of plant species (e.g., Prestoea montana in the riparian zone and Dacryodes excelsa on ridgetops; Basnet 1992) or if there is a localized introduction of non-native tree species (Lugo 1992b). One dominant mechanism causing these functionally different spatial units is the selective accumulation of nutrients by tree species (e.g., Prestoea accumulating calcium and aluminum, Guarea accumulating phosphorus, Inga fixing nitrogen, and Cecropia accumulating nitrogen [Bloomfield et al. 1993]). Interspecific differences in litter production (e.g., foliar turnover) also contribute to localized accumulation of nutrients. Plants also feed back into the abiotic environment by producing secondary chemicals that influence decomposition, and by influencing the spatial patterns of organic matter by inhibiting movement of litter.

Workplan - Soil will be sampled around five of the more common tree species (Dacryodes excelsa, Prestoea montana, Guarea guidonia, Inga laurina, and Cecropia schreberiana) to determine if they are influencing their surrounding environment and to what relative degree (e.g., Hobbie 1992). The tree-plots to be sampled will be located throughout the LEF to ensure as large a data pool as possible for correlative and quantitative ecological statistics (e.g., see H2). Soil analyses will initially consist of total and extractable nutrients and light- and heavy-fraction carbon. Soil samples will be obtained from three depths and along four radii from each tree. Other parameters to be recorded at each tree plot are factors such as aspect, slope, neighboring tree and shrub species, soil type, parent material/bedrock type, topographic position on the slope, presence of any disturbance and type, etc. Any positive correlations found in this phase may then be followed up by specific species testing in the next LTER phase as well as monitoring of species' influences on ecosystem "processes" (e.g., decomposition rates, N mineraliztion rates, etc.).

H5: The disturbance regime prevailing in tabonuco forest over evolutionary time has led to the development of a plant community whose members have varied and complementary ecological characteristics.

Background - We assume that disturbance is an important factor producing and maintaining gradients in resource availability in tabonuco forest. Trade-offs in tree life histories and other ecological characteristics result because investment of energy or nutrients into adaptations that maximize abundance at one point within N- dimensional hyperspace precludes the investment of the same energy or nutrients to any other adaptations (Hall et al. 1992, Tilman 1994). It is these "trade-offs" that govern the distribution and abundance of tree species along environmental gradients. In the Neotropics, there has been considerable interest in tree regeneration in treefall gaps (Denslow 1980, 1987, Hubbell and Foster 1983, 1986, Brokaw 1985, 1987, Platt and Strong 1989, Welden et al. 1991, Clark and Clark 1992). Most of these studies have focused on the extremes of the life history continuum: fast-growing shade-intolerant vs. slow-growing shade-tolerant species. Most studies of tropical tree life histories have focused on specific life-history stages (Clark and Clark 1992), particularly seeds (e.g., Vazquez-Yanes and Smith 1982), seedlings (e.g., Augspurger 1984), and saplings (e.g., Welden et al. 1991). A few studies have described complete tree life histories (Hartshorn 1972, McCormick 1994), but they have not always explicitly tested the effect of resource levels (e.g., light) on life history variation.

General Approach - We propose to build on a series of studies of the life history of tree species in the LEF over the past 30 years (Bannister 1970, Lebron 1977, Mu¤iz Melendez 1978, Silander 1979, Sastre-Jesus 1979, Nieves 1979, Lugo and Rivera-Battle 1987, You 1991; summarized by McCormick 1994). Life history traits and other ecological characteristics of species will be determined for selected species (Table 7). These 14 species were derived from 88 species occurring on the HRP prior to Hurricane Hugo that had at least one individual >10 cm DBH (see Appendix A). We propose to measure a wide variety of ecological characteristics of these species to test the following hypotheses.

H5A: Ecological characteristics of canopy trees in tabonuco forest exhibit trade-offs because of limitations of nutrients and energy. (Zimmerman, Aide, Fetcher, Haines, Myster, Pulliam, Sabat, K. Vogt)

Rationale - An important paradigm in ecology, the principle of allocation (Gadgil and Bossert 1970, Harper and White 1974) simply states that in order to be efficient at one thing requires being inefficient at doing other things. For trees, this has been expressed in the relative ability of species to withstand deep shade by being slow-growing vs. those that are fast- growing and shade intolerant. There should be additional trade-offs in ecological characteristics, parallel to those involved in resource acquisition, related to seed production and dispersal, growth and mortality, regeneration strategies, tree architecture, and herbivore defense (Swaine and Whitmore 1988).

H5B: Canopy trees in tabonuco forest can be separated into two distinct groups corresponding to "pioneer" vs. "non-pioneer” life history types. (Zimmerman, Aide, Fetcher, Haines, Myster, Pulliam, Sabat, K. Vogt)

Rationale - This hypothesis, outlined by Swaine and Whitmore (1988), proposes two distinct groups of tree species: "pioneers" are shade-intolerant species that are fast-growing and have low levels of herbivore-defense chemicals. They produce an abundance of small, highly dispersable seeds that remain dormant in the soil until a disturbance exposes them to light. "Non-pioneers" (sometimes referred to as "Climax" species) have the opposite characteristics. Analysis of hurricane damage to trees on the HRP appears to conform to this view of tropical tree life histories (Fig. 19). Some argue that there are not distinct groups of species but that species distribute themselves uniformly between extremes (Alvarez-Buylla and Martinez-Ramos 1992). A continuous distribution of the ecological characteristics of species would suggest that each species carries a unique role in forest dynamics following disturbance and would provide one explanation for the co-occurrence of many species in tropical forests.

Workplan - A wide variety of ecological traits (Table 8) will be determined for the selected species in and around the HRP at El Verde. Here we summarize the approach towards measuring each of these traits. Additional details on methodology are provided in Appendix A.

Carbon gain - Physiological characterization of the different species will focus primarily on leaf carbon gain under field conditions. Carbon gain will be estimated using models most recently described by Gross et al. (1991) and Ogren (1993), and a steady state modeling approach developed by Fetcher (unpublished). Nutrient uptake kinetics and VAM dependency - Kinetics of phosphorus and calcium uptake by excised roots will be determined according to Epstein et al. (1963) using 32P and 45Ca. The dependence of plant growth on infection of the roots by vesicular-arbuscular mycorrhizae (VAM) will be tested in shadehouse experiments using the methods of Calderon (1993). Two of the 14 study species (Prestoea montana and Cecropia schreberiana) have already been studied by Calderon (1993). Regeneration - A series of observations and experiments will investigate the regeneration strategies of the key species (Table 8). We will measure seed rain and the occurrence of seeds in the seed bank (Garwood 1989). Shadehouse experiments will be used to investigate light-dependent germination (Vazquez-Yanes and Smith 1982, Everham et al. in review) and shade tolerance (Augspurger 1984). We will also investigate species' ability to resprout following mechanical damage (Putz and Brokaw 1989, Zimmerman et al. 1994) and to produce adventitious roots when stems come into contact with the soil (Sagers 1992, Greig 1993). Tree growth and mortality - Using the methods of Clark and Clark (1992), we will estimate changes in mortality and height growth in four diameter classes of each species across a range of light environments. Architecture - Much of the variation in tree architecture is reflected in changes in the relative size of lateral branches to main stems (Stevens and Perkins 1992). This yields differences in mass attenuation curves (with increasing tree height) that can be summarized by a single value - the per cent linear attenuation. Herbivory - Aide (1988, 1993) studied patterns of insect herbivory and the phenology of leaf production in 32 species of trees in the lowland forest of Panama. Using these same methods, the timing of leaf flush as a defense against herbivory of young leaves will be tested in tabonuco forest. Nutrient conservation mechanisms and foliage quality - Nutrient retranslocation will be measured in each species by comparing nutrient contents of fresh adult leaves and freshly fallen leaves. Secondary chemistry of fallen leaves will also be measured to determine how defense chemistry may affect the decomposition of leaf litter. Two species have already been studied (P. montana and D. excelsa; Bloomfield et al. 1993). Synthesis - Each researcher will publish separate reports on their work with the 14 study species. Studies of individual species will be linked together by a multivariate analysis (e.g., principal components analysis, multidimensional scaling) that will directly test H5A and H5B. From a statistical perspective, we expect to observe that ecological characteristics will be described by a few principal axes, but will not exhibit significant clustering in multivariate space. Critical life-history traits determined at El Verde will also be used in the ZELIG gap-based stand dynamics model (Urban and Shugart 1992), and predicted post- disturbance community dynamics will be tested against measured forest dynamics at Bisley. Thus, these studies will provide a link between long-term monitoring studies (HRP), permanent plots at Bisley, and seedling dynamics plots at El Verde and will help validate models of vegetation dynamics following disturbance.

REQUIRED TOPICS

Long-Term Experiments

The principal long-term experiments established in LTER 1 are listed below. We will continue to follow these experiments in LTER 2. In addition, we propose a series of new long-term experiments that include removal of functionally-important plant species, manipulation of herbivores, and manipulation of higher-order predators. These manipulations are described in the previous text. A further long-term experiment arising from LTER 1 has been funded through a separate grant from NSF to K. Vogt (DEB- 9317258). Under this proposal, coarse litter deposited by Hurricane Hugo will be manipulated to examine the long-term effects of this litter fraction on nutrient dynamics, SOM formation, and stream food webs. Project participants include D. Vogt and A. Covich from the Luquillo LTER.

Hurricane Recovery Plots - The principal long-term experiments proposed in LTER 1 included tree harvests and biomass manipulations at a range of intensities to examine the effect of gap size on forest regeneration. During the first year of LTER 1, we completed the tree harvest experiment on two 40x40 m plots at Bisley. When Hurricane Hugo struck two months later, we re-ordered our priorities to take advantage of the natural experiment and established hurricane recovery plots at El Verde and Bisley. These plots are designed to measure long-term ecosystem recovery across a gradient of hurricane effects from severe at Bisley to less severe at El Verde. Initial results of this work have been published (Walker et al. 1991a, Basnet et al. 1992) and a synthesis of results covering the first five years after disturbance is forthcoming in 1995.

Biomass removal - The two 40x40 plots that were harvested at Bisley immediately before Hurricane Hugo were designed to examine the effects of complete above-ground biomass removal on below-ground nutrient pools and forest regeneration. Initial results have been published (Silver 1992, Scatena et al. 1993, Silver and Vogt 1994) and the experiment will be expanded in LTER 2 to include a comparison of human and hurricane disturbance.

Soil organic matter formation - Experimental plots were established at Bisley to evaluate the effect of litter quality, source (root vs. leaf litter) and soil texture on SOM formation. This experiment will provide data to help calibrate the CENTURY model and test its ability to simulate SOM dynamics in tropical soils. Litter of different qualities and sources are being added to experimental plots with soils of high and low clay content. The experiment is designed to last 10 years.

Long-term Data Sets

Long-term data sets available from the LEF are listed in Table 9. This list includes data generated by the LTER program and by agencies such as the USDA Forest Service, U.S. Geological Survey, and the USDA Soil Conservation Service.

The Five Core Areas

The Luquillo LTER has emphasized the five core areas common to all LTER sites since its inception. A broad range of studies relevant to each of the core areas is funded through other sources (see below). A summary of ongoing and proposed research in each core area follows.

Pattern and Control of Primary Production - Long-term studies of primary production in the LEF are based on a series of permanent plots established by the USDA Forest Service and measured periodically since 1943. The most recent remeasurement was in 1992-93. The long-term plots span the range of forest types in the LEF and provide a detailed record of patterns of growth, mortality, and compositional change (Crow 1980, Weaver 1983, Frangi and Lugo 1985, Lugo and Rivera Battle 1987, Johnston 1992, Lugo 1992, Lugo et al. 1994). These long-term records are complemented by studies at El Verde and Bisley that focus on spatial patterns of production and response to disturbance. Measurements of litterfall at both El Verde and Bisley provide another index of production. Measurements of belowground productivity in tabonuco forest were initiated in LTER 1 at both primary sites. A complementary project also funded by NSF is examining the controls on primary production in both tabonuco and dwarf forest (see below). Results from this latter study were integrated with LTER modeling efforts to develop long-term projections of production under different regimes of disturbance and nutrient availability (Zimmerman et al. in review). In LTER 2, long-term measurements of above- and belowground production will be continued at both El Verde and Bisley. Photosynthetic rate measurements in closed forest, hurricane gaps, and landslides will document species and population growth responses to disturbance, complementing the longer term measurements. Results from these studies will be used to calibrate the CENTURY and FORGROW models, which will then be validated in other sites in tabonuco forest.

Spatial and Temporal Distribution of Populations Selected to Represent Trophic Structure - Intensive study of focal species initiated in LTER 1 provided the opportunity to measure population responses of a wide range of organisms to Hurricane Hugo. The number of focal species under observation will be expanded in LTER 2 to include parts of the food web that were unrepresented in LTER 1, and new measures of ecological characteristics will be initiated for canopy tree species. At present, populations of woody plants, herbaceous plants, ferns, fungi, stream periphyton, fish, stream decapods, soil invertebrates, termites, spiders, frogs, lizards, snails, birds, and bats are under study at one or both of the LTER primary sites by LTER researchers or affiliated scientists. Synthesis of information on the trophic structure of tabonuco forest will be published in book form in 1994 (Reagan and Waide in review). LTER 2 will focus on understanding the pivotal role of certain species in the ecosystem through long-term manipulations. These experiments will address the effect of consumers on ecosystem processes like succession and nutrient cycling.

Pattern and Control of Organic Matter Accumulation in Surface Layers and Sediments - The development of SOM was studied through direct experimentation in LTER 1 as a means of calibrating the CENTURY model. Modeling was used to develop long-term projections of SOM dynamics under different disturbance conditions and the interactions between SOM and carbon, nitrogen, and phosphorus (Sanford et al. 1991). Decomposition rates of key plant species (Bloomfield et al. 1993; Bloomfield 1993) and mixed species samples (Zou et al. in review) addressed the controls of SOM formation. Studies of belowground decomposition rounded out our knowledge of SOM forming processes. Long-term experiments on SOM formation that were initiated in LTER 1 will be brought to a conclusion in LTER 2. The assumptions of our SOM model will be tested by evaluating its predictions at new sites. Decomposition studies will be continued with more attention devoted to the effect of secondary chemistry on decomposition processes. We will chart biogeochemical recovery on a sequence of landslides in LTER 2 and relate the development of SOM to anthropogenic and hurricane disturbance alone and in combination. We will further examine the response of SOM to plant species removal.

Patterns of Inorganic Inputs and Movements of Nutrients Through Soils, Groundwater, and Surface Water - A substantial record of wet and dry deposition inputs and stream outputs was completed during LTER 1 (Table 9; McDowell et al. 1990, McDowell and Asbury 1994). We will expand on these measures in LTER 2 with additional dry deposition estimates. Factors controlling nutrient cycling and the recovery of nutrient cycling following disturbance will be emphasized in LTER 2. Removal experiments of focal tree species will address the role of these organisms in influencing spatial patterns of nutrients. We will examine the role of terrestrial herbivores and higher level consumers on nutrient fluxes. In addition, we will conduct experiments to evaluate the effect of varying coarse litter quantities on nutrient cycling in both terrestrial and aquatic habitats. We will also develop stream water concentration/discharge relationships for several watersheds, and compare those with "pre-hurricane" relationships where data are available. LTER 2 will focus on increasing the spatial scales where we can estimate biogeochemical fluxes. This effort will involve combined efforts of innovative field research, GIS, and biogeochemical modelers.

Patterns and Frequency of Disturbance - LTER 1 accumulated information on the spatial and temporal distributions of treefalls, landslides, and hurricane damage and initiated synthesis of this information using the GIS. We also began to examine the distribution of historical land uses in tabonuco forest by classifying and digitizing these uses from 1936 and 1989 aerial photography. In LTER 2 we will expand this work to include four other sets of historical photography. We will continue our landscape-level analysis of hurricane susceptibility using the HURRECON and EXPOS models. Disturbance overlays will be incorporated into the LEF GIS and provide additional information for our modeling efforts.

Synthesis and Modeling

The Luquillo LTER has emphasized synthesis of research results through publications designed to draw together related research results and the interactive development of models incorporating knowledge from different subject areas of the project. The goals and approach of LTER 1 are summarized in Waide and Lugo (1992). A review of our current knowledge of ecosystem processes in the LEF was developed as an LTER exercise (Lugo and Scatena 1994). Two special issues of journals (Biotropica and the Kansas Journal of Entomology) are dedicated to the short-term effects of Hurricane Hugo (Walker et al. 1991) and the biology of stream invertebrates in the LEF, respectively. Two books treat the history and future of long-term research in the LEF (Lugo and Lowe in press) and the dynamics of the terrestrial and aquatic food webs at El Verde (Reagan and Waide in review). Modeling at the Luquillo LTER has focused on three parallel efforts: 1) adapting existing models from other sites (CENTURY, PROSPER) to the conditions of a tropical montane forest, 2) developing models specific to the needs of the Luquillo LTER (see Table 10 and 3) creating interfaces between models and the LEF GIS and displaying model output across the landscape using geographical ecosystem modeling tools (GEOPLOT). Other models of LEF ecosystems have been developed by cooperating scientists at other LTER sites (O'Brien et al. 1993). Models are used by LTER scientists to synthesize information, to generate hypotheses and predictions about ecosystem behavior, and to examine the implications of our results over extended time periods or under different environmental conditions. A detailed description of how modeling will contribute to LTER 2 is given under H1.

Data Management

During LTER 1, the Luquillo Data Management group had 11 principal tasks: 1) establish a structure for data management activities and document this structure, 2) acquire and implement hardware and software for data management, 3) identify, document, and archive existing non-LTER data sets, 4) acquire existing long-term data sets from other projects or agencies, 5) identify, document, archive, and update LTER data sets, 6) enter data, 7) perform quality control on data entry, 8) manipulate data, 9) fill requests for data from LTER and non-LTER scientists, 10) maintain inventories of data sets and publications, and 11) document their activities in reports and presentations. The human resources available to accomplish these tasks included the Data Manager (Eda Melendez, M.S.), two full-time technicians, and a half-time student assistant. The protocols established for filing, managing, and requesting data from the Luquillo LTER are described in a handbook revised periodically by the Data Manager and available to all LEF scientists (Appendix B). To date, 108 LTER data sets have been identified and filed with the Data Manager; 76 of these are completely documented and 32 are in the process of documentation. An additional 93 data sets from non-LTER studies have been identified as relevant to the LTER program and documented by the Data Manager. The data base for the LEF therefore contains 201 data sets. So far during LTER 1, the Data Manager has received 128 requests for data.

Intersite and Network Activities

The Luquillo LTER has attempted to foster cross-site interactions since the inception of our project. Several of our investigators are also participants in LTER projects at other sites (Parton, Pulliam, CPR; Foster, HFR; Haines, CWT; McDowell, HFR; Vogts, AND & HBR; Johnson, HBR; Schowalter, AND, CWT, KNZ). This in itself assures constant flow of information and ideas among sites. In addition, we have attempted to develop closer relationships with several sites whose research agendas are similar to ours (Table 11). The effect of hurricanes on forested ecosystems is an interest shared by the Luquillo and Harvard Forest sites. The processes affecting soil organic matter are being studied at several sites, including Central Plains and Luquillo, using the CENTURY model. Understory plant and litter invertebrate dynamics are interests that scientists at Coweeta and Luquillo have in common and which are being pursued both through LTER interactions and separate proposals. The Hubbard Brook and Luquillo sites are developing comparisons of whole watershed response to disturbance as well as the factors influencing soil nutrient dynamics both in disturbed and undisturbed forests. As closer relationships develop with other sites in the network, we anticipate the evolution of mutual research interests into full-fledged intellectual collaboration. For example, ideas on the importance of disturbance to ecosystem processes currently being examined at the Virginia Coast and Bonanza Creek sites correspond very closely to concepts developing at Luquillo. At the Virginia Coast site, the hypothesis that the superimposed effects of disturbances at different temporal and spatial scales give rise to state changes parallels our ideas about the synergistic effect of different disturbance types and the importance of legacies of past disturbance. The central hypothesis of the Bonanza Creek site is very similar to our ideas that the course of succession is determined by initial physical and chemical gradients and influenced by subsequent biotic feedback. Work from Cedar Creek proposes that high-diversity systems exist because of limiting similarity and interspecific trade-offs and suggests a test of the hypothesis in tropical forests (Tilman 1994). The convergence of our ideas with those of other LTER sites offers promise for the development of general ecological principles through intersite comparisons and synthesis. We have given the development of a regional perspective for the Luquillo LTER considerable attention. Sites within the Caribbean Basin share climatic, floristic, and disturbance characteristics with Luquillo and are the primary targets for regionalization of our program. Within Puerto Rico, the IITF has developed a research program in dry forest in the Guanica Biosphere Reserve that has many elements comparable to the Luquillo LTER. We have established comparative projects and cross-site interchanges with sites in Costa Rica (La Selva), Panama (Barro Colorado Island), Argentina, Venezuela, Jamaica, Brazil, China, Spain, and French Guiana. We have collaborated with researchers studying the effects of hurricanes in Mexico, Jamaica, Nicaragua, and the Virgin Islands, and we are establishing connections with the research group studying the effects of Hurricane Andrew in Florida. We have linked up with other tropical networks, including a worldwide group of sites examining forest dynamics in large plots such as the HRP. Our close relationship with these tropical sites provides access for the interchange of ideas with the LTER Network.

Related Research Projects

There have been a variety of research projects at our site that have been funded by outside sources (Table 12). The University of Puerto Rico (UPR) has a Minority Research Center of Excellence funded by NSF that includes LTER investigators from both the Terrestrial Ecology Division (TED) and the Department of Biology. Our original project was a comparison of controls of primary productivity in tabonuco and cloud forests following hurricane disturbance. This "bottom-up" study of the two forest types includes regular fertilization of forest plots at both sites. Funding for the center was recently renewed and the project was expanded to include many ecological processes related to tropical forest biodiversity. Among other things, we are investigating the effect of increased primary productivity, resulting from increased nutrient availability, on secondary production and consumer diversity. Additional projects were mostly related to ecosystem dynamics and nutrient budgets in terrestrial and aquatic habitats in tabonuco and colorado (Cyrilla racemiflora) forest types in the Luquillo Mountains (Table 12) and reflect a wide diversity of funding sources. Other studies include the Smithsonian Biodiversity Plot located at Bisley, paleoecological studies in the floodplains surrounding the mountains, growth ring studies of C. racemiflora, and management of the endangered Puerto Rican Parrot. Projects most related to LTER work include a soil map of the HRP conducted by scientists from USDA Soil Conservation Service. Studies of soil nitrogen and trace gases and stream chemistry studies contributed greatly to our understanding of the ecosystem effects of Hurricane Hugo (Steudler et al. 1991). The University of Puerto Rico is one of the most important institutions of higher learning in the United States for Hispanic and African-American undergraduate and graduate students. Minority students have been funded each year by NSF's Research Experience for Undergraduates Program to conduct a wide variety of research projects at the Luquillo LTER site. Investigators from the LTER program have participated in the Topics in Biology course given each semester at the Rio Piedras campus.

Dissemination of Information - In addition to the usual methods of communicating research results via publications and presentations at scientific meetings, scientists at the Luquillo LTER have explored several other avenues to make their research public. The Luquillo LTER was one of the principal sponsors of the 1993 annual meeting of the Association for Tropical Biology in San Juan. This meeting provided an audience of more than 300 scientists for the dissemination of LTER research results. The LTER program figured prominently in a video to describe ecological research at the University of Puerto Rico. This video has been shown frequently on educational television channels in Puerto Rico, and future international distribution is anticipated. The project Principal Investigators are frequently requested to discuss LTER research at public forums and at all academic levels. R. Waide presented LTER research in a television interview and two radio call-in shows within the last year. An in-depth article on the TED's ecological programs appeared in the university newspaper Dialogo. Requests for published information are handled both by the Data Manager and the individual units involved in the LTER. The IITF library, for example, filled over 15,000 external requests for information in 1993, many of which related to the LTER program. The Luquillo LTER Newsletter has a distribution of 150 scientists and decision-makers interested in ecological issues in Puerto Rico. The IITF annual letter, which has a worldwide distribution of over 2500, highlights LTER research. The UPR has recently prepared both a poster and a brochure explaining research opportunities in ecology in Puerto Rico. LTER scientists participate in the programs of the Puerto Rico Alliance for Minority Progress, which provides speakers for university groups and classes. A cooperative agreement between IITF and the Barranquitas High School Science program resulted in the establishment of a long-term forest dynamics plot which is used for science fair projects and student training.

Archives and Inventories

Analytical samples are archived in the laboratories of the TED and the IITF following established protocols. Soil samples collected by scientists of the Soil Conservation Service in connection with a joint project on the HRP have been described and archived. Soil samples from Bisley are stored at IITF with duplicates at Yale. Plant specimens are stored in the herbarium at the El Verde Field Station, with duplicate specimens at the Missouri Botanical Garden and the New York Botanical Garden. Animal specimens are kept in the collection at El Verde. Inventory lists of plants are available for El Verde (Lawrence in review) and Bisley (Chinea et al. 1993), and lists of species of vertebrates (Reagan and Waide in review), invertebrates (Garrison and Willig in review) and microorganisms (Lodge in review) are available for El Verde. Many other publications describe the flora and fauna of the LEF. A GIS developed by the USDA Forest Service contains information on soils, vegetation, infrastructure, and historic and cultural sites. An inventory of historical land use for the LEF is being prepared by Co-PI David Foster at Harvard Forest. More detailed GIS maps are available for Bisley and El Verde.

Leadership, Management, and Organization

The management structure of the LEF LTER program is shown in Fig. 20. The overall structure has functioned well during the last six years, and only minor modifications are planned for LTER 2. F. N. Scatena and J. K. Zimmerman will join A. E. Lugo and R. B. Waide as signatory PIs. Their addition to the management structure will help spread out the administrative responsibility, plus provide them with the experience to manage the project in the future. Scatena has been one of the most active participants during the first six years of the project and Zimmerman has acted as the El Verde site manager during the last two years and has become a key collaborator in various aspects of the project. During the next funding cycle, Waide and Lugo will continue to share responsibility for the scientific and administrative direction of the project. Scatena and Zimmerman, while continuing to serve as Site Managers for Bisley and El Verde, respectively, will act on the project directors' behalf or in their absence. Interaction among LEF LTER participants, which include scientists, graduate students and staff, is accomplished through at least three modes. Rapid communication among virtually all participants has been facilitated by the electronic mail connections established in LTER 1. Monthly meetings bring together scientists resident on site to share results and discuss modifications of the research agenda. A yearly meeting of all collaborators provides the opportunity for in-depth program review by the National Advisory Committee, whose members for LTER 2 are Paul Risser, Wayne Swank, Dick Wiegert, Julie Denslow, and John Wiens. These meetings are useful for determining the project's progress and for establishing new collaborations among LEF investigators

New Projects and Technologies

New projects to be undertaken in the next phase of LTER operations are described in detail in the discussion of the five hypotheses. This section of the text will be confined to a description of novel technologies to be employed at the LEF over the next 6 years. Geographic Information Systems - We are currently concentrating on data input to a GIS of the HRP. As the data layers are added, we are developing a menu-driven query and analysis system, so that the GIS will be usable by all researchers needing spatial analysis of their data sets. As a parallel effort, additional data layers are being input to a forest-wide GIS; this will be used both for large-scale studies and investigation of scaling phenomena as we apply results from the HRP to the entire LEF, and ultimately to other tropical areas. Remote Sensing and Image Analysis - We are investigating the utility of remotely- sensed data at LEF. Cloud cover in satellite images is variable, but frequently near to 100 percent. Aircraft-borne sensors may have greater success in capturing data because of the greater flexibility in timing overflights. We intend to compare satellite-derived imagery with that obtained from aircraft, in an effort to relate the two data types. The results will be input to the LEF GIS and will be used, in conjunction with conventional aerial photographs, for change analysis, vegetation characterization, and scaling investigations. Global Positioning Systems - We intend to test the applicability of global positioning systems (GPS) sensors in the LEF. With the high relief and dense, tall, vegetation, it is expected that they will prove to be of limited use; however, it may be possible to use GPS to locate gaps. We will attempt to determine what size and orientation of forest openings are necessary to be able to use GPS. Climate Monitoring - We will purchase and evaluate inexpensive, portable climate monitoring stations (from Davis Instruments) modified to log data to microcomputers and to monitor light levels under field conditions. These stations permit synoptic monitoring of environmental gradients at 20% of the cost per unit of popular brand equipment. In conjunction with other, hand-held, monitoring equipment, the portable stations will allow us to characterize environmental conditions over a range of spatial and temporal scales. Dry Deposition Monitoring - We will use chloride to monitor dry deposition and assess watershed hydrological tightness.

Supplemental Support

Supplemental support for the Luquillo LTER program (Table 13) has taken the form of technical supplements and allotments under five NSF programs: Research Experience for

Undergraduates (REU), Research Opportunity Awards (ROA), Small Grants for Exploratory Research (SGER), Research Opportunities for Women (ROW), and Enhanced Research Opportunities at LTER Sites (EROL). The principal benefit of these sources of support has been to equalize the technical capabilities of the Luquillo LTER with those of sites chosen earlier. The establishment of local-area and wide-area networks has resulted in much closer communication and collaboration among our widely-spread group. The development of GIS/Remote Sensing technology has led us into research areas that were closed to us before LTER. The funds provided through the REU program have allowed us to provide LTER research opportunities to more than 50 minority undergraduate students. The EROL, ROA, ROW, and SGER programs have provided opportunities to expand the range of scientists working in the LEF and to bring fresh ideas into the research group.

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Tables

Table 1. The five working hypotheses to be addressed in LTER 2.

H1:	The ecosystem patterns and processes that are active at El Verde and Bisley are continuous over increasing spatial scales, so that understanding of system attributes gained at these two points can lead toaccurate predictions at other sites within tabonuco forest.
H2:	At any point in geographical space, the short-term response to disturbance and the subsequent trajectories of recovery are determined by 1) the location of the point along abiotic gradients (physical), 2) the abiotic and biotic conditions at the time of disturbance (historical), and 3) biotic conditions subsequent/consequent to disturbance (successional). The relative importance of these three factors will vary with the severity of the disturbance.
H3:	Anthropogenic disturbances (e.g., agriculture, charcoal production, timber harvesting, etc.) have different spatial patterns, intensities, and recovery trajectories than individual natural disturbances (hurricanes, landslides, treefall gaps).
H4:	Tabonuco forest contains plant and animal species (or groups of species) that alter critical ecosystem processes and successional pathways by modifying the attributes of ecological space in their vicinity.
H5:	The disturbance regime prevailing in tabonuco forest over evolutionary time has led to the development of a plant community whose members have varied and complementary ecological characteristics.

Table 2. Participants in LTER 1 and LTER 2. PIs have responsibility for directing the research program under the core grant. Co-PI's are funded directly from the core grant. Unless otherwise indicated, scientists participating in LTER 1 will continue in LTER 2.

	Participants	Present Affiliation	Specialty	Years of Tropical Experience
PIs	Waide, R.	University of Puerto Rico	food webs, avian ecology	23
	Lugo, A.	Int. Inst. Tropical Forestry	ecosystem analysis, nutrient cycling	34
	Scatena, F.	Int. Inst. Tropical Forestry	geomorphology, hydrology	7
	Zimmerman, J.*	University of Puerto Rico	plant ecology, phenology	7
COPIs	Aide, M.	University of Puerto Rico	restoration ecology, herbivory	12

	Brokaw, N.	Manomet Bird Observatory	regeneration patterns, disturbance	21
	Covich, A.	Colorado State University	decomposition, stream organisms, GIS	18
	Crowl, T.*	Utah State University	stream ecology	6
	Fetcher, N.	University of Puerto Rico	regeneration patterns & disturb.	14
	Foster, D.	Harvard University	forest response to hurricanes	7
	Haines, B.	University of Georgia	nutrient cycling in plants	32
	Hall, C.	SUNY-Syracuse	modeling, stream ecology	8
	Johnson, A.*	Universityof Pennsylvania	soil chemistry	7
	McDowell, W.*	University of New Hampshire	soil solution chemistry	12
	Melendez, E.	University of Puerto Rico	data management	6
	Myster, R.*	University of Puerto Rico	landslides, revegetation	3
	Parton, W.	Colorado State University	meteorology, nutrient cycles	9
	Pulliam, W.*	Colorado State University	nutrient cycling, modeling	1
	Reagan, D.	Env. Scient. & Eng.	reptiles, behavior, ecology	16
	Schaefer, D.*	University of Puerto Rico	nutrient cycling, atmospheric deposition	3
	Schowalter, T.*	Oregon State University	insect ecology, nutrient cycling	3
	Silver, W.*	Yale University	belowground processes	13
	Vogt, D.*	Yale University	belowground processes	5
	Vogt, K.	Yale University	belowground productivity	5
	Walker, L.	University of Nevada	succession, primary productivity	10
	Willig, M.	Texas Tech University	ecology & behavior of bats, insects	17
	Woolbright, L.	Siena College	ecology & behavior of frogs	22

	Zou, X.*	University of Puerto Rico	nutrient dynamics, forest ecology	5
LTER	Asbury, C.**	U.S. Geol. Survey	nutrient cycling, waters	7
	Berish, C.**	Env. Protection Agency	belowground productivity	7
	Lawrence, W.**	University of Maryland	remote sensing, physiol. ecology	8
	Lodge, D.**	Forest Products Lab	mycorrhizae, fungal systematics	12
	McCormick, J.**	University of Tennessee	life history studies	29
	Pfeiffer, W.**	none	insect ecology	5
	Sanford, Jr., R.**	University of Denver	soil organic matter	18
	Stewart, M.**	SUNY-Albany	ecology & behavior of frogs	31
	Swanson, F.**	Oregon State University	geomorphology	5

*Scientists added to the project since the beginning of LTER 1
** Scientists who have left the project since the beginning of LTER 1

Table 3. Scientists affiliated with the Luquillo LTER but not funded from the core grant. These people have developed research programs that contribute to the overall goals of the LTER.

Participants	Present Affiliation	Specialty
W. Arendt	IITF	avian ecology
L. Bishop	Earlham College	ecology & behavior of arachnids
E. Boose	Harvard University	modeling, GIS, hurricanes
S. Brown	University of Illinois	biomass, decomposition, and productivity
G. Camilo	University of Puerto Rico (Post-doctoral Associate)	food webs, modeling
L. Ferrington	University of Kansas	taxonomy of stream insects
M. Gannon	Penn State - Altoona	ecology of bats
R. Joglar	University of Puerto Rico	ecology of amphibians
N. Hemphill	University of Louisville	ecology of stream insects
M. Keller	IITF	atmospheric chemistry

J. Lodge	Forest Products Lab	mycorrhizae, microbial systematics
E. Masteller	Penn State - Erie	taxonomy of stream insects
L. Nieves	UPR-Humacao	fish biology
H. Odum	University of Florida	ecosystem studies, modeling
C. Pringle	University of Georgia	stream ecology
J. Sharpe	no institutional affiliation	biology of ferns
J. Thomlinson	University of Puerto Rico (Post-doctoral Associate)	GIS, remote sensing
P. Weaver	IITF	secondary forest dynamics
J. Wunderle	IITF	avian ecology
D. Zarin	University of Pennsylvania	landslide recovery

Table 4. Long-term monitoring in association with the Luquillo LTER research program. Legend: B = Bisley, E = El Verde, R = Rio Blanco, LEF = other areas in the Luquillo Experimental Forest.

Measure	Initiation	Funding	Location	Frequency
VEGETATION				
Total Plant Inventory	1987 1990	IITF NSF	B E	Continuous Every 5 years
Seedlings	1989	NSF	E, B	Every 4-6 months
Plant tagging	1988	IITF/NSF	B, E	Continuous
Wood volume	1988	IITF/NSF	B	Yearly
Basal area	1988	IITF/NSF	B, E	Yearly/Every 5 years
Biomass	1988	IITF/NSF	B, E	Yearly/Every 5 years
Litterfall	1988	NSF	B, E	Every 2 weeks
Litter decomposition	1988	NSF	B, E, LEF	Periodically
Leaf area index	1989	NSF	B, E	Yearly
Canopy closure	1989	NSF	E, B	Every 3 years
Flowering phenology	1989	NSF/IITF	B, E,	Weekly
Landslide revegetation	1988	NSF	3 intensive 17	Every 4 months

			extensive	Every 6 months
GEOMORPHOLOGY				
Stream cross-section	1987	IITF	B, LEF	Yearly
FAUNA				
Key species inventory	1988	NSF	E, B	Yearly (wet and dry season)
Food web structure	1988	NSF	E, B	Yearly
DISTURBANCE				
Inventory of gaps and landslides	1988 1989	0NSF/USGS NSF	B, R, E Four life zones in LEF	Continuous Yearly by transects and aerial photos
METEOROLOGY				
Rainfall	1987	IITF/NSF	B, E, R, LEF 6 stations at different elevations	Continuous measurement with Level 3 Stations and vertical profiles at El Verde
Temperature	1987	IITF/NSF		
Humidity	1988	IITF/NSF		
Wind speed and direction	1988	IITF/NSF		
HYDROLOGY				
Discharge (water level recorders in weirs)	1987	IITF	B, E, LEF	Continuous
Throughfall	1987	IITF/NSF	B	Continuous
Stemflow	1988	IITF/NSF	B	Continuous
Transpiration	1988	IITF/NSF	B, E	Twice/yr
Evapotranspiration	1988	IITF/NSF	B	Twice/yr
CHEMISTRY (major cations and anions)				
Air chemistry	1994	NSF	E, B, LEF	Seasonally
Throughfall	1988 1994	UPR/NSF UPR	B E	Weekly composites Weekly composites
Streamflow	1988	UPR/NSF	B	Weekly composites
Groundwater	1988	UPR	B, R	Weekly
Stream water	1986	UPR	B, E, LEF	Weekly
Litterfall	1989	NSF	B, E	Continuous

Table 5. Key animal species selected for intensive long-term population studies in the

Luquillo LTER.	
Species	**Life Form**
Atya lanipes	shrimp
*Macrobrachium crenulata**	shrimp
Epilobocera sinuatifrons	crab
Lamponius portoricensis	insect
Caracolus caracolla	snail
*Nenia tridens**	snail
*Gaeotis nigrolineata**	snail
Geotrygon montana	bird
Coereba flaveola	bird
Todus mexicanus	bird
Otus nudipes	bird
Eleutherodactylu s coqui	frog
Anolis stratulus	lizard
Anolis gundlachi	lizard
*Anolis evermanni**	lizard
Leucauge regnyi	spider
Stasina portoricensis	spider
Modisimus signatus	spider
*Stenoderma rufum**	bat

*New additions

Table 6. Characteristics of the El Verde and Bisley study sites.

	El Verde	**Bisley**
Geology	Volcanoclastics of the upper Cretaceous Hato Puerco formation	Volcanoclastics of the lower Cretaceous Fajardo formation
Topography	less dissected	more dissected
Daily Rainfall Pattern	afternoon	morning
Elevation	250-480 m	260-400 m
Aspect	N-NW	N-NW
Holdridge life zone	Subtropical wet	Subtropical wet
Annual rainfall	3600 mm	4000 mm

Annual streamflow	250 cm	290 cm
Average throughfall	56-60%	59%
Bat populations	0.008 ind/net-hour	0.172 ind/net-hour
Bird populations	4.36 ind/count	3.92 ind/count
Lizard populations	649/ha	785/ha
Frog populations - adult	750/ha	996/ha
Frog populations - juv.	2317/ha	1350/ha
Shrimp detritivores	20.0 ind/m^2	0.1 ind/m^2
Shrimp predators	0.01 ind/m^2	0.20 ind/m^2
Aquatic invert. grazers	900 ind/m^2	3600 ind/m^2
Aquatic invert. shredders	520 ind/m^2	180 ind/m^2
Aquatic invert. gatherers	210 ind/m^2	500 ind/m^2
Aquatic invert. predators	30 ind/m^2	5 ind/m^2
Tree density (>10 cm dbh)	819/ha	957/ha
Tree species richness	47.62.97 species/ha	35 species/ha
Gap frequency	1.4/ha/yr	1.6/ha/yr
Gap size	54.8 m^2	76.0 m^2
Hurricane tree mortality	7.1%	20.0%

Table 7. Tree species selected for detailed study of ecological characteristics. Included are the species' rank abundance in the overstory (> 10 cm DBH) of the HRP at the time of Hurricane Hugo and in the understory (1-10 cm DBH) approximately three years post-Hugo.

Life history characteristics to be studied in these species are displayed on Table 8

Species	**Rank Abundance**

	Pre-Hurricane	Post-Hurricane
Prestoea montana	1	4
Casearia arborea	2	2
Dacryodes excelsa	3	13
Manilkara bidentata	4	7
Inga laurina	5	9
Sloanea berteriana	6	5
Tabebuia heterophylla	7	16
Guarea guidonia	8	12
Matayba domingensis	9	45
Casearia sylvestris	10	6
Alchornea latifolia	11	9
Cordia borinquensis	55	7
Schefflera morototoni	12	3
Cecropia schreberiana	21	1

Table 8. Life history characteristics to be studied in species indicated in Table 7.

Characteristic	Investigator
Night respiration	Fetcher
Parameters of light response curve (dark respiration, initial slope of curve, and light-saturated photosynthesis)	Fetcher
Rate of photosynthetic induction	Fetcher
V_{max} , (maximum uptake rate) for P and for Ca	Haines
K_m, (Michaelis-Menten half saturation constant) for P and Ca	Haines
VAM dependency	Myster
Seed mass	Zimmerman
Seed bank	Zimmerman
Seed rain	Zimmerman
% germination in shade, partial shade & sun	Zimmerman
Seedling growth rate in shade, partial shade & sun	Zimmerman
% resprouting following branch or frond removal	Zimmerman

% rooting when stems contact soil	Zimmerman
"Sapling" annual height growth & mortality	Sabat
"Pole" growth & mortality	Sabat
"Small tree" growth & mortality	Sabat
"Large tree" growth & mortality	Sabat
Architecture (per cent mass attenuation)	Sabat
Leaf development time and leaf life span	Aide
Toughness of young and old leaves	Aide
% herbivory rate on young and old leaves	Aide
Phenology of leaf production	Aide
Nutrient contents of fresh and fallen leaves	Vogt
Secondary chemistry of fallen leaves	Vogt

Table 9. Data sets available for locations within the Luquillo Experimental Forest. Data currently collected are indicated by .

Data Category	Tabonuco	Colorado	Palm	Dwarf	Plantation
CLIMATOLOGY	none	none	none	none	none
Air temperature	1909	1993	1980-81	1960's	none
Daily precipitation	1909	none	1980-81	1960's	none
Instant precipitation (NADP)	1984	none	none	none	none
Relative humidity	1958-62, 63-66, 91	1965-66, 91	1980-81, 91	1958-62	none
Solar radiation	1958-62, 63-66, 91	1965-66, 91	1991	1958-62	none
Wind speed, direction	1958-62, 63-66, 91	1965-66, 91	1991	1958-62	none
Streamflow	1940-53, 76	1979	1980-81	none	none
CHEMICAL COMPOSITION	none	none	none	none	none
Animal tissue	1979-82	none	none	none	none
Bulk soil	1965-69	1980	1980-81	1991-92	1982-85
Cloudwater	none	none	none	1984-86, 89-90	none
Dryfall (NADP)	1984	1990	none	none	none

Fungal tissue	1983-86	none	none	none	none
Litter	1987	none	none	1990-91	none
Plant tissue	1966-69	none	1980-81	1987-91	1982-85
Precipitation (NADP)	1984	1990	none	none	none
Precipitation (bulk)	1964-69, 84	1990	none	1964-69, 83-85, 91-92	none
Soil solution	1965-69, 83-84, 88-90	1988-90	1980-81	none	none
Groundwater	1988-92	198 8-92	none	none	none
Stemflow	1966-69, 87-88	none	198 0-81	199 1-92	1988-92
Streamwater	1966-69, 83	1983	1980-81	none	none
Throughfall	1966-69, 83-84, 87	1988-90	1980-81	none	none
VEGETATION	none	none	none	none	none
Biomass	1957-62, 66-67	1984-85	1980-81	1977	1982-85
Composition	1965-69, 89	1984-85, 89	1980-81	1968, 1989	1982-85
Litter decomposition	1964-65, 68-71, 81-82, 87-91	none	1980-81	none	1982-85
Litterfall	1964-66, 70-73, 81, 87	1984-85	1980-81	1991-92	1982-85
Mychorrhizal associations	1983-86	none	none	none	none
Tree growth/mortality	1943	1943	1943	1943	1943
Wood decomposition	1940	1940	1940	1940	1940
MICROFLORA	none	none	none	none	none
Biomass	1984-85	none	none	none	none
Composition	1960-69, 80-83	none	none	none	none
FAUNA	none	none	none	none	none
Biomass	1958-59, 81	none	none	none	none
Composition/population	1958-59, 64-66, 81	1960's	1960's	1970's	none
MAPS AND REMOTE SENSING	none	none	none	none	none
Aerial Photos	9x since 1936	8x since	8x since	8x since	8x since

		1936	1936	1936	1936
Detailed topography	1964, 1986, 1990	none	none	none	none
Landsat TM, TMS, TIMS, CAMS, AVHRR	1983	1983	1983	1983	1983
Landslide mapping	1936-90	1936-90	1936-90	1936-90	1980

Table 10. Models developed for or adapted to the Luquillo LTER site during LTER 1. Detailed descriptions are provided in Everham et al. (1993)

Model Name	Description	Reference
CENTURY	Ecosystem soil nutrients	Sanford et al. 1991
TOPOCLIM	Spatial mesoclimate	Wooster 1989
TABONUCO	Forest energy flow	Everham et al. 1993
FORGROW	Climate sensitive forest growth	Everham et al. 1993
DISTURB	Gap distribution	Pederson et al. 1991
TREEMAP	Mapping tree distributions	Everham et al. 1993
HURRECON	Surface hurricane winds	Boose et al. 1994
EXPOS	Exposure to hurricane winds	Boose unpublished
PROSPER	Forest hydrology	Huff and Swank 1985
QBRADA	Stream energy flow	Everham et al. 1993
CATENA	Soil and vegetation storages	Everham et al. 1993
LITFLOW	Stream leaf litter retention	Everham et al. 1993
GEOPLT	Landscape ecosystem model	Hall et al. 1992

Table 11. Intersite and network activities of the Luquillo LTER program.

Project Description	Luquillo Investigator	Other LTER site	Other Investigator
Soil invertebrates	X. Zou	AND CWT	A. Moldenke D. Crossley
Geological processes	F. Scatena	AND	F. Swanson
Root dynamics	K. & D. Vogt	AND, HBR	K. & D. Vogt
Canopy invertebrates	T. Schowalter	AND	T. Schowalter
Soil organic matter dynamics	B. Parton B. Pulliam	CPR	B. Parton B. Pulliam
Seedling recruitment and growth	B. Haines	CWT	J. Clark

Light penetration to forest floor	B. Haines	CWT	B. Haines
Nitrogen mineralization in forest floor	B. Haines	CWT	B. Haines
Soil temperature modeling	B. Haines	CWT	J. Vose
Woody debris retention in streams	A. Covich	CWT	J. Webster
Seed rain	F. Scatena J. Zimmerman	CWT	B. Haines
Soil extraction, nutrient pools	F. Scatena W. Silver	HBR	A. Johnson T. Siccama
TFA binding in soils	X. Zou	HBR	C. Driscoll
Cloud chemistry	B. McDowell	HBR	G. Likens
Groundwater chemistry	B. McDowell	HBR	B. Bowden
Temperate and tropical forest hurricane comparison	D. Foster	HFR	D. Foster E. Boose
Temperate and tropical hurricane comparison	R. Waide	NIN	E. Blood
Landscape heterogeneity	J. Thomlinson	NTL	J. Magnuson
LIDET	D. Schaefer	Network	M. Harmon
Network climate monitoring	D. Schaefer	Network	various
LTER/NASA/MODIS	D. Schaefer	Network	W. Kaplan
Biodiversity inventory	R. Waide	Network	J. Lattin
Cross-site stream CO2 dynamics	B. McDowell	Network	G. Kling
Cross-site food web comparison			
T. Crowl	Network	J. Meyer	

Table 12. Additional funded projects at the Luquillo LTER site.

Principal Investigator(s)	Project	Funding Source
R. Waide, J. Zimmerman, X. Zou, D. Schaefer, M. Aide, N. Fetcher, L. Walker, A. Sabat, and Others (UPR)	Ecological processes and patterns of diversity in tropical forests	NSF-MRCE
M. Larsen and R. Stallard (USGS)	Water, energy, and biochemical budgets in the Luquillo Experimental Forest (WEBB)	USGS
F. Dahlheimer (Smithsonian)	Biodiversity in tropical forests	Smithsonian
A. Johnson (U. Penn.), T. Siccama (Yale)	Tropical soil nutrient pools	Mellon Foundation
F. Scatena, C. Rodriguez (IITF)	Effects of human activity along forest corridors	USDA-FS

H. Mount and others (USDA-SCS)	Soil map of the Hurricane Recovery Plot	USDA-SCS
W. McDowell, B. Bowden (U. New Hampshire)	N dynamics in riparian zone	NSF
K. Vogt, D. Vogt (Yale), A. Covich (Colorado State), others	Wood decomposition and nutrient cycling	NSF
G. Brush (J. Hopkins)	Paleoecological studies of Luquillo flood plains	Mellon Foundation
P. Steudler, J. Mellilo (The Ecosystem Center)	Soil nitrogen and trace gas exchange	Texaco
A. Drew (SUNY-ESF)	Growth and phenology of C. racemiflora	USDA-FS
S. Brown (U. Illinois)	Coarse woody debris and forest carbon budgets	USDA-FS, DOE
J. Meyer (DOI-F&W Serv.)	Puerto Rican Parrot project	DOI-F&W Serv.
N. Fetcher (UPR-Rio Piedras)	Spatial variability in leaf area index	NASA
J. Norat (UPR-Medical Sciences)	Effect of land use on water quality	NASA
J. Gonzalez (UPR-Mayaguez)	Development of a center to study tropical atmospheric chemistry	NASA/EPSCoR (Pending)
B. Weiner (UPR-Rio Piedras)	Land use in the tropics and its effect on the global environment	NASA (Pending)
D. Schaefer (UPR/TED)	National Atmospheric Deposition Program	DOE/USDA
G. Lovett (IES), B. McDowell (U. New Hampshire) and C. Asbury (TED/UPR)	Cloud deposition processes	Mellon Foundation
Caribbean Water Resource Division	Streamflow monitoring	USGS
X. Zou, T. Schowalter, and D. Coleman (UPR/TED, Oregon State, Georgia)	Responses of invertebrates to "new forestry" practices in wet forests	EPA/EMAP (Pending)
W. Silver (IITF)	Ecosystem processes in cloud forest	Mellon Foundation
B. McDowell, C. McSwiney (U. New Hampshire)	N2O fluxes in riparian habitats	NASA
K. Basnet and M. Alvarez (IITF)	Tabonuco root grafting	IITF

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K. Basnet and M. Alvarez (IITF)	Tabonuco root grafting	IITF

Table 13. Supplemental support from NSF for the Luquillo LTER program.

Lead PI	Type	Period	Amount	Objectives
W. Lawrence	Technical Supplement	88-89	$80,254	Install local and wide area network connections; acquire hardware and software for GIS/RS lab; train staff in GIS
R. Waide	REU	89-90	$15,994	Undergraduate research support
R. Waide	Equipment Supplement	89-90	$74,323	Acquisition of automated ion analyzer and micro-meteorological stations in response to research needs resulting from Hurricane Hugo
W. Lawrence	Technical supplement	89-90	$49,926	Maintenance of GIS hardware and software; acquisition of plotter, digitizer, thermal printer, and laser printer for GIS lab
R. Waide	REU	90-91	$30,186	Undergraduate research support
R. Waide	Technical Supplement	90-91	$40,000	Maintenance of GIS hardware and software, purchase of software and an optical disk for storage, salary of GIS technician
R. Waide	Technical Supplement/REU/ROA	91-92	$61,242	Summer internships for minority undergraduates; research on spider ecology by Dr. Leslie Bishop; acquisition of backup tape drive and uninterruptible power supplies; acquisition of modeling software; software maintenance
R. Waide	Technical Supplement/REU/ROA	92-93	$75,000	Summer internships for minority undergraduates; research on spider ecology by Dr. Leslie Bishop; acquisition of 486 computer and color printer; acquisition of TCP/IP software for LAN; software maintenance

J. Lodge	ROW	90-91	$17,908	Timing of nutrient mineralization from leaf litter internal cycling by fungi
J. Lodge/ C. Taylor	SGER	90-91	$49,896	Establishment of a permanently gridded rainforest plot for assessment of hurricane damage and studies of ecosystem recovery
C. Pringle	EROL	92-93	$50,000	Nutrient assays of algal periphyton growth
C. Pringle/ N. Hemphill	EROL	93-94	$50,000	Effects of nutrient perturbations on trophic cascades in tropical montane streams
J. Schall	EROL	91-92	$50,000	Biogeography and ecology of the lizard malarial parasite Plasmodium azurophilum
L. Tieszen	EROL	90-91	$50,000	Isotopic changes during the conversion of green biomass to soil organic matter at several LTER sites

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Table 14. History of support during LTER 1

The Luquillo LTER program has been a major focal point for research in the Luquillo mountains. Not only has the effort increased the interactions between island-resident but has also resulted in a significant increase in additional funding and outside research activities at the site. A history of support of the primary institutions conducting research at the LTER site is shown in Table 14. Additional extramural projects, and supplemental NSF support are given in Tables 12 and 13, respectively.

Table 14. Other related support for the Luquillo LTER program

Amount in Thousands of Dollars	Recipient	Source	Research Objective
Increased from 2200$/yr in 1987 to 3300$/yr in 1994.	International Institute of Tropical Forestry	USDA Forest Service	Total research budget
$150/yr	Terrestrial Ecology Division	University of Puerto Rico	Supplement LTER activity
$50/yr	International Institute of Tropical Forestry	USDA Forest Service	Supplement LTER activity
Variable $10/yr	LTER collaborators	Oak Ridge Associated Universities, U.S. DOE	Travel to perform research at the El Verde Field Station

$150	Caribbean Water Resource District	Puerto Rican Planning Board, USGS WEBB program	Increased number of scientist and professionals working from 1 in 1987 to 5 in 1994
$200	Puerto Rican Parrot recovery program	U.S. Fish and Wildlife Service, USDA Forest Service	Conservation biology of Puerto Rican Parrot