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Division Biotic Systems & Resources

PROGRAM ANNOUNCEMENT/SOLICITATION NO./CLOSING DATE
Long-Term Ecological Research / 2 FEB 1988

SUBMITTING INSTITUTION CODE (if known)

FOR RENEWAL ☐ CONTINUING AWARD ☐ ACCOMPLISHMENT BASED RENEWAL ☐ REQUEST, LIST PREVIOUS AWARD NO.:

IS THIS PROPOSAL BEING SUBMITTED TO ANOTHER FEDERAL AGENCY? Yes____ No X; IF YES, LIST ACRONYM(S)

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Center for Energy & Environment Research, University of Puerto Rico

ADDRESS OF ORGANIZATION (INCLUDE ZIP CODE)
G P O Box 3682, San Juan, P R 00936

IS SUBMITTING ORGANIZATION ☐ For-Profit Organization; ☐ Small Business; ☐ Minority Business; ☐ Woman-Owned Business

TITLE OF PROPOSED PROJECT
Long-Term Ecological Research on the Luquillo Experimental Forest

REQUESTED AMOUNT	PROPOSED DURATION	DESIRED STARTING DATE
$2,088,927	5 years	October 1, 1988

CHECK APPROPRIATE BOX(ES) IF THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW:

- ☐ Animal Welfare
- ☐ Endangered Species
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NSF FORM 1207 (1-87)
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LONG-TERM ECOLOGICAL RESEARCH ON THE LUQUILLO EXPERIMENTAL FOREST

A proposal to the
National Science Foundation
from the

CENTER FOR ENERGY AND ENVIRONMENT RESEARCH
UNIVERSITY OF PUERTO RICO

INSTITUTE OF TROPICAL FORESTRY
U. S. DEPARTMENT OF AGRICULTURE - FOREST SERVICE

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February 1, 1988

PROJECT SUMMARY

The Luquillo Experimental Forest (LEF) is proposed as the site of a long-term ecological research program. The LEF is a National Forest and a MAB Biosphere Reserve, which contains several research natural areas within its 11,231 ha. The objective of the proposed LTER is to tie studies of disturbance regime and forest structure and dynamics to a landscape perspective. The two primary research questions address the relative importance of different disturbance types within the four tropical rain forest life zones of the LEF, and the importance of the biota in restoring ecosystem productivity after disturbance. A combination of long-term (10-40 year) and short-term (3-5 year) experiments will examine research components addressing pattern, frequency, and intensity of disturbance; environmental properties expected to vary with disturbance size, age, and origin; biological properties expected to vary with environmental properties; and system properties emergent from the effects of disturbance pattern, severity, and frequency on the mutual interaction of environment and biota. Existing and projected data sets are being incorporated into a comprehensive data management system to insure prompt data reduction, timely dissemination of information to collaborators and other LTER sites, and secure long-term data storage.

I. INTRODUCTION

Studies of response of forested ecosystems to disturbance have been historically important in ecology and have contributed to a developing view of forest systems as dynamic in structure and function. Forest ecosystems are subject to a variety of disturbances, differentiated along scales of severity, spatial extent, frequency, and duration (e.g., Karr and Freemark 1985, White and Pickett 1985, Jordan 1985, Lugo et al. 1986, Foster 1988a and b). Many studies of forest disturbance and its consequences have been undertaken, some with a long-term perspective; however, relatively few such studies have occurred in the humid tropics. Extending studies of forest disturbance to the tropics is potentially valuable because: 1) comparison of a wider variety of ecosystems will assist in forming generalizations about disturbance, 2) tropical forests are different from temperate forests in many aspects that may affect response to disturbance, such as type of soil, amount and half-life of organic matter, and community complexity, and 3) anthropogenic disturbance is occurring widely in tropical forests.

Most investigations of disturbance in tropical forests focus on a limited subset of the broad spectrum of ecosystem disturbances, partly because most tropical research is short-term due to logistic difficulties and lack of long-term institutional support. Long temporal series of observations are necessary to unravel short- from long-term responses to events with complex return frequencies. Hence, long-term research is a necessary tool for the eventual understanding of tropical forests. NSF's Long-Term Ecological Research (LTER) program provides an ideal framework for examining ecological events that occur on a temporal scale of decades or centuries.

We propose to conduct long-term studies of the relationship between disturbance regime and forest structure in the Luquillo Experimental Forest (LEF) of Puerto Rico (Fig. 1). Our objectives are 1) to investigate the relative importance of different types of disturbance within the four life zones (Ewel and Whitmore 1973) constituting the landscape of the LEF, and 2) to analyze the importance of the biota in restoring ecosystem productivity after different types of disturbance within representative watersheds in one of these life zones.

The history of disturbance in the LEF is well known through measurements of long-term plots (Fig. 2), although ecosystem responses have not been well studied for each type of disturbance (Brown et al. 1983). Frequent human-related and natural disturbances to the forest have created a mosaic of areas in various stages of succession. The major forms of disturbance in this humid tropical forest are natural treefalls, landslides, hurricanes, and selective cutting. The integral role of disturbance in the LEF was shown by Doyle's (1982) close simulation of actual relative abundances of tree species, using a forest dynamics model that incorporated treefalls and

Figure 1. Landsat 5 Thematic Mapper false color image of the eastern end of Puerto Rico. In the early dry season (January 21, 1985), the rain and wet forest life zones of the Luquillo Experimental Forest (LEF) stand out in contrast to surrounding moist forest and agricultural lands. North is toward the top of the photograph.

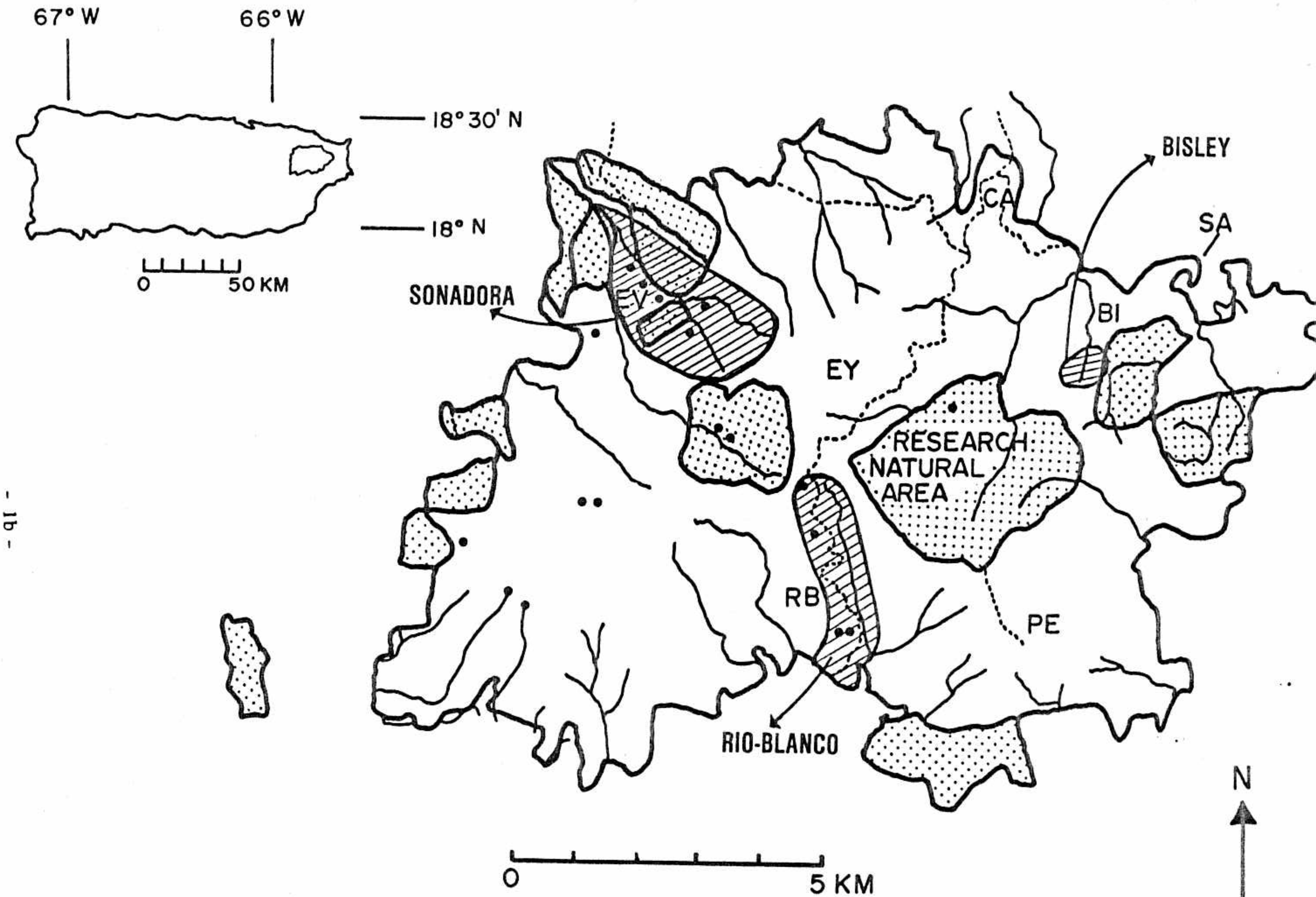

Figure 2. Map of the LEF showing 1) 12 reserved research tracts (dotted areas), 2) the Bisley, Sonadora, and Rio Blanco watersheds (shaded areas), 3) long-term growth plots under study by the Institute of Tropical Forestry (points), and 4) other sites for which long-term data sets exist (EV = El Verde, CA = Catalina, BI = Bisley, SA = Sabana, EY = El Yunque, RB = Rio Blanco, PE = Pico del Este). The inset shows the location of the LEF in Puerto Rico.

hurricanes (Fig. 3).

Components of the current proposal include examination of:

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, rates of recovery, and displacement from and return to steady state).

Specific experiments under each of the research components will emphasize the five core research topics common to existing LTER sites:

1. Pattern and control of primary production,
2. Spatial and temporal distribution of populations selected to represent trophic structure,
3. Pattern and control of organic matter accumulation in surface layers and sediments,
4. Patterns of inorganic inputs and movements of nutrients through soils, groundwater, and surface waters, and
5. Patterns and frequency of disturbance to the research site.

II. RATIONALE

Speciation and hence high biotic diversity in the tropics is driven by "environmental challenges" that, according to Dobzhansky (1950), stem chiefly from "the intricate mutual relationships among the inhabitants." This quotation reflects a central idea of tropical ecology, namely, that the benign and relatively constant tropical environment allows biotic interactions to be the dominant factor in determining the structure and function of forest ecosystems (Giller 1984). This view has led to impressive progress in evolutionary tropical biology and has resulted in particular emphasis being given to the importance of predation, competition, pollination, and fruit dispersal (Leigh et al. 1982, Janzen 1983, Giller 1984, den Boer 1986).

This traditional paradigm of tropical ecology, however, is now under close scrutiny (Ho et al. 1986). For example, Sousa (1984, p. 338) stated: "There is a growing realization that disturbance may play as great a role in community dynamics as do biological interactions such as competition and predation, which have received far more empirical and theoretical attention from

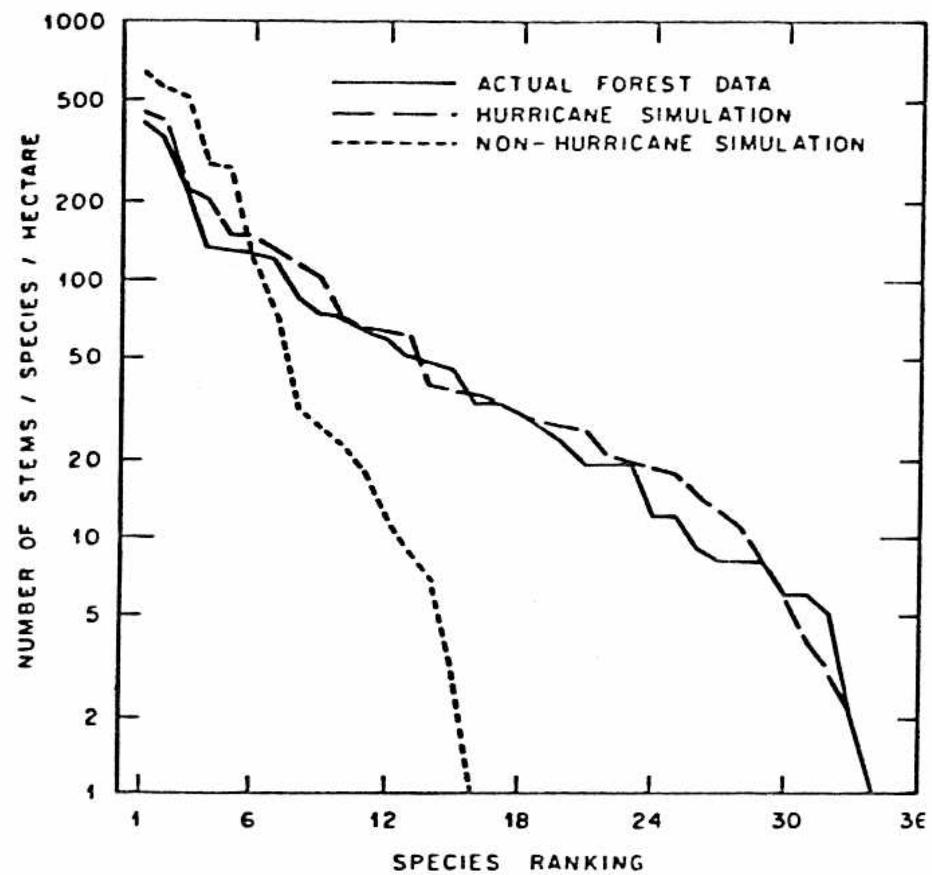

Figure 3. Dominance-diversity curves for model simulations with and without hurricane effects compared to tabonuco (Dacryodes excelsa) forest data. Species rank ranges from most abundant (1) to least abundant (36). Species abundance is represented as the total number of stems (above 4 cm dbh) per hectare (Doyle 1982).

ecologists. The interplay between disturbance and these biological processes seems to account for a major portion of the organization and spatial patterning of natural communities." Several types of evidence have triggered alternative interpretations of the driving factors of ecosystem structure and function in the tropics. For example: 1) the possibility that extraterrestrial forces caused mass species extinctions (Alvarez et al. 1980) and that such extinctions follow recurrent cyclic patterns (Fischer 1981) has stirred considerable debate over traditional thinking about speciation and extinction in the tropics (Raup 1984, Spepkoski and Raup 1986, Officer et al. 1987, Donovan 1987); 2) the debate over the existence of species refugia in the tropics (Haffer 1982, Benson 1982, Endler 1982) has challenged the assumption that the tropics were not affected by glaciations; 3) the formulation of a "new concept" in ecology ("patch dynamics"; Pickett and White 1985) and the realization of the importance of canopy gaps for the regeneration of canopy tree species (Whitmore 1975, Hartshorn 1978, Brokaw 1982) has caused a re-evaluation of the way tropical ecologists view forest succession; and 4) the recent fire that burned millions of hectares of tropical moist forest in Borneo (Leighton 1984), the discovery of charcoal in the soil profiles at La Selva, Costa Rica, San Carlos, Venezuelan Amazon, and many other locations (Sanford et al. 1985), and paleoecological data from lake sediments (Covich 1978, Deevey 1984) have forced a re-examination of the concept of what a primary tropical forest is or is not.

Parallel to this change in paradigms, and implicit in the evidence that motivates the change, is the realization that disturbances are stressors that operate at many scales, frequencies, and intensities (Fig. 4). Scale can vary from very local (e.g., the small area affected by a falling branch) to global disturbances (e.g., biomes affected by meteorite impacts [Raup 1984] or human deforestation of the tropics [Lanly 1982]).

Severity of disturbance (the impact of the stressor on the ecosystem; Lugo 1978, White and Pickett 1985, Jordan 1985) may or may not be related to scale. For example, a tree fall gap is a less severe stress than a landslide of similar size because only structure is removed from the system and the productive capacity of the soil is unaffected (Lugo 1978). The evaluation of the impact of a given type of disturbance event is complicated further by the frequency of return of the event. Usually, less severe events have higher frequencies of return than do more severe ones (Fig. 4). A less severe disturbance, however, could be highly stressful to a system if its period of return is sufficiently frequent. The challenge to ecologists is to unravel the mechanisms of ecosystem response to disturbances that differ in scale, frequency, and severity of action.

Most tropical research in the area of disturbance ecology is focusing on systems dominated by small gaps whose frequency of occurrence is high (Denslow 1980, White and Pickett 1985, Denslow 1987). Although small gaps are important in maintaining diversity in certain forest

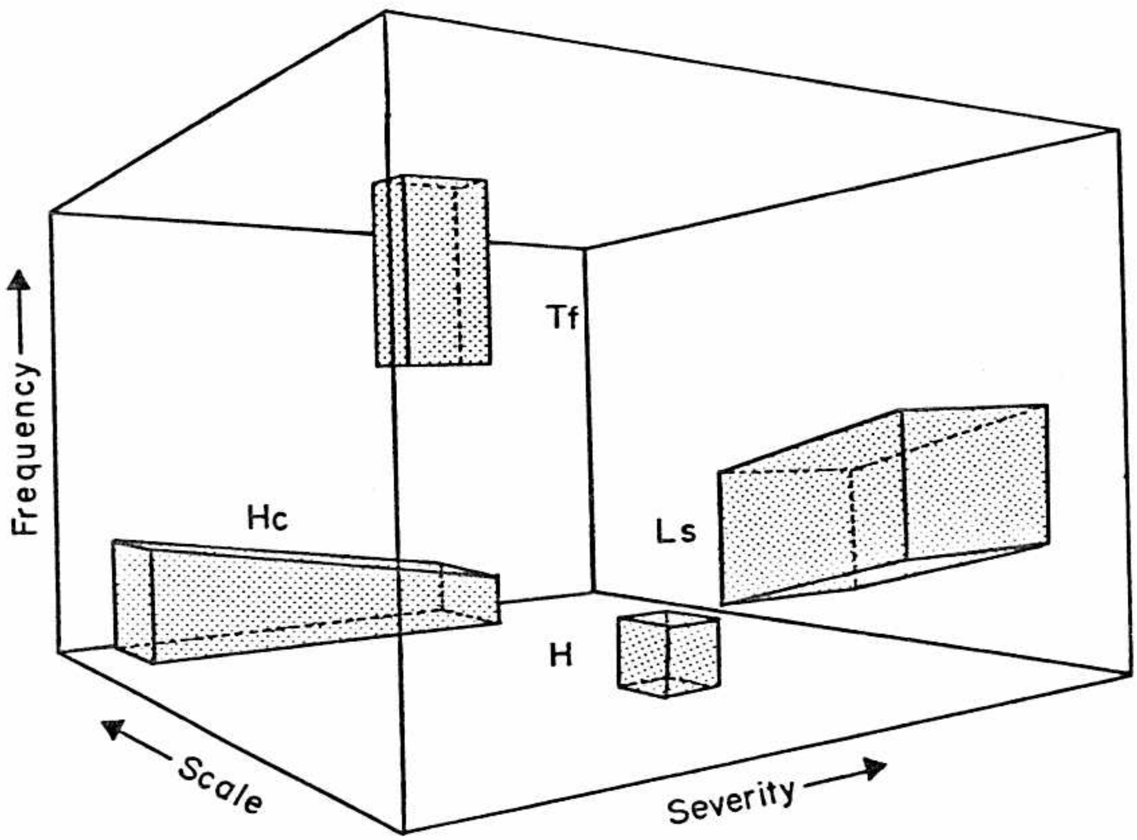

Figure 4. Conception of the relationship of four common types of disturbance in the LEF along dimensions representing disturbance severity, scale, and frequency. Tree fall (Tf), landslides (Ls), hurricanes (Hc), and harvest (H) are the four kinds of disturbance. In this figure, the relationships among the disturbance types can be seen. For instance, tree falls are frequent, but low in severity and scale, while hurricanes are infrequent (especially severe hurricanes), have moderate to very severe effects, and act on a large scale. The effects of these disturbances and the responses of ecosystems should be equally dissimilar.

types, this situation represents only one end of a continuum of disturbance severity and frequency. Tropical forests comprise large numbers of species that must face natural disturbances of all scales and intensities, each with a different frequency of return, yet relatively little is known about the effects of infrequent, large-scale disturbance. Forest response to small-scale, low-severity disturbance with a frequency of 10 years is likely to be much different from response to large-scale, high-severity disturbance with 100-year frequency. Treefalls are the most common form of natural disturbance in tropical forests. Landslides also occur in many tropical forests, but differ in their importance based on geology and topography. In the Caribbean, southeast Asia, Australia, and some parts of Central America (Fig. 5), hurricanes are the disturbance events that operate at scales and intensities that are most conducive to long-term ecological research and that offer an opportunity to answer questions about the mechanisms of action of physical forces relative to long-term behavior of the biota. Hurricanes occur in the Caribbean with predictable frequencies (Fig. 6), on the order of centuries for hurricanes with very severe effects and on the order of several decades, decades, or years for lesser storms (Weaver 1986).

Tropical forestry research in Puerto Rico has already produced observations that suggest certain patterns of biotic response to both large- and small-scale phenomena. For example, the estimated age of large colorado trees (Cyrilla racemiflora; Fig. 7) and palms (Prestoea montana; Fig. 8), can be related to hurricanes in 1867 and 1932, respectively (Weaver 1986, Lugo and Rivera-Battle 1987). Studies show that frequently measured forest parameters such as biomass, tree density, number of tree species, basal area, wood volume, wood density, above ground primary productivity, and complexity index will change in predictable patterns over periods of 40 years following a hurricane (Crow 1980, Weaver 1986, Fig. 9). Variation in annual rainfall that is unrelated to hurricane events can also elicit biotic responses since periods with more frequent and higher rainfall increase the probability of landslides and can result in a doubling of annual stream runoff (Fig. 10). Because hydrologic fluxes are critically important to many ecosystem processes (Lugo 1986), infrequent but large fluctuations in rainfall will have significant effects on ecosystem functions such as organic matter export (Asbury and Lodge, in prep.), nutrient cycling, and productivity. Long-term records are necessary to measure and understand infrequent events (Fig. 10). Clearly, both time and spatial scale are critical factors in the design of any ecological research in tropical forests subjected to such types of disturbances. The LEF offers significant background understanding (Section V) and sufficient records of long-term ecosystem processes to permit the formulation of specific hypotheses for long-term ecological research (Brown et al. 1983).

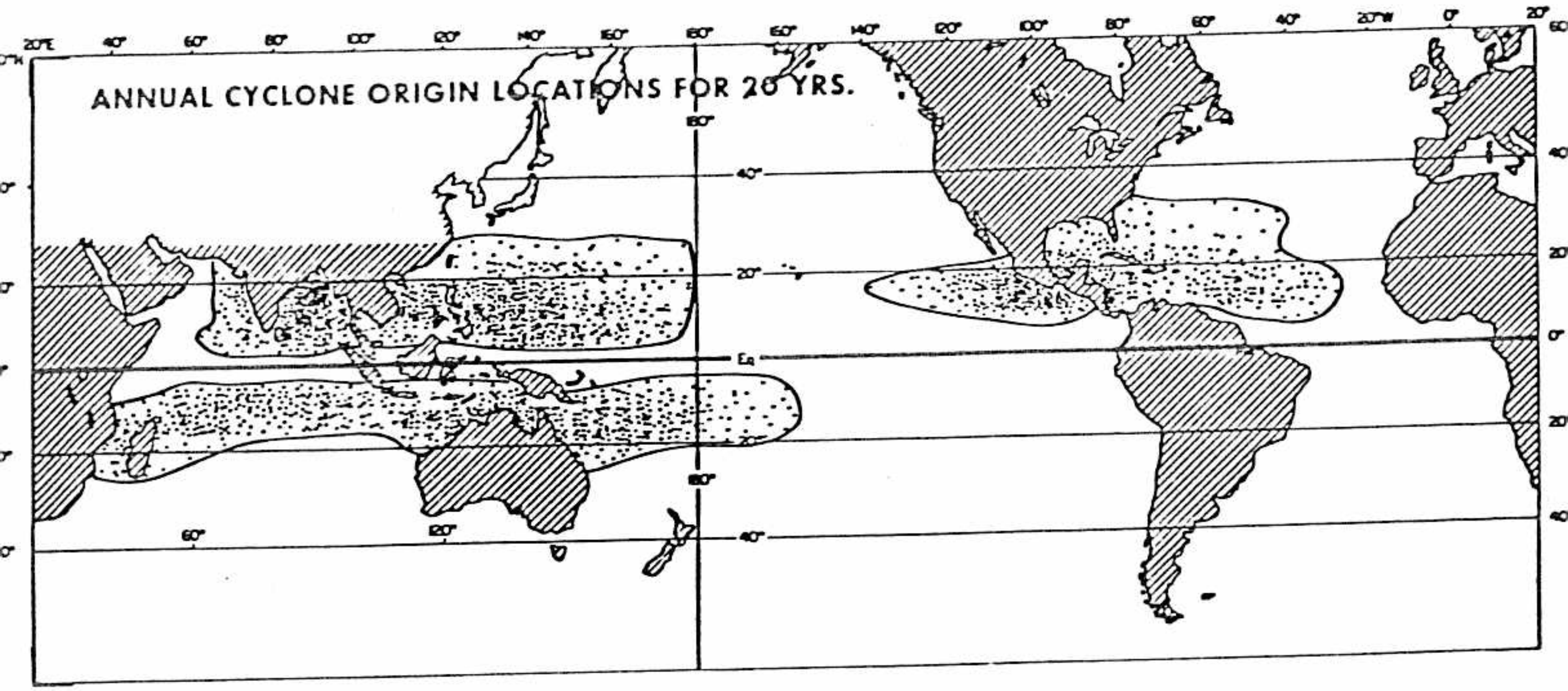

Figure 5. Location of genesis points of tropical cyclones for a 20-year period (Gray 1979).

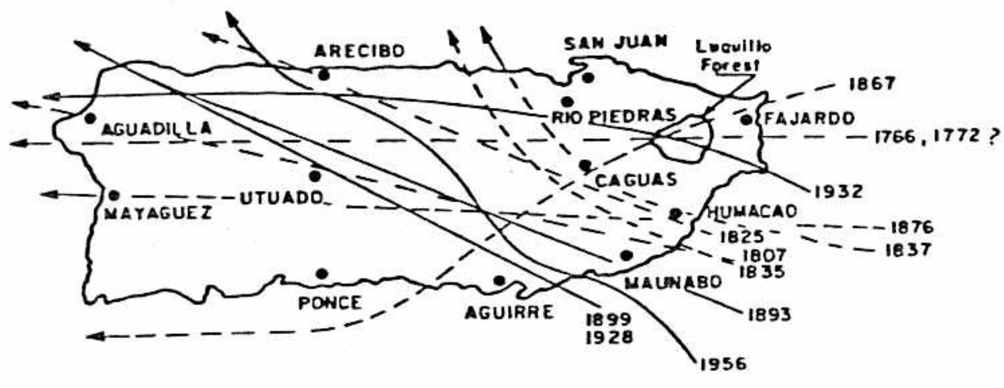

Figure 6. Paths of severe hurricanes over Puerto Rico from 1700 to 1960. Solid lines are known trajectories and dashed lines are assumed trajectories based on literature descriptions (Weaver 1986).

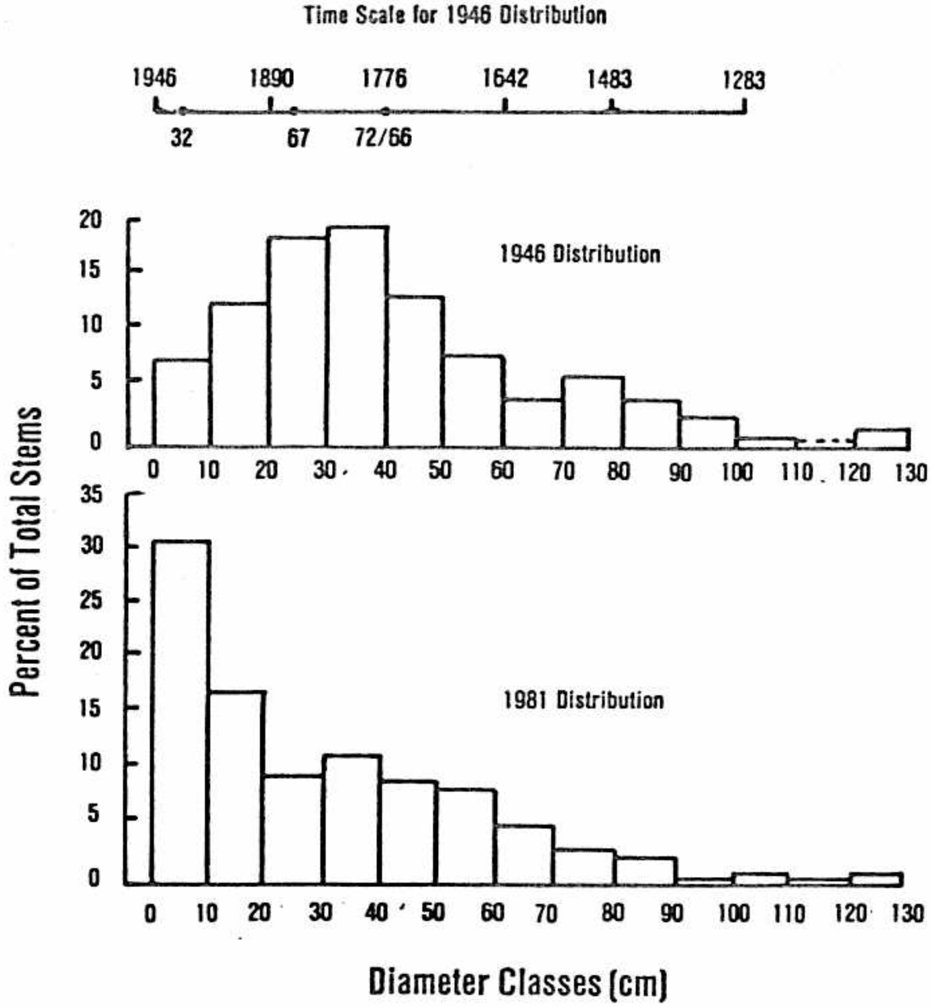

Figure 7. Diameter class distribution of Cyrilla racemiflora on undisturbed long-term research plots within the colorado forest of the Luquillo Mountains in two different years. The time scale indicates the years to which the diameter class corresponds as well as the years that severe storms passed directly over the LEF (Weaver 1986).

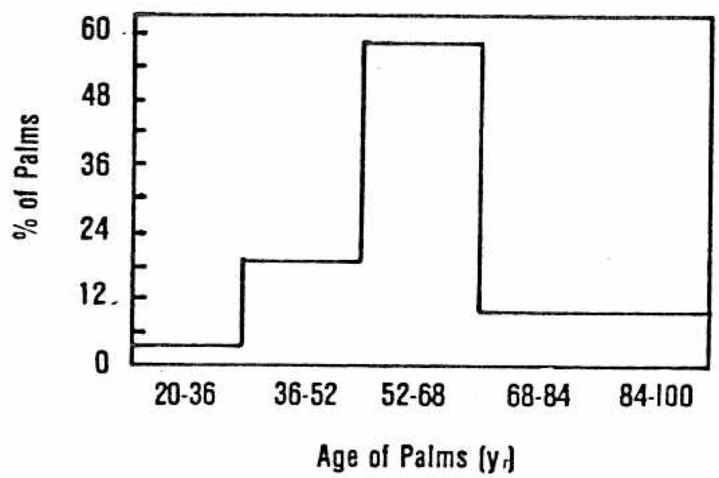

Figure 8. Age of palms (Prestoea montana) in the LEF. Individuals in the dominant age class were seedlings at the time of passage of the 1932 hurricane (from Lugo and Rivera-Battle 1987).

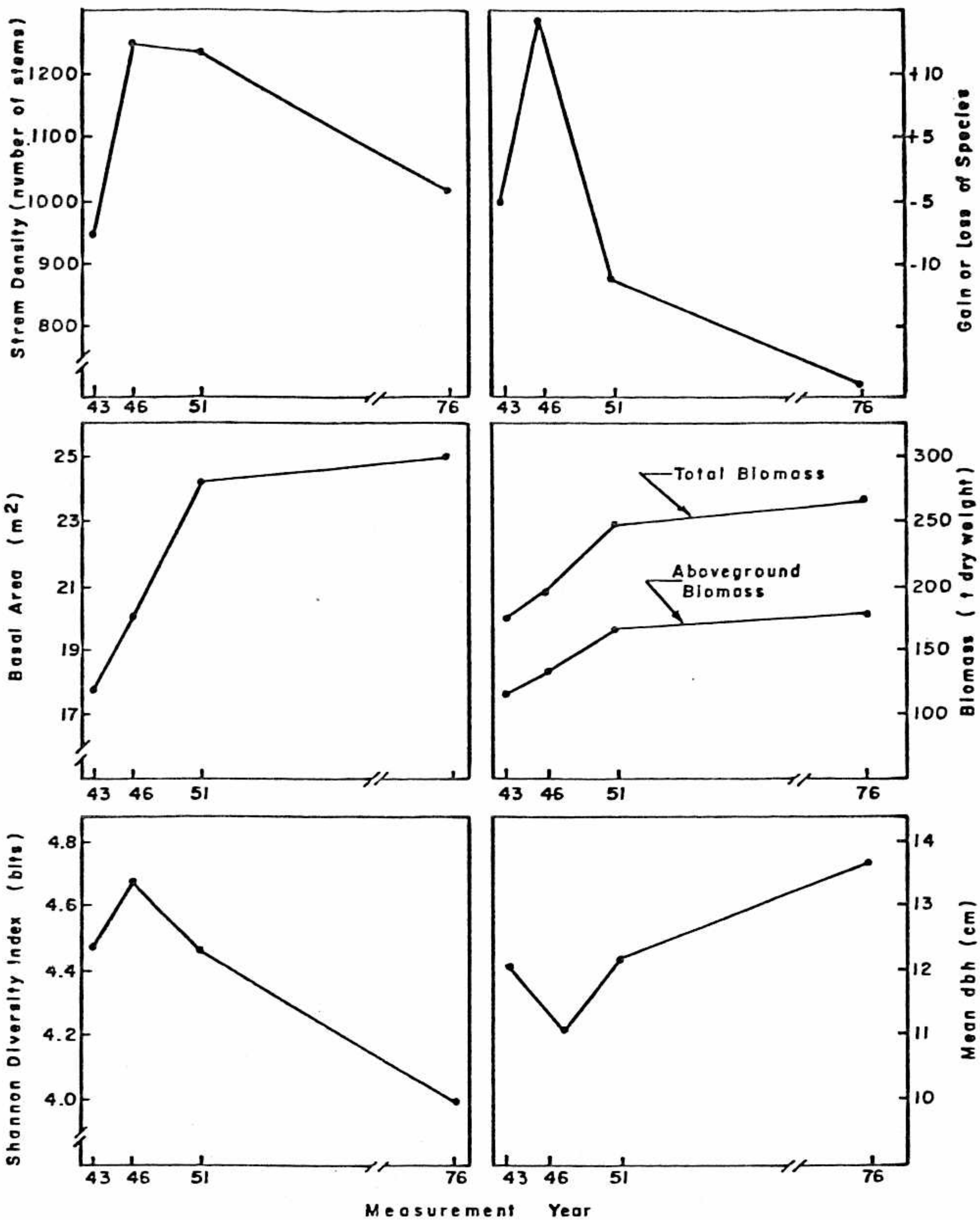

Figure 9. Changes in stand characteristics for the El Verde plots during the period 1954-1976. Measurements are based on all trees with dbh > 4 cm in a 0.75 ha plot (Crow 1980). The graphs show patterns of increasing biomass, basal area, and mean dbh and decreasing stem density, species richness, and diversity, reflecting recovery from hurricanes that struck the LEF in 1928 (San Felipe), 1931 (San Nicholas), and 1932 (San Ciprian).

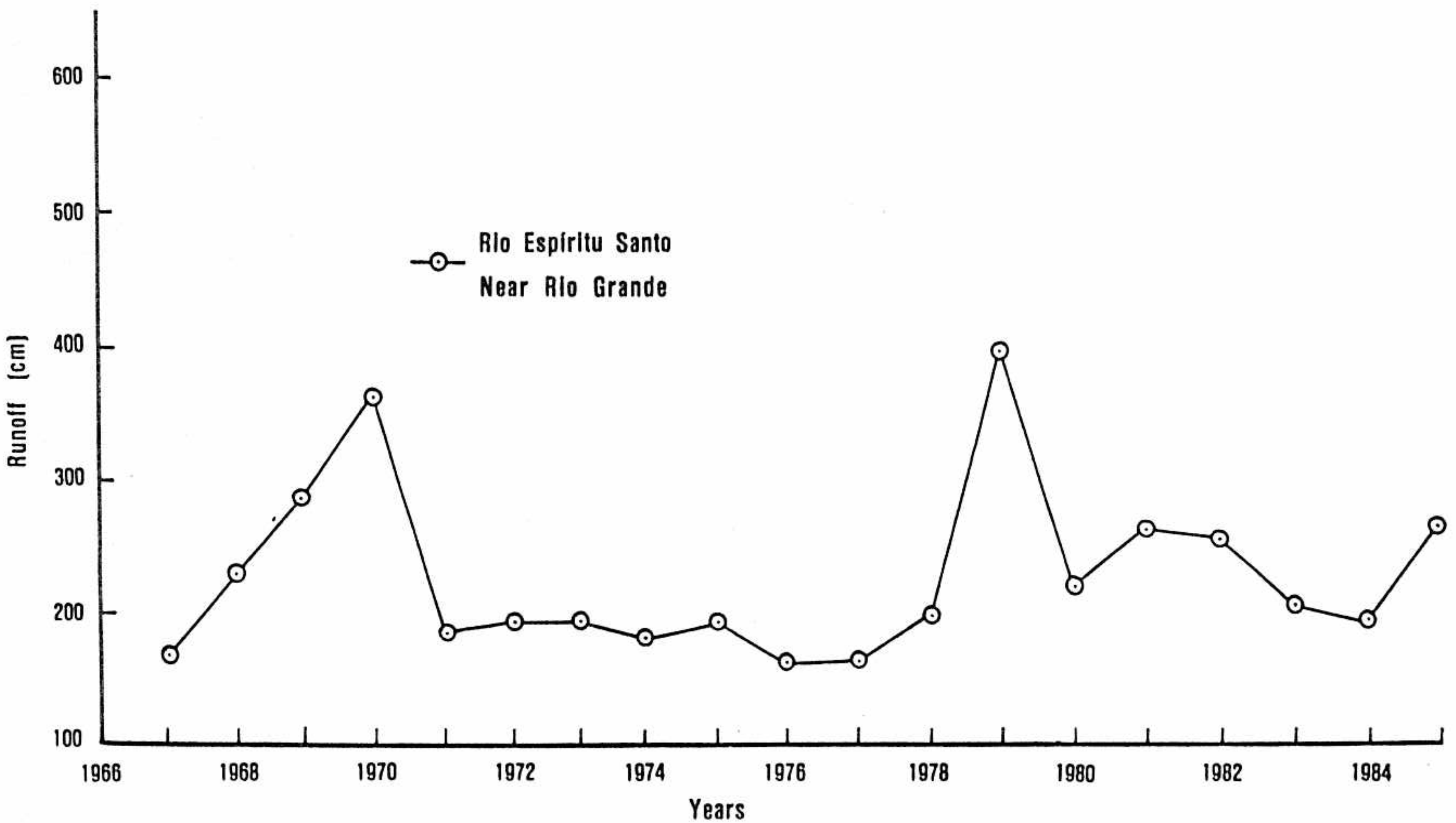

Figure 10. Long-term records of annual runoff in the Espiritu Santo River show recurrent peaks (1970 and 1979) separated by eight years of low flow. This pattern occurs in other gaged rivers in the forest (Brown et al. 1983). This record illustrates the need for long-term data collection in this forest which is greatly affected by infrequent meteorological events (data are from U. S. Department of the Interior).

II.A. Main Research Questions

We will use a combination of experimental and observational studies to address questions about the response of the terrestrial and aquatic biota to disturbances of different scales, severities, and frequencies in five watersheds in the Luquillo Mountains. By response we mean both the impact of disturbance as well as the feedback from the biota to site quality following disturbance. The main questions addressed by this proposal are:

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?

These questions stem from the observation that the end results of secondary succession after different types of disturbance in the LEF are virtually indistinguishable despite quite different initial conditions. The type of disturbance that initiated succession at a site is difficult or impossible to determine through examination of the regenerated mature forest. We base our approach on the hypothesis that the mode of resistance of an ecosystem to disturbance is a function of the stressor (intensity, periodicity, sector of the ecosystem that it affects, and area affected). After disturbance of any severity, the path of site recovery is influenced by the physical and chemical properties of the soil, water, and atmosphere, by the activity of the biota, or by a complex interaction among all four (soil, biota, hydrosphere, and atmosphere).

II.B. Explanation of the Main Research Questions

Most tropical research has concentrated on interactions within the biota or the effect of environment on the biotic community. However, the biota's effect on site characteristics is also a key component in the post-disturbance recovery process. We hypothesize that the potential for a return to the previous level of productivity after disturbance is conditioned by the biota. This follows from the premise that different types of disturbance produce different types of environments conducive to different rates and pathways of recovery. Our research will focus on that period of time when the biota exerts its main influence over the physical environment (the recovery phase; sensu Bormann and Likens 1979a). We expect that with increasing severity of disturbance the feedback function of the biota becomes more critical to the recovery process.

Some examples of biotic feedbacks that act during recovery illustrate the point: 1) The capacity of plants to retranslocate nutrients from senescent leaves prior to leaf fall affects litter quality, decomposition rates, and nutrient availability in the soil. Plants in some environments have high rates of retranslocation while those in others have low rates, and these are reflected in the ratio of nutrient use efficiency proposed by Vitousek (1982, 1984). Plants that exhibit high use efficiency ratios enhance nutrient recirculation and minimize potential losses due to leaching. Studies in Puerto Rico (Frangi and Lugo 1985) and Venezuela (Cuevas and Medina, in press) suggest that high efficiency ratios are associated with degraded sites and sites exposed to high leaching potential (Frangi and Lugo 1985). 2) Increasing complexity of root morphology, root functions, and spatial distribution of roots significantly increase the availability of nutrient pools to plants, enriching many substrates with organic matter, and improving the aeration and physical properties of soils. 3) Increased interception of rainfall by developing vegetation reduces soil erosion, leaching, and overland runoff. 4) The range of decomposition constants of complex biochemical materials (wood, bone, and shell) spreads nutrient releases over time. This provides stability to nutrient cycles in terms of storage and slow steady release. 5) As food web complexity increases through successional time, system resilience decreases (Pimm 1982). DeAngelis (1980) has shown theoretically that system resilience is inversely related to the "tightness" of nutrient cycling. Hence, as food web resiliency decreases during succession, the probability of retaining vital nutrients in biotic circulation increases (Odum 1969, Pimm 1982).

High rainfall areas such as the LEF (average = 3775 mm/yr; Lugo 1986) are subjected to the mechanical impact of rain drops and winds, potential land movements, and constant leaching of nutrients. These potential stressors, if unchecked, can deplete soil nutrients, remove soil from the site, and lower site productivity. To the extent that the biota mitigates such a series of events, it represents a collection of mechanisms that conserve soil and nutrients and maintain the capability of the site to support biological productivity (Budowski 1965). Successional species are known to grow rapidly, bind nutrients in biomass, protect soil by closing the forest canopy, and moderate forest microclimates (Odum 1969, Budowski 1965, Marks 1974, Ewel 1980). However, these generalizations do not address the more important question of how the complexity of an ecosystem is rebuilt from different initial conditions. This issue can be addressed only through long-term study of specific sites that have been subjected to different severity, frequency, or scale of disturbance.

III. PROPOSED LONG-TERM ECOLOGICAL RESEARCH PROGRAM

III.A. Outline of research and data management components

III.A.1. The Luquillo Experimental Forest (LEF) - Four life zones occur in the LEF (subtropical wet forest, subtropical rain forest, lower montane wet forest, and lower montane rain forest; Ewel and Whitmore 1973), and four major vegetation types occupy these life zones (Table

1). Below 600 m the dominant tree is the tabonuco (Dacryodes excelsa), which is best developed on protected, well-drained ridges. Above the average cloud condensation level (600 m), palo colorado (Cyrilla racemiflora) is the dominant tree except in areas of steep slope and poorly drained soils, where the sierra palm (Prestoea montana) occurs in nearly pure stands. The dwarf forest occupies ridge lines and is composed of dense stands of short, small diameter trees and shrubs that are almost continually exposed to winds and clouds. Both the palm and dwarf forests are dominated by only a few plant species. A detailed description of the LEF is given in Section V.

Table 1. Distribution of forest types within the Luquillo Experimental Forest (adapted from Brown et al. 1983)

SITE	Approximate area (ha) of each forest type* 1	2	3	4	5	TOTAL
Higher elevation (600-1,070 m)	5,868					5,868
Medium elevation (300-600 m)	59	1,076	2,499	215	76	3,925
Lower elevation (100-300 m)		56	1,094	163	125	1,438
Increasing human disturbance	-->					
Total	5,927	1,132	3,593	378	201	11,231

1. Colorado, palm, and dwarf forest*
2. Old growth tabonuco forest
3. Secondary tabonuco forest
4. Plantations
5. Deforested

The tabonuco forest has been the subject of the most extensive ecological studies of any of the four forest types, and data from these studies will form part of the LTER data base. Long--term studies of forest growth have been conducted by Wadsworth (1951) and represent a 40 year record of tabonuco forest dynamics. In addition, the tabonuco forest has been the subject of studies of tree growth (Crow and Weaver 1977) and community composition (Crow and Grigal 1979), and the extensive data base has served in the development of simulation models of forest regeneration (Doyle 1981, Doyle et al. 1982).

The most detailed study of the tabonuco zone was the Rain Forest Irradiation Project of the U. S. Atomic Energy Commission, which took place from 1963 to 1968 (Odum and Pigeon 1970). The principal goals of this project were to determine the effects of gamma irradiation on a rain forest ecosystem, to examine the cycling of fallout elements, and to develop an understanding of vertical and horizontal forest structure and various system processes including nutrient cycling, energy flow, and forest regeneration mechanisms.

The Center for Energy and Environment Research (CEER) has continued to conduct studies of nutrient cycling and energy flow in tabonuco forest since the end of the Rain Forest Project in 1968. This research has been sponsored by the U. S. Department of Energy (AEC, ERDA) and the University of Puerto Rico. The initial phase of the current Rain Forest Cycling and Transport Project (1980-83) concentrated on the structure of terrestrial and aquatic food webs and their possible roles in the biotic control of ecosystem processes. The current phase examines nutrient import, export, and immobilization, decomposition, primary productivity, and forest regeneration as well as continuing work on food webs. The accumulated work of 50 years makes the tabonuco forest the best known of the four forest types in the Luquillo Mountains and probably the best known site in the tropics. In addition, the El Verde Field Station and research area has served as a focus for local and mainland ecologists, whose work has greatly enhanced knowledge of forest processes.

III.A.2. General procedures - The proposed LTER program addresses the question of variance in the disturbance regime at the scale of the LEF landscape and the question of forest response at scales from the individual organism to the watershed. Investigation of disturbance regimes will take advantage of the full range of life zones, elevation, slope, aspect, and geomorphology available in the LEF. Interpretation of satellite and photographic images and ground surveys will be combined with a geographic information system (GIS; Fig. 11) to develop an understanding of how the predominant disturbance type and size varies throughout the LEF. This breadth of sites will satisfy the need to study systems subjected to disturbances of different intensity, frequency, and scale. Integration of results and predictions for future disturbance events will be made using the Map Analysis Package (see below) and simulation modeling.

Studies of regeneration will be restricted to five watersheds (Bisley 1, 2, and 3; Sonadora; Rio Blanco; Fig. 2) within a single forest type (tabonuco; see above and Section V). We propose to study regeneration intensively in areas affected by four types of disturbance common in the LEF and many other tropical moist forests: treefall gaps, landslides, hurricanes, and selective harvesting (hereafter called harvest). Disturbances of the first three types occur naturally throughout the LEF. Harvest will initially take the form of a selective cut of trees in one watershed, either Bisley 1 or 2 (see below). Bisley 3 will be preserved as a control watershed. The harvest will be conducted by the U. S. Forest Service. The result of this manipulation will be a mosaic of untouched forest and gaps of varying size. Further treatments are discussed in the following sections. Measurements of forest response to disturbance at Bisley will range from the level of single organisms to the entire experimental and control watersheds.

Artificially-created gaps in the experimental Bisley watershed and naturally-occurring

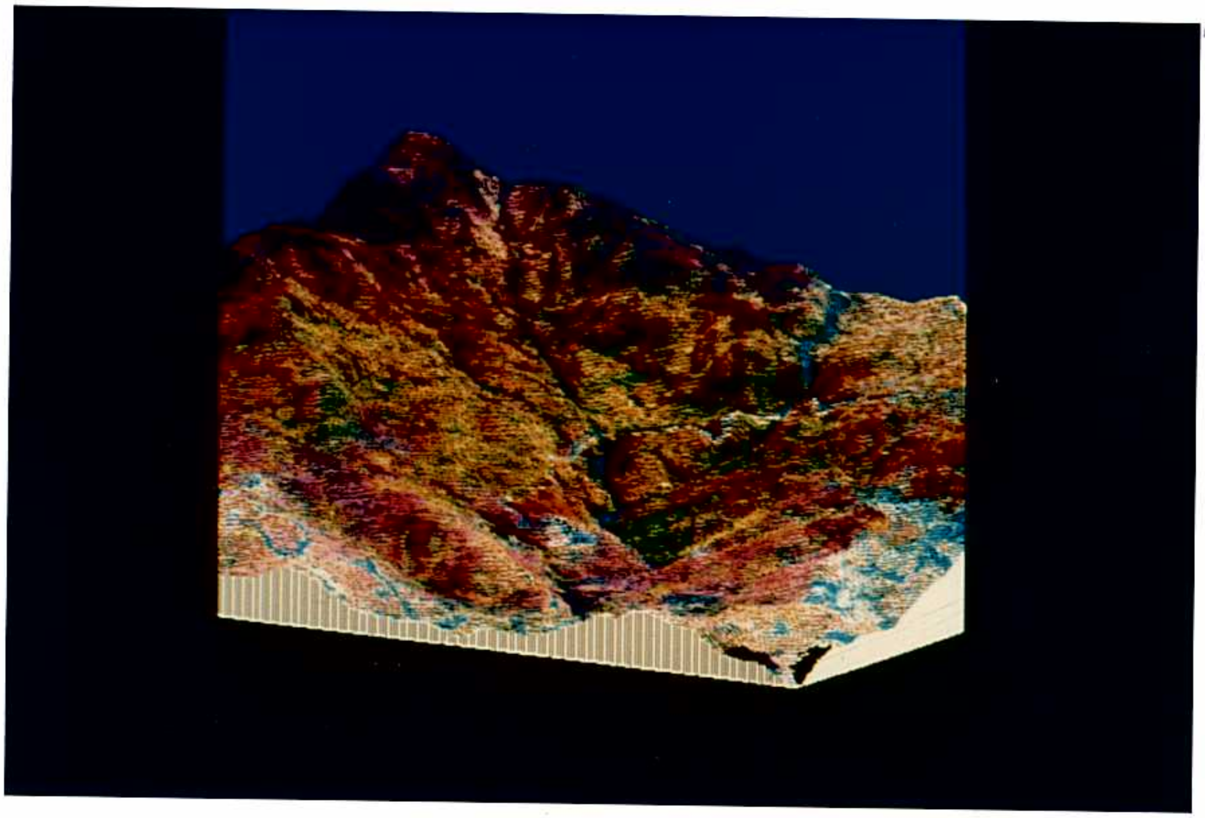

Figure 11. A three-dimensional image of the Luquillo Experimental Forest, looking towards the southeast. The image was generated from the Geographic Information System being developed for the LEF by combining Landsat Thematic Mapper data with digital elevation. Yellow areas on the lower slopes represent tabonuco forest whereas colorado forest at higher elevations appears red. The Rio Espiritu Santo and its tributary the Quebrada Sonadora are visible in the image.

landslides and treefalls located in the Bisley and Sonadora watersheds will provide sites for the regeneration studies. Heavy rains in December, 1987, resulted in many small-to-medium sized landslides within the LEF, including at least 31 in and around the El Verde Field Station in the Sonadora watershed. These recent slides offer an excellent opportunity for regeneration studies. Both new and previously recorded treefall gaps (Odum and Pigeon 1970; Perez Viera 1986; Wunderle et al. 1987) will provide additional sites in both Sonadora and Bisley watersheds. A large (2 ha), active landslide in the Rio Blanco watershed will be the focus of studies of regeneration after large-scale, high-intensity disturbance. The Rio Blanco watershed has been the site of several large landslides in the past 20 years and offers a unique opportunity to study this kind of disturbance. An equally large landslide occurred at East Peak during heavy rains in December, 1987, and future studies are planned at this site. The Bisley, Sonadora, and Rio Blanco watersheds are all within tabonuco forest (Odum and Pigeon 1970) at 200-500 m elevation and 3,500-4,500 mm rainfall. Temperature differences among sites are not significant.

III.A.3. Conceptual framework - In designing the proposed Luquillo LTER program, we have taken advantage of the extensive research history of the forest by combining new approaches to ecosystem study with those that have traditionally proven effective in the LEF. The framework for the current proposal was developed at a workshop at El Verde in October, 1987, at which the collaborating investigators clarified the relationship between individual research goals and the theme of the proposal. A conceptual model of the main forcing functions and subsystems of a watershed in tabonuco (D. excelsa) forest provides a unifying focus for the proposed research (Fig. 12, top). The forcing functions of this ecosystem model are hurricanes, climate (including heavy rainfall events and resultant landslides), solar energy, geological substrate, and human management. The main subsystems are vegetation, animals, and soil and associated microbiota. The processes within the system include hydrologic flows, biotic interactions, and energy and nutrient fluxes, all of which are subject to disturbances generated by the forcing functions. Forcing functions, disturbances, subsystems, and flows will be studied as part of the proposed LTER program. However, the measurements and experiments of the proposal range widely in scale and detail depending of the hypothesis to be tested.

Questions about disturbance and the response of the biota will be addressed through a series of research topics that correspond closely to the core research topics of the LTER program. The lower part of Fig. 12 describes the relationship of these research topics to one another and to the conceptual model of the watershed. Each research topic is associated with one or more simulation models that serve to focus the investigation (see below). The investigators associated with each of the research topics reflect foci of interactions within the research team. Strong interactions between groups are indicated by arrows.

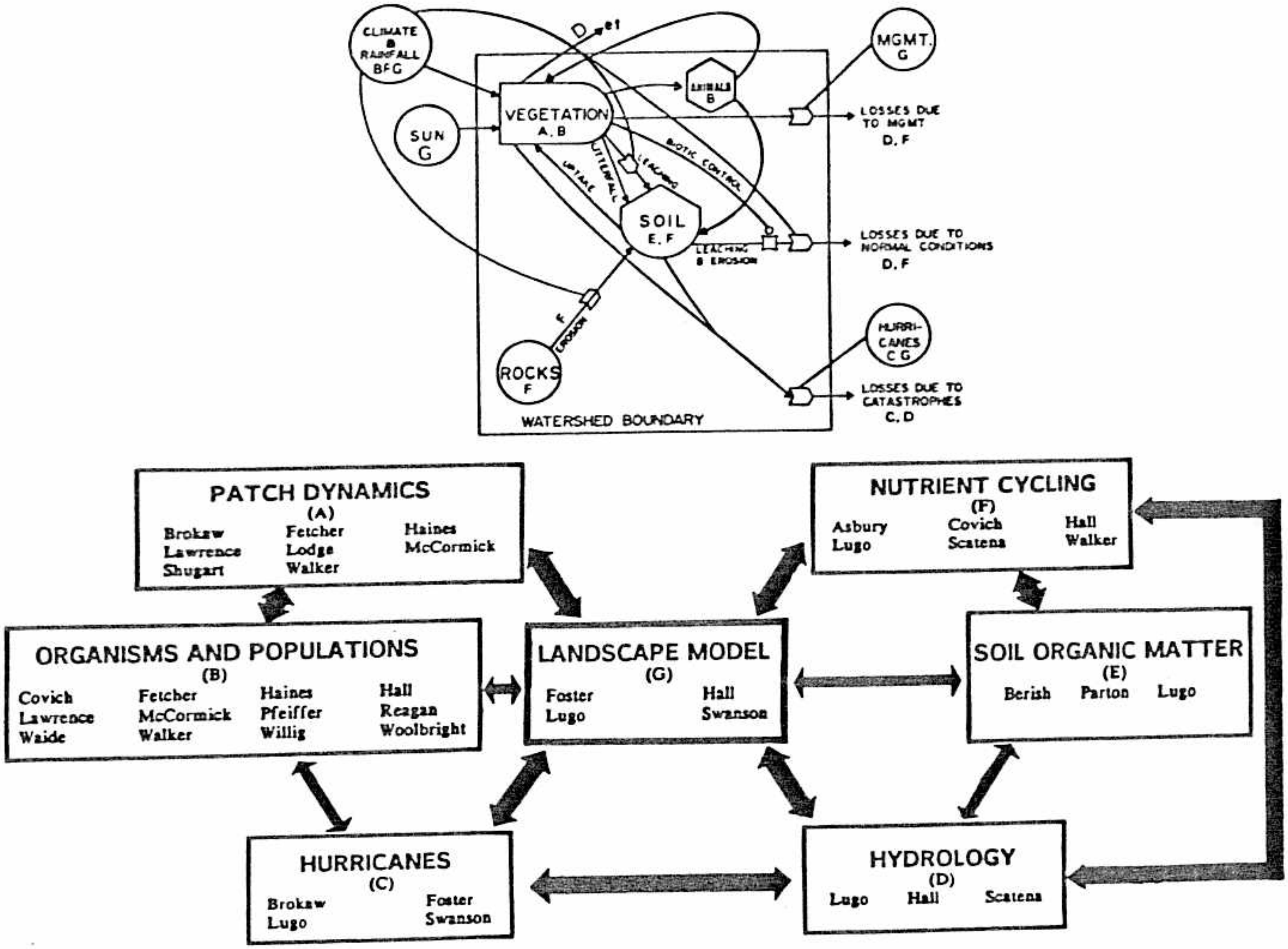

Figure 12. Conceptual model of watershed dynamics in tabonuco forest (top) and the relationships among research components and investigators involved in these components (bottom). Symbols in the watershed model are after Odum (1983). Management is abbreviated MGMT, and evapotranspiration is abbreviated **et**. Interactions among components are shown by arrows, with the thickness of the arrow reflecting the strength of the interaction. Results from each research component feed into the watershed model and into a central landscape model of disturbance. Further explanation of the figure is given in the text.

The patch dynamics group will interact strongly with investigators conducting organismal and population studies (see Sections III.C.2.e and f) that represent the smallest scale of focus of the LEF LTER program. Investigations of organisms and populations are based on over 25 years of research and observation of animals and plants at Luquillo. Organism and population studies focus on the biotic compartments of the forest ecosystem as represented in the model at the top of Fig. 12.

Patch dynamics and nutrient cycling groups will also interact through common interests in the fate of nutrient stocks after different kinds of disturbance. Nutrient loss or retention will be greatly influenced by the way revegetation proceeds in different disturbance patches.

The hurricane group will integrate abiotic factors related to disturbance and biotic response to disturbance to develop models of disturbance regime at the ecosystem and landscape scale (see Section III.C.1). These models will provide a mechanism to scale up intensive studies of the watersheds into a comprehensive view of disturbance and response throughout the LEF.

The soil organic matter (SOM) group (see also Section III.C.2.c) focuses on the interactions of the biota and the physical environment through the production, decomposition, leaching, and storage of soil organic matter. Because the group involved in developing this topic will also address soil nutrients, it will interact strongly with the nutrient cycling group (see Section III.C.2.b and g). The nutrient cycling group will in turn depend on studies of the hydrology of the tabonuco forest ecosystem (see Section III.C.2.g). This set of integrated studies and research groups will focus their attention on the fluxes and storages of matter (nutrients and organic matter) in the ecosystem.

We propose to integrate simulation models and the GIS data base as a tool for addressing landscape-level questions. We will develop general models that can be applied to all of the sites in the GIS grid network and thereby represent the response of the biological systems to the specific driving variables at each of the grid cells (see below). The output of landscape-level modeling, analysis, and synthesis are twofold. First, new hypotheses and alternative explanations of phenomena are fed back to research groups working on component parts of the landscape. Second, the principles of landscape behavior (Risser et al. 1984, Forman and Godron 1986, Risser 1987) under tropical conditions of multiple and frequent disturbance will be used for extrapolation to other Caribbean and tropical regions and for comparison with similar results from other LTER sites.

III.A.4. Intra- and inter-site synthesis - Within the LTER format, synthesis of research results must take place on three levels: 1) within each LTER research group, 2) among subsets of sites within the LTER network, and 3) at the level of the whole LTER network as well as other locations where long-term research is being conducted. The unique strength of the LTER approach is in the contribution of ideas which arise from a comparison of a broad range of ecosystems each studied in depth. We recognize the importance of each of these levels of synthesis, and we have made specific plans for integration at each of these levels.

III.A.4.a. Intra-site synthesis - Published syntheses of information are already available for the tabonuco forest (Odum and Pigeon 1970) and the whole landscape (Brown et al. 1983) of the LEF. A book synthesizing information on populations and feeding relationships of animals will be published by the University of Chicago Press (Reagan and Waide 1989). For the current study, we propose to use several synthesis mechanisms that include group interactions among project participants, development of a Geographic Information System (GIS) incorporating ground-based and remotely-sensed data, and hierarchical simulation modeling.

Group interactions - The research activities of many of the members of our research team are already tightly coordinated through participation in other group projects (Fig. 13). Members of the LEF LTER research team have a broad range of tropical experience and are led by a core group of resident scientists who have collaborated on a variety of ecosystem studies in Puerto Rico. An NSF-funded workshop for all collaborators was held in October, 1987, at El Verde and served to integrate the new members of the team into the core group. At the El Verde workshop, the group reached a consensus on the research goals of the LEF LTER and on the strategies for achieving them. We will continue to emphasize such fruitful interactions among study participants through monthly meetings of resident scientists, annual scientific meetings for all group participants, collaboration in field studies, and easy communication among all members of the team via the BITNET system.

GIS system - The development of a GIS system for the Luquillo Experimental Forest involves a grid overlay that has cells 30 x 30 m on a side. Our GIS data base will include basic physical, chemical and biological information for each cell including elevation, aspect, slope, climatic variables (rainfall, temperature), geology, soils, biological information (e.g., plant species distribution, estimated plant biomass) and historical land use information. In addition, the GIS will contain multiple sets of remotely-sensed data from different sensors and at different scales (see below). The Earth Resources Laboratory of NASA's National Space Technology Laboratories is developing both mainframe and PC-based versions of the LEF-GIS through a graduate student based at the University of Georgia.

Remotely-sensed data for the LEF includes multiple sets of aerial photography and other data acquired from both aircraft and satellite platforms: Landsat Thematic Mapper (TM), Thematic Mapper Simulator (TMS), and Calibrated Airborne Multispectral Scanner (CAMS). Further TM data and SPOT data from the French satellite will be acquired in 1988. In addition, NASA will fly a mission over Puerto Rico using the Ocean Color Imager in January 1988. Future data

(1) WATERSHED PROJECT	(2) TROPICAL SOIL BIOLOGY	(3) LIMITS TO PRODUCT-IVITY	(4) RAIN FOREST CYCLING	INVESTIGATORS		Other sites
X				F. Scatena	USFS	Dominican Republic, Jamaica, Colomb
X	X	X		A. Lugo	USFS	
X	X	X	X	R. Waide	CEER	Colombia, Mexico, Bahamas, Jamaica
X		X	X	C. Asbury	CEER	Brazil
X		X	X	W. Lawrence	CEER	Florida
X	X	X	X	J. Lodge	CEER	Costa Rica
X	X		X	W. Pfeiffer	CEER	
		X		N. Fetcher	U. Puerto Rico	Costa Rica, Panama
		X		L. Walker	U. Puerto Rico	Hawaii
				F. McCormick	U. Tennessee	
			X	A. Covich	U. Oklahoma	Panama, Mexico, Belize, Guatemala
			X	D. Reagan	CEER-Adjunct	Africa
			X	M. Stewart	SUNY-Albany	Africa, Jamaica, Mexico
			X	M. Willig	Texas Tech U.	Brazil
			X	L. Woolbright	Siena College	
				N. Brokaw	Manomet Bird Obs.	Panama, Belize
				D. Foster	Harvard U.	
				F. Swanson	Oregon State U./USFS	Ecuador
				C. Berish	Emory U.	Costa Rica, Belize, Mexico
				W. Parton	Colorado State U.	Peru
				B. Haines	U. Georgia	Costa Rica, Panama, Venezuela, Afri
				C. Hall	SUNY-Syracuse	Costa Rica

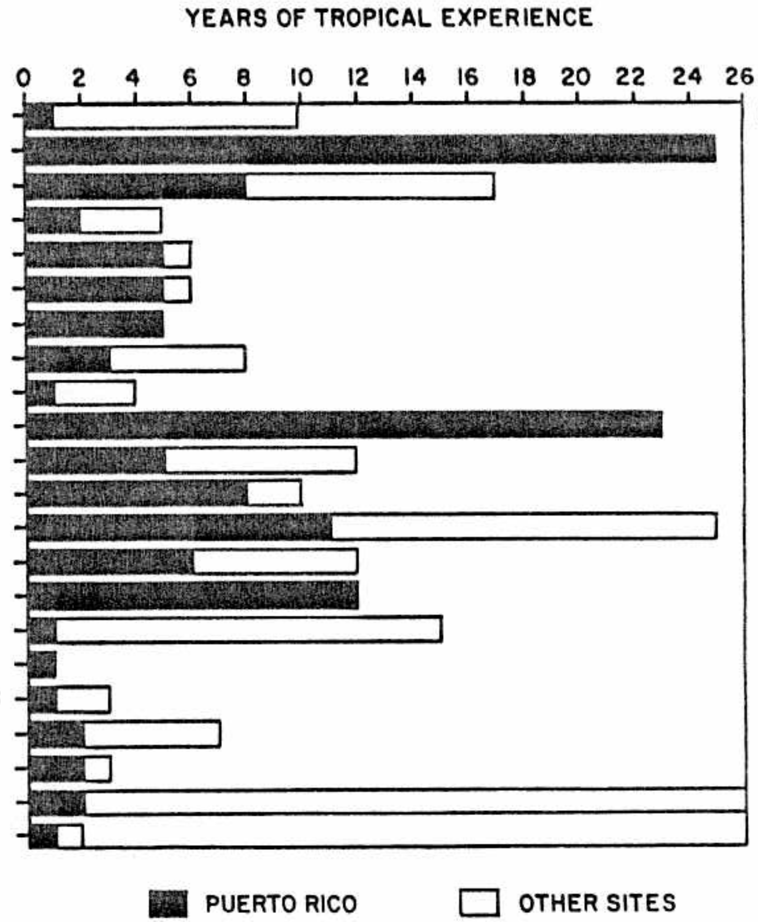

Figure 13. The LEF LTER research group. Investigators and their institutional affiliations are shown in the middle columns. The first four columns list current or proposed research programs in Puerto Rico that involve subgroups of the research team. The Watershed Project (1) forms one base of the current proposal (Section III.A.5). The Tropical Soil Biology and Fertility Program (2) is an international network of sites using a common methodology to investigate soil processes. The Limits to Productivity project (3) is a proposal to the Minority Research Centers of Excellence Program of NSF to establish a center of excellence in tropical ecology in Puerto Rico (Section III.A.5). The Rain Forest Cycling and Transport Program (4) is the research sponsored by the U. S. Department of Energy at El Verde. The bar graph shows years of research experience in Puerto Rico and other tropical countries, which are listed in the final column.

acquisitions will be made through a joint University of Puerto Rico/NASA Cooperative Research Program now in its third year (see letter of endorsement in Appendix 3).

Simulation models - Our goal is to understand how the biota (e.g., from individuals to the landscape) responds to and restores productivity after many kinds of disturbances acting at different scales of time and space. To maintain integration among these different scales, we will use a series of simulation models. These models have three additional uses: 1) to plan research so that field measurements encompass all information needed to test hypotheses, 2) to express current understanding of phenomena and to generate new hypotheses, and 3) to extrapolate site- and experiment-specific information to different locations in space and time. Modeling will be used to formalize various hypotheses presented in this proposal to provide non-trivial predictions about the characteristics of ecosystems and their components in the Luquillo Mountains. Each aspect of the research work in this proposal feeds into a model, and all models are coordinated to the core research topics and to the GIS landscape model (Fig. 12). This coordination assures that data collected at all levels of biotic organization contribute towards synthesis at either a higher level of aggregation (e.g., the landscape) or towards greater detail (e.g., population-level models).

We will develop simulations based on the general model (an aggregated model of watershed dynamics) and five models representing the core research topics in Fig. 12: 1) the model of succession in the tabonuco forest developed by Doyle (1982), 2) a model of soil organic matter dynamics (Parton et al. 1987; Fig. 14), 3) the MAP hurricane model (see Section III.C.1), 4) a hydrologic model, 5) and a detailed model of nutrient cycling in a forest stand (Fig. 15). We will implement the models in the order given above. The soil organic matter model (Century Model), the plant succession model, and the MAP model have already been developed and show great promise for simulating the impact of disturbance on nutrient cycling, soil organic dynamics, and plant succession. All of these models use long time steps (monthly to yearly) and are appropriate for simulating the long-term (50 to 500 year) response of the system to disturbance. The major activities in implementing these models include parameterization and modification of the MAP model for disturbance regime and the Century SOM model for soils in the LEF and linking the Century SOM model to the plant succession model so that it includes the impact of nutrients on plant succession. Dr. Hank Shugart has agreed to collaborate with us in the development of a linked plant succession and SOM model. Inter-site comparison will be enhanced by the use of the SOM and plant succession models selected; versions of these models have been identified by the LTER Coordinating Committee as examples of successful applications of ecological models to long-term research, and the two models will form one focus of the LTER modeling workshop proposed by the Coordinating Committee for 1988.

We propose to use a patch dynamics model (Doyle 1982), as recommended for comparative studies of disturbance (Pickett and White 1985), to guide our research on disturbance and regeneration in the tabonuco forest. This model describes disturbance-mediated ecosystem processes by taking into account: a) the frequencies, dispersion, and environmental characteristics of all types and sizes of disturbances; and b) the recovery rates from all types and sizes of disturbances. The basic premises of the model are adapted from Levin and Paine (1974):

1. The community is a mosaic of different patch types, many of which originate as disturbances.

2. The patch is the fundamental unit of ecosystem structure. When recovery within individual patches is coupled to events generating patches, a bridge is built between patch processes and ecosystem processes.

The frequency, scale, and severity of disturbances affect the recovery process because there is a "continuum of biogeochemical, hydrological, and radiant energy responses at the forest floor, depending on the scale of the disturbance" (Bormann and Likens 1979a). This environmental continuum among disturbances induces a corresponding continuum of biological responses, which in turn influence the environment and ecosystem state (Bormann and Likens 1979a) of recovering patches.

Our ultimate goal is to use our knowledge of these properties to predict the frequency and size-class distribution of different states - reorganization, aggrading, transition, steady state (Bormann and Likens 1979a; see below) in the forest mosaic, thus leading to an understanding of the structure and function of the system as a whole (Levin and Paine 1974).

The hydrologic and nutrient cycling models will use daily time steps and will be appropriate for simulating the short-term response of the system to disturbance. Both regression and physically-based hydrologic models will be tested and compared (Loague and Freeze 1985, Heggen 1986). A detailed nutrient cycling model will be developed by combining the parts of existing models (e.g., Hunt 1978, McGill et al. 1981). The effects of disturbance will then be evaluated using the dummy variable technique (Hewlett et al. 1984). In this case the effects of disturbance are assessed by comparing the residual error from a full model containing the disturbance with a reduced model without the treatment. A principal objective during the second LTER funding period will be to link the watershed model to the nutrient cycling model and thus create a combined model that can simulate the impact of disturbance on nutrient losses from watersheds.

The component investigations and models proposed herein are linked to the landscape level of ecosystem organization through a landscape model generalized to each cell of a geographic information system (GIS) covering the LEF. Whereas there is a relatively rich literature available for modeling forest stands (Shugart 1984, Dale and Gardner 1986), most of these models are based on growing a series of individual species in plots of about 0.1 hectare. There does not exist to our knowledge an explicit transfer of this approach to a geographically complex system except to solve the initial equations for one site vs. another (Shugart, personal communication). We propose to develop an explicit scheme for translating geographical information, derived from geographical space, into model parameter space (equivalent to ecological space) using a gradient approach (Whitaker 1975, Austin 1987). We will determine micrometeorological conditions for many locations in the LEF landscape by integrating a GIS physical-specifications system with a statistical analysis that predicts meteorological data as a function of site location and related topographical characteristics (Fig. 16). The parameters derived from this analysis plus other GIS-derived physical and biotic parameters that act as forcing functions operating on the ecosystem can then be used to predict the behavior of individuals, populations, and ecosystems throughout the entire landscape.

III.A.4.b. Inter-site synthesis - Response to the preparation of an LTER proposal for the LEF has been very strong, and many investigators have indicated a willingness to cooperate in various projects. Most of these collaborative efforts will be funded separately from this proposal. We list below notable cooperative efforts with individuals from recognized centers of long-term ecosystem research. Those efforts that will be funded in part from this proposal are indicated with an asterisk. These will receive approximately 25% of the total budget.

Andrews	Swanson	role of geological processes*
	Vogt	root dynamics
Coweeta	Berish	root dynamics*
	Crossley	litter organisms
	Haines	nutrient uptake and allocation*
	Fitzgerald	soil sulphur dynamics
	Meyer	stream nutrient cycling
	Swank	sulphur cycling
	Wallace	stream nutrient cycling
Hubbard Brook	McDowell	stream nutrient additions
	Bowden	stream nutrient additions
	Johnson	soil nutrient pools
Central Plains	Parton	soil organic matter dynamics*
Harvard Forest	Foster	hurricane impact on forests*
Northern Lakes	Covich	aquatic invertebrate population dynamics*
Venezuelan Institute for Scientific Investigation	Medina	plant ecophysiology
	Cuevas	root dynamics
Oak Ridge	Huston	plant productivity

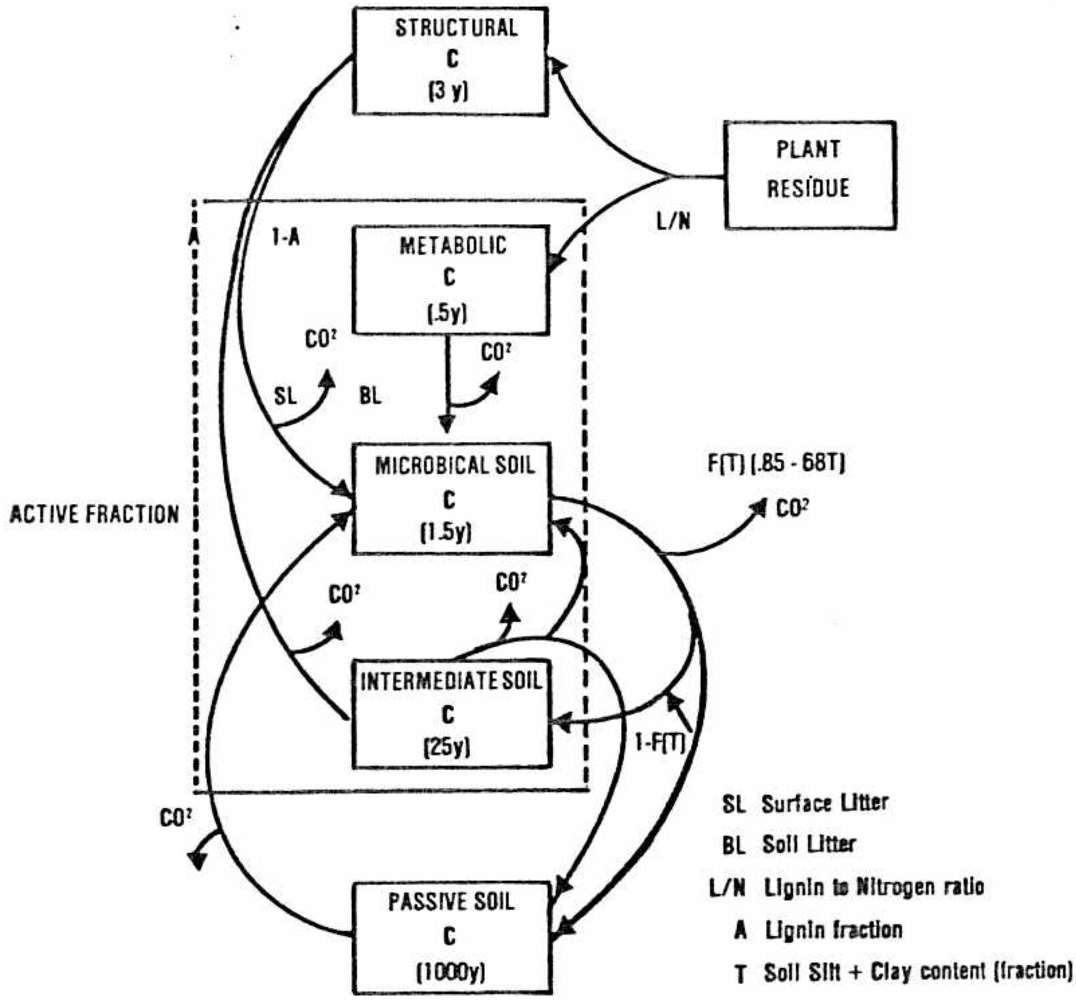

Figure 14. Soil Organic Matter (SOM) Model (Century Model). This conceptual model shows plant residue flowing either into a structural or a metabolic pool depending on the quality of the material, based on the lignin:N ratio. Soil organic matter (SOM) turnover is affected by soil texture (T). The active fraction is composed of the metabolic SOM, the microbial SOM (biomass plus products), and the intermediate soil SOM. This structure is presently implemented in our simulation model.

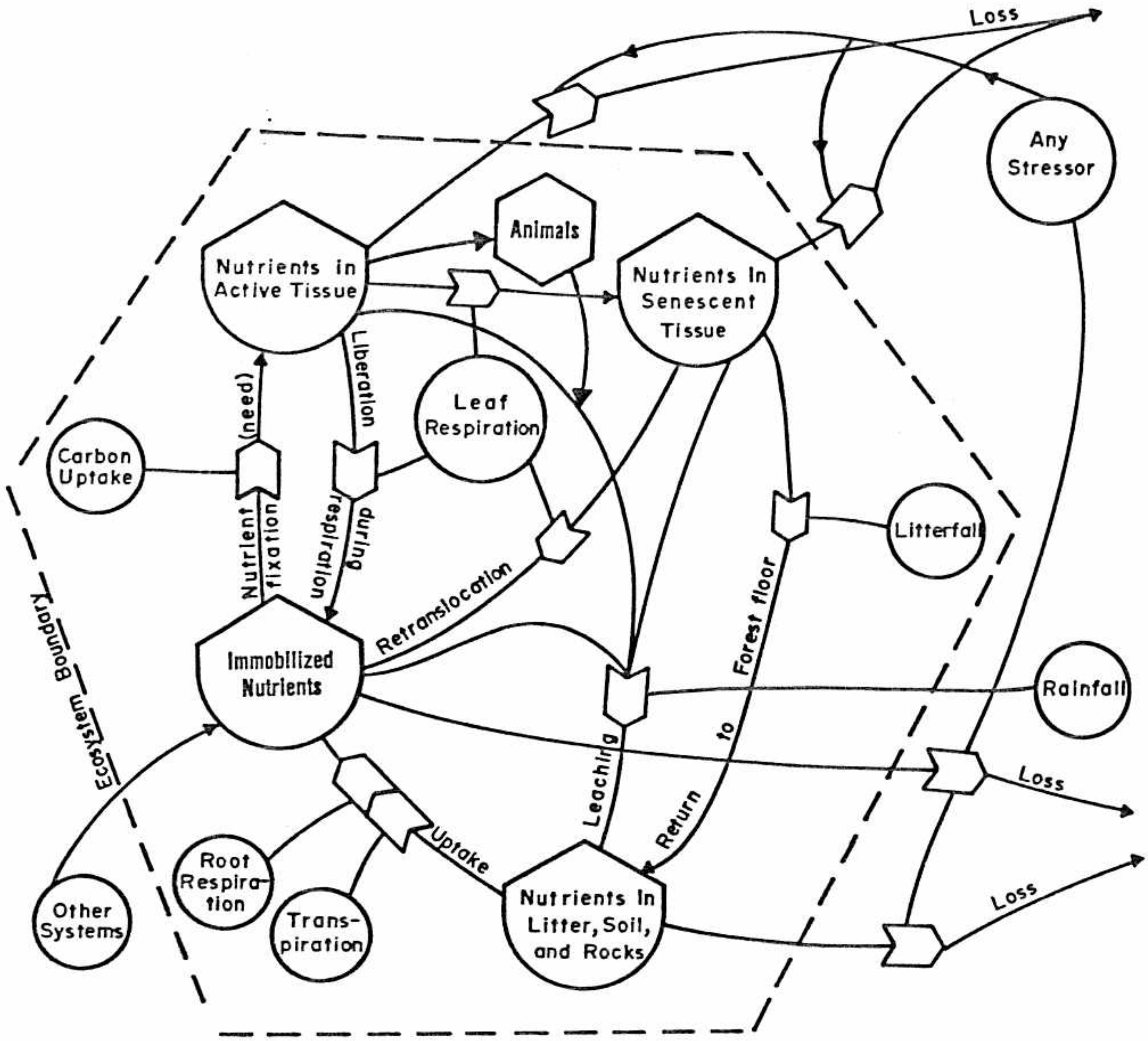

Figure 15. Model of nutrient cycles and nutrient use efficiency in tropical forests. The model shows four nested pathways of internal nutrient cycling (uptake and liberation during respiration, retranslocation, leaching, and nutrient return by litterfall) as well as inputs and exports to and from the forest ecosystem. Nutrient cycling pathways are either under biotic control (circles inside the ecosystem boundary) or abiotic control (circles outside the ecosystem boundary). Symbols are from Odum (1983).

In addition, the LEF LTER will also benefit from coordination with long-term programs already existing at CEER and the Institute of Tropical Forestry (ITF). These include cooperation with National Environmental Research Park sites and national laboratories through CEER's connection with DOE and participation in the Man and the Biosphere Program, the National Atmospheric Deposition Program, and the Tropical Soil Biology and Fertility Program.

III.A.4.c. LTER Network Synthesis - The LTER Coordinating Committee has proposed a series of activities for 1988-1991 that are designed to synthesize information over the entire LTER network. If our proposal is funded, we intend to participate fully in these activities. As a first step in this participation, we have organized a small workshop of LTER scientists for March, 1988, that will discuss the range of models in use across the LTER network and how to apply them to our site. This workshop will facilitate our entry into the network modeling initiative. We anticipate that we could make significant contributions to Coordinating Committee programs in climatic variability, atmospheric chemistry, productivity and its controls, and disturbance and dynamics of ecosystems soon after our acceptance as a LTER site.

We have planned for network-wide syntheses of results by adopting LTER protocols for data management and meteorological data collection, and by modeling our research design in gap dynamics and soil processes on widely-used protocols. We will continue to implement LTER protocols as they are developed.

III.A.5. Coordination with ongoing studies - The proposed LEF LTER program will expand on several ongoing studies in the LEF. Coordination among these studies and the proposed LTER work is discussed below.

Watershed dynamics - A study of watershed dynamics being conducted by the Institute of Tropical Forestry (ITF) provides the foundation for proposed LTER studies. The purpose of the watershed dynamics study is to determine the level of harvest that is possible without the loss of long-term site productivity. Three watersheds in the Bisley area of the LEF were selected for their representative forest structure, size (6-10 ha), and accessibility. Preliminary measurements (Table 2) have been completed at all three sites. A calibration phase will last for two years (1988-90) during which the climate, chemistry, biology, and hydrology of the three watersheds will be studied in detail. The overall objective is to develop equations and models that describe watershed response to specific events. All hydrological measures will be accompanied by chemical determinations including all major cations and anions. The Bisley watersheds will also be calibrated to the Sonadora watershed, where similar measures have been taken for four years.

In 1990, after two years of calibration, one of the two experimental watersheds (Bisley 1 and 2) will be selected for manipulation. Prior to any manipulation, ITF will conduct a workshop

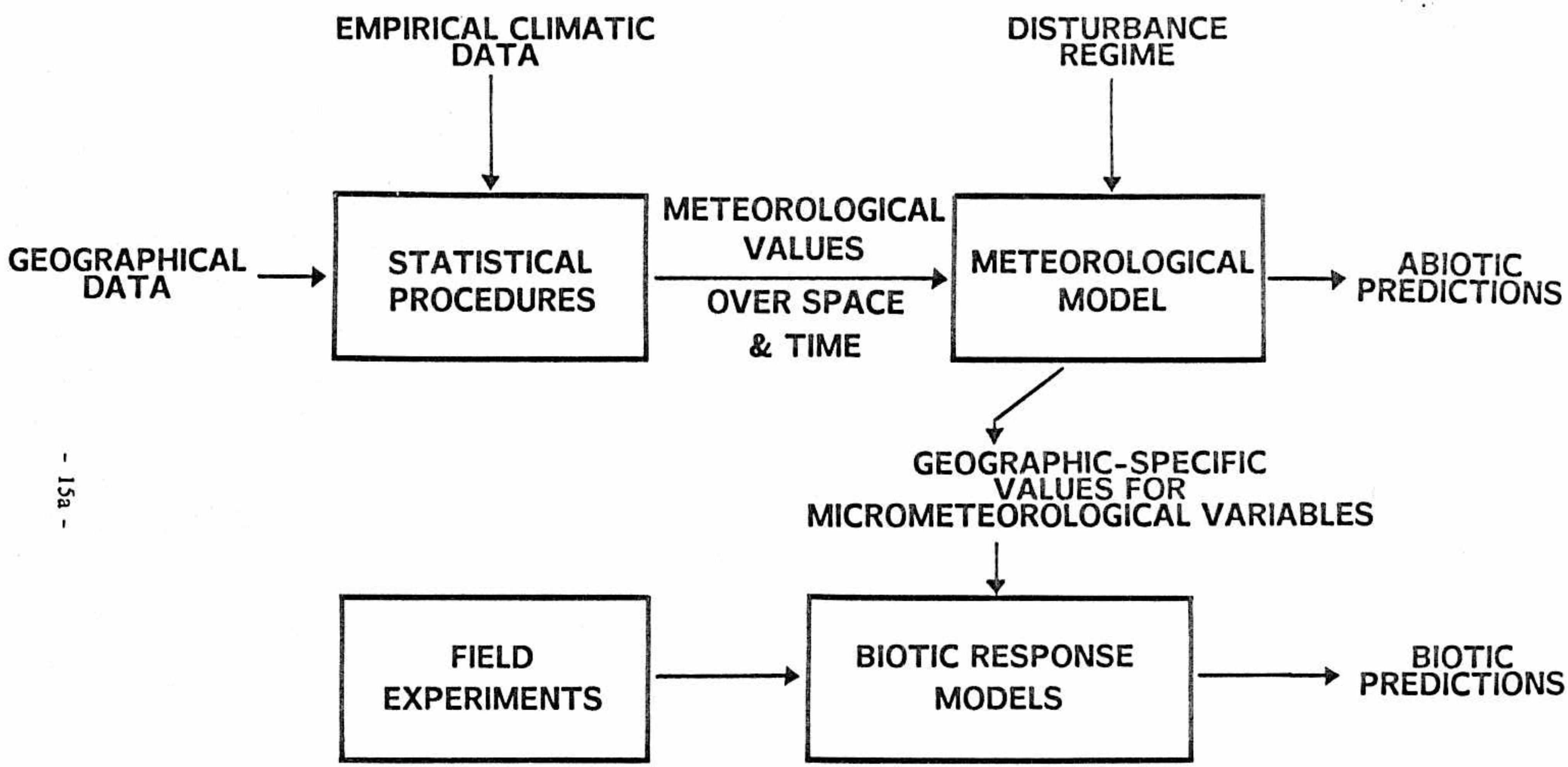

Figure 16. Overview of modeling integration.

Table 2. Scheduled measurements for proposed LEF LTER research program. Other measurements are discussed in the text. Where funding responsibility passes to NSF/LTER, the agencies involved are separated by a /. B = Bisley watersheds, S = Sonadora watershed, R = Rio Blanco watershed, DA = disturbed areas.

Measure	Initiation	Funding	Location	Frequency
Vegetation				
Total Plant Inventory	1987	ITF	B	Continuous
	1989	NSF	DA	Before and 6 mos after; then yearly
Plant tagging	1988	ITF/NSF	B	Continuous
Halle's profiles	1988	ITF	B	Once
Wood volume	1988	ITF/NSF	B	Yearly
Basal area	1988	ITF/NSF	B	Yearly
Biomass	1988	ITF/NSF	B	Yearly
Litterfall	1988	NSF	B + DA	Continuous
Litter decomposition	1988	NSF	B + DA	Once
Leaf area index	1989	NSF	B + DA	Yearly
Geomorphology				
Topography	1986	ITF+USGS	B, R	Once
Soil profile descriptions	1987	ITF+USGS	B, R	Once
Soil mapping	1987	ITF	B	Once
Soil chemical and physical characteristics	1988	ITF/NSF	B + DA	Once
Stream cross-section	1987	ITF	B	Yearly
Fauna				
Key species inventory	1988	UPR/NSF	B, S, DA	Yearly (wet and dry season)
Food web structure	1988	UPR/NSF	B, S, DA	Yearly
Disturbance				
Inventory of gaps and landslides	1988	ITF+UPR +USGS	B, S, R	Continuous Once by transects
	1989	NSF	Four life zones in LEF	yearly by satellite and aerial photos
Meteorology				
Rainfall	1987	ITF/NSF	B, S, DA	Continuous
Temperature	1987	ITF/NSF	3 stations	measurements
Humidity	1988	ITF/NSF	at different	with portable
Wind speed and direction	1988	ITF/NSF	elevations	Level 3 sta-
Light intensity	1988	NSF		tion on demand in DA
Hydrology				
Discharge (water level recorders in weirs)	1987	ITF	B, S	Continuous
Throughfall	1987	ITF/NSF	B, DA	Continuous
Stemflow	1988	ITF/NSF	B, DA	Continuous
Transpiration	1988	ITF/NSF	B, DA	Twice/yr
Evapotranspiration (by difference and gas exchange)	1988	ITF/NSF	B, DA	Twice/yr
Chemistry (major cations and anions)				
Soil solution	1988	UPR/NSF	B, S, DA	Weekly composites
Throughfall	1988	UPR/NSF	B, S, DA	Weekly composites
Stemflow	1988	UPR/NSF	B, S, DA	Weekly composites
Ground water	1988	UPR	B, S	Weekly
Stream water	1986	UPR	B, S	Weekly
Vegetation - leaves, stems, roots	1989	NSF	B, DA	Once
Litterfall	1989	NSF	B, DA	Continuous
Litter decomposition	1989	NSF	B, DA	Once
Root decomposition	1989	NSF	B, DA	Once

with expert silviculturists and ecologists to develop a prescription for the logging and regeneration of the site. The initial manipulation will extract wood products from the forest with the purpose of obtaining an economic return while maintaining long-term site productivity. We ask whether it is possible to achieve these two objectives simultaneously in high rainfall areas. If the manipulation is successful (i.e. the system returns quickly to its initial state), a second watershed will be manipulated using a higher intensity of disturbance to find out at what intensity of disturbance irreversible change occurs. If however, the first manipulation proves to be damaging to site long-term quality, the second watershed will be treated at a lower intensity of disturbance so that long-term productivity is protected. The economic gain of this second manipulation will then be evaluated.

Continuous measurements of biotic and abiotic phenomena will take place in both the control and two experimental watersheds as part of a monitoring program (Table 2). These data are critical for evaluating system response to disturbance, understanding the disturbance events, building long-term data bases for models and other synthesis techniques, and for evaluating experiments and hypotheses. Most measurements conducted in the survey and assessment phases will be repeated periodically as part of the monitoring phase of the study.

The watershed dynamics study is funded by the Institute of Tropical Forestry (ITF) and the University of Puerto Rico, and considerable baseline data (Table 2) have already been collected. Our proposed LEF LTER program is designed to complement and enhance the scientific benefits derived from the basic program. This will be accomplished in part by continuing a series of measurements that were begun by ITF and in part by initiating new studies. In order to separate funding responsibility clearly, we show in Table 2 the location and frequency of specific measurements and how these measurements will be funded.

Landslides - Landslide work will benefit from the collaboration of the U. S. Geological Survey (USGS) Water Resources Division currently conducting research with ITF and CEER on landslides. The objective of the USGS work is to estimate landslide potential for combinations of shear strength, moisture, and topographic conditions, to determine the importance of ground water seepage forces on the potential for slope failure, and to quantitatively assess magnitude and frequency of recent and past slides so that landslide-hazard predictions can be extended to similar sites. One of our sites (Rio Blanco) is also being used by USGS for their study, and measurements that they take on physical parameters will assist us in interpreting our data on regeneration.

Primary production - A subset of the research team (see Fig. 13) has submitted a proposal for $750K to study limits to primary production in tabonuco and dwarf forest under NSF's Minority Research Centers of Excellence Program. This proposal has two goals: 1) to encourage participation of minority students and faculty at the University of Puerto Rico in joint CEER-/ITF/UPR ecological studies, and 2) to develop a research program on the controls of primary productivity that will be a component of a future LTER renewal proposal. Should the MRCE proposal be funded, it will complement studies of primary productivity described below and will build on the already strong local research group.

Regeneration - Nora DeVoe, a graduate student in the Yale School of Forestry, is conducting an experiment on the requirements for establishment and growth of five key tree species in the tabonuco forest (Dacryodes excelsa, Manilkara bidentata, Sloanea berteriana, Didymopanax morototoni, and Cecropia peltata) in two 20x60 m clearings in the Sonadora watershed. The objective of this study is to determine the effects of light exposure on regeneration (germination, establishment and early growth). The hypotheses being tested are: 1) that exposure level will determine which species are regenerated where and 2) that light exposure will affect growth and dry matter production in a manner unique to each species. The experimental plots that have been established in Puerto Rico provide an opportunity for studies of regeneration of plants and recolonization of animals under different management conditions. Members of the LTER research team have begun studies of these phenomena in these plots.

III.B. Guiding questions about disturbance and recovery

Our efforts are guided by a series of questions about disturbance and recovery in forested ecosystems. Although not exhaustive, these questions reflect commonly formulated inquiries about disturbance properties in a variety of ecosystems (West et al. 1981, Picket and White 1985). We use the questions as a framework for specific hypotheses.

A. Concerning the disturbance regime in the LEF, we ask the following questions:
   1. What kinds of disturbances occur in the LEF?
   2. What is the distribution, size, and age-class frequency of these disturbances?
   3. What is the rotation period (mean time needed to disturb an area equal to the study area [White and Pickett 1985]) of the ecosystem due to each type of disturbance?
   4. What are the characteristic shapes of disturbed patches?
   5. How do the size, shape, and dispersion pattern of patches relate to recovery trends?

B. Concerning the environmental characteristics of disturbances in the tabonuco forest we ask: How do light, humidity, soil moisture, temperature, and soil nutrient levels vary with disturbance type, size, and age?

C. Concerning the biological properties of recovery from disturbances we ask: As a function of disturbance type, size, and age, how do the following vary?

1. Sources of plant recruitment (seed, advance regeneration, sprouts)
2. Plant species composition, diversity, and life history types including nutrient acquisition strategy.
3. Recruitment and stem density
4. Growth, biomass, and leaf area index
5. Growth efficiency (sensu Waring and Schlesinger 1985)
6. Animal species richness, community composition, population density
7. Structure and complexity of the food web

D. Concerning the system properties of recovery from disturbances we ask:

1. For which types and sizes of disturbance are there recognizable phases of recovery (Vitousek 1985), e.g., reorganization, aggrading, transition, steady state (sensu Bormann and Likens 1979a)?
2. Do rates of recovery vary as a function of disturbance type and size?
3. What proportion of the tabonuco forest is in each recovery phase? How do these proportions compare with those in tropical and extra-tropical continental forests?
4. What are alternative mechanisms of nutrient conservation under different disturbance regimes?
5. How do nutrient-use efficiencies change with time after disturbance?
6. What functional attributes of the forest correlate with disturbance regime?
7. What nutrient retention or export mechanisms occur in streams under different disturbance regimes?

These questions are addressed in the sections that follow using studies at levels of organization and complexity ranging from an examination of the whole LEF landscape and the investigation of whole ecosystems and ecosystem compartments to the study of plant and animal populations and ecophysiological processes.

III.C. The description of individual research components

III.C.1. Disturbance regime - (Brokaw, Foster, Swanson)

The disturbance regime of a landscape is characterized by the types of disturbances, their areal extent, severity (e.g., degree of soil removal), frequency, and geographic distribution (Heinselman 1973). Garwood et al. (1979) show that frequent, endogenous tree deaths have a shorter rotation period than large, infrequent, exogenous disturbances in many forests. However, some forests, particularly in the hurricane belt, have a higher frequency of large-scale disturbance (Foster 1988a). The island of Puerto Rico, for example, is subject to frequent hurricanes

(Wadsworth 1951; Fig. 17); they are frequent enough and affect sufficient area that their rotation interval may be the shortest, and their importance the greatest, of disturbances in the tabonuco forest. Moreover, frequent large disturbances may prevent substantial areas of the tabonuco forest from maturing to the point when gap dynamics, driven by episodic death of large trees, becomes an important process (Bormann and Likens 1979a).

Abiotic (topographic, pedologic) and biotic (vegetation composition, structure) factors mediate the relative importance and effects of disturbances, so that the severity of forest damage can be predicted from knowledge of abiotic and biotic characteristics of the ecosystem. Within this framework we address two hypotheses concerning temporal and spatial aspects of disturbance:

H.1: In the LEF broad-scale disturbance by hurricanes is the dominant factor in the disturbance regime, thereby minimizing the importance of smaller scale disturbances, such as gaps and landslides.

H.2: The disturbance regime varies substantially across the LEF in response to controls of topography (slope steepness, aspect, position), geology (geotechnical properties of soil and rock), and vegetation (structure, composition).

Approach - The first step in addressing these hypotheses is to characterize the disturbance regime of the LEF landscape. This will be accomplished by analysis of aerial photographs (1936, 1954, 1964, 1983, 1985, 1987) , long-term plot data (e.g., Wadsworth 1950, Weaver 1986), written records, and retrospective field studies (e.g., as developed for other ecosystems, Foster [1988a and b] for hurricanes, Brokaw [1985] for gaps, Swanson and Dyrness [1975] for landslides, Raup and Carlson [1941] for land-use history). The landslide, hurricane, land-use history, and gap inventory will cover the entire LEF; in addition data on new hurricane damage and gaps will be recorded for study sites distributed across the LEF with specific concentration in the Sonadora and Bisley watersheds. The frequency, size class distribution, and spatial distribution of disturbance due to treefalls will be determined by annual ground surveys of newly created gaps. Censuses of new gaps will be made throughout the five watersheds under study in tabonuco forest. Elsewhere, surveys will follow transects selected to characterize gap formation in the range of topography in tabonuco, colorado, dwarf, and palm forests. We will also investigate the possibility of assessing gap creation from aerial photographs made in 1983, 1985, 1986, and 1987 (cf. Sanford et al. 1986), from records of the long-term ITF and CEER plots, and from historical reconstruction based on presently occurring patches of Cecropia peltata, a pioneer tree species that is common in the tabonuco forest and that is an obligate gap species (Silander 1979, Perez Viera 1986). These raw data characterizing the disturbance regime will be compiled in the GIS as actual map overlays of specific disturbances and measures of stand disturbance for hurricanes and gaps (e.g., areal turnover rate for gaps and percent of area reset by hurricane).

By examining the relations among disturbances and site characteristics, such as geology, topography, vegetation, and hydrology, we will seek to determine causes of the apparent pattern of the disturbance regime. Using the GIS and these interpretations of site influences on disturbance, maps will be derived to show the sensitivity of landscape units (pixels or landform elements defined in terms of slope steepness, aspect, or elevation classes) to disturbance. The disturbance regime of a site on the landscape can then be approximated as the composite of the regimes of all significant disturbance types. To our knowledge this multi-type characterization of the disturbance regime of a landscape has not been attempted before.

To test H.1 we consider that disturbance intensity is regulated in part by the stage of vegetation development (e.g., root strength influence on landslide potential, stand structure influences on gap and hurricane blowdown potential; Fig. 18). If stands are reset by direct hits from hurricanes at a frequency of 80 years (a reasonable estimate for the LEF; see Fig. 17), gaps play a only minor role in forest disturbance (40% of the area is reset by gaps whereas 60% is reset by hurricanes). In contrast, if stands are reset by hurricanes less frequently, say every 400 yrs, gap formation dominates forest dynamics. In the hypothetical scenario of Fig. 18, gaps turn over 340% of the landscape whereas hurricanes reset only 60% of the area.

We expect that geography is an important regulator of disturbance at LEF (H.2) because of the high relief, the variety of hillslope aspects, the resulting strong orographic effects of landforms, varied geologic conditions, and the rather consistent direction of hurricane winds. Information on disturbance occurrence (maps of location, age, size, shape) will be integrated into a geographical information system (GIS) currently being prepared for the LEF by NASA's National Space Technology Laboratories. The GIS data set will include topography, soils, vegetation, geology and land-use information in digital form. This data base will be converted into a form compatible with the Map Analysis Package (MAP; Tomlin 1983), which is an IBM-XT system that will be available for use by all LEF LTER participants. MAP can be used to generate maps of attributes such as topographic slope and aspect, watersheds, wind shadows, and the distance nearest to selected site features. Associations among disturbance type, forest attributes, landform features, and site physical characteristics will be tested using associated statistical programs integrated into MAP (SYSTAT, DECORANA, TWINSPAN, EMSTAT).

We see many opportunities to apply the algorithms for mapping disturbance regime developed at LEF to other sites, including Andrews LTER where wildfire, rather than hurricanes, is the dominant large-scale disturbance, and to other sites in temperate forests (e.g., Harvard Forest, central Massachusetts; Foster 1988a and b, 1988 unpubl.; Tionesta Forest, Pennsylvania; Pickett and Foster unpubl.). For our study of gaps, the definition of gaps and the protocol for sampling gaps developed at workshops at the Harvard Forest in 1986 (Franklin et al. in prep.) and Andrews Forest in 1987 (Runkle et al., in prep.) will be used to facilitate comparisons with studies of gap dynamics in both temperate (Andrews LTER, Harvard Forest, North Carolina Piedmont, Great

Smoky Mountains, Hubbard Brook LTER) and tropical (Barro Colorado, Panama; La Selva, Costa Rica) ecosystems.

The analysis of disturbances that occur with low frequency is generally possible only in retrospective studies. The LEF LTER program would provide an opportunity for predictive studies of disturbance based on the information generated in the studies described above, especially for broad scale processes, such as hurricanes. Predictions from such models can be used to refine our understanding of the effects of biotic and abiotic factors on hurricane damage.

A simulation model of hurricane damage has been developed for the Harvard Forest using the MAP GIS and will be implemented for the LEF. In brief, the model involves the assignment of damage probabilities to each cell cartographic point. The probabilities are calculated as the product of site susceptibility (defined by factors such as aspect, slope, elevation, and soils) and vegetation susceptibility (a function of vegetation composition and structure). Damage from storms of different intensities and directions can be predicted from the model. The model can be refined by comparing predictions against 1) historical records and 2) observations of damage from future storms. Aerial photography, taken annually, and permanent plots will be used to ensure pre- and post-disturbance records. Immediately after future storms we will use aerial photographs to locate and document areas of damage, such as blowdown areas and landslides, for future ground-based studies as described below.

III.C.2. Recovery after disturbance

III.C.2.a. Environmental properties - (Lawrence, Fetcher)

Quantifying the changes in environmental parameters that occur after disturbance is a vital precursor to understanding the mechanism of regeneration (Bazzaz 1979). Data on light availability, soil moisture, and soil nutrient levels in tropical forest disturbances have been collected by Denslow (1980), Uhl et al. (1982), Chazdon and Fetcher (1984), Perez Viera (1986), and Vitousek and Denslow (1987).

A comprehensive data base on general climate and gap environments in tabonuco forest exists as a legacy of the Rain Forest Irradiation Project (Odum and Pigeon 1970). Hourly, daily, and monthly records of insolation, illumination, temperature, humidity, rainfall, wind, evaporation, and carbon dioxide levels are available for the period 1963-1966 (Odum et al. 1970). Comparisons of gap and understory records for these parameters are also available for the period of gap formation at the radiation site (Smith 1970). Vertical profiles of environmental variables within tabonuco forest were also determined by Odum et al. (1970).

Given the detailed records of environmental conditions that exist for the tabonuco forest, we propose that further measurements be directed to evaluating specific hypotheses on a request basis. We will conduct these measurements with a portable Level 3 meteorological station

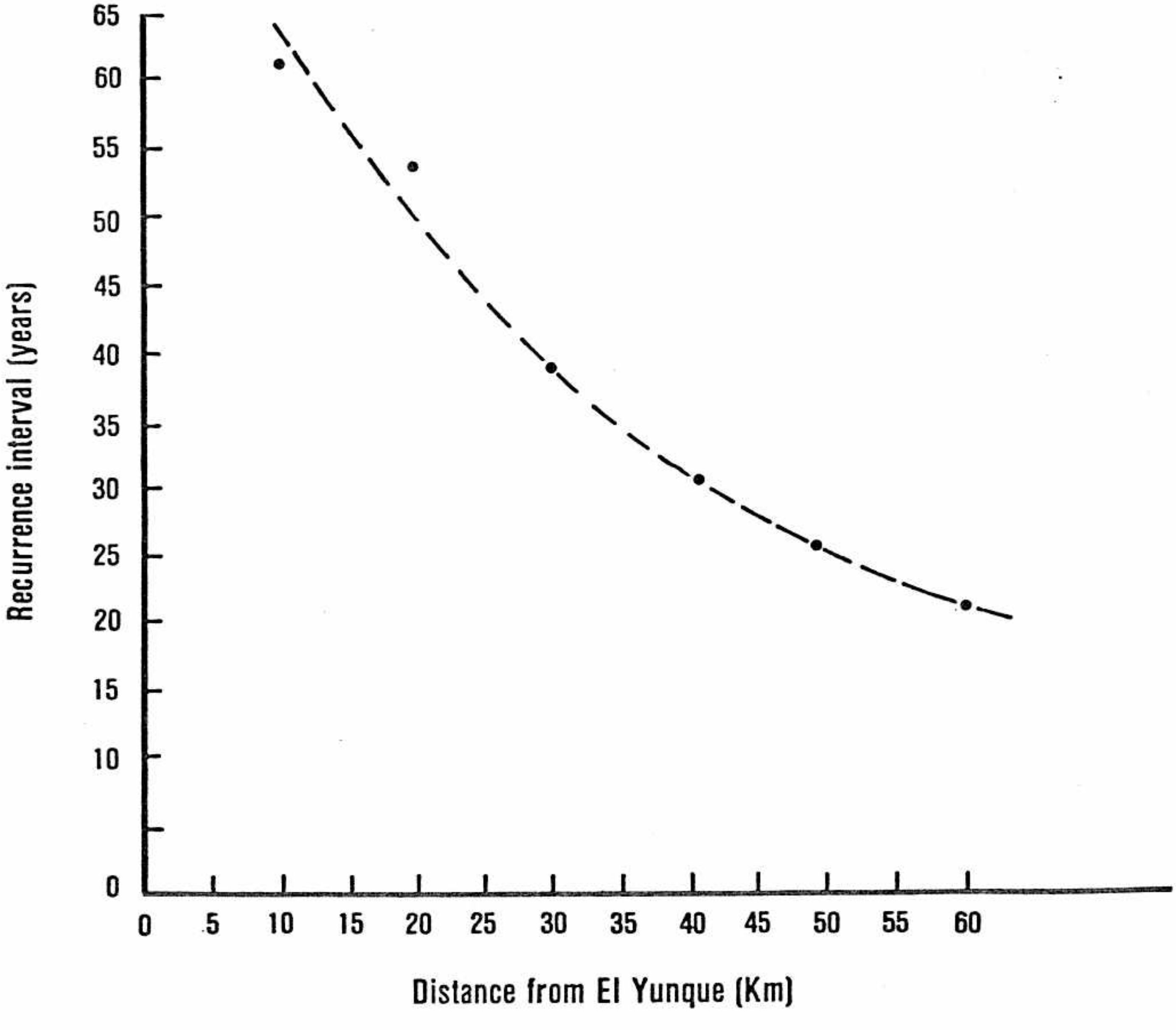

Figure 17. Estimated recurrence interval of type A (severe) hurricanes passing within a given distance from the center of the LEF. The figure is based on trajectories of type A hurricanes from 1700 to 1970 (Weaver 1986).

(Greenland 1986). This portable instrument will be dedicated to the comparison of the environmental regime of undisturbed forest and nearby disturbed sites. This instrument package will allow us to examine the relationships among terrain, disturbance type and size, and environmental conditions (especially light) for a variety of different slope and aspect conditions. Long-term meteorological data will be recorded by three permanent Level 2 stations at different elevations (in the Bisley, Sonadora, and Rio Blanco watersheds) and by existing stations.

III.C.2.b. Nutrient storage - (Asbury, Lugo, Parton, Scatena)

Nutrients stored in the vegetation of the various disturbed areas serve as an index to rate of nutrient recovery and give an indication of mechanisms for nutrient conservation. We propose to conduct an initial inventory of above- and belowground C, N, and P for the various disturbed areas and in the surrounding undisturbed vegetation. Chemical analyses will be performed on leaves, small and large woody material, live and dead roots, and litter in the Bisley watersheds. Allometric computations will be made to estimate total nutrients stored in the vegetation of the study area. A total nutrient budget will be estimated by the inclusion of soil analyses.

Soil analyses will be performed by Dr. Art Johnson of the University of Pennsylvania. Dr. Johnson has performed similar analyses in the manipulated watershed at Hubbard Brook Experimental Forest (HBEF), and his work will provide an immediate comparison of pre- and post-harvest soil nutrient capital in temperate and tropical LTER sites. The three objectives of this comparative study are 1) to compare the effectiveness of plant regrowth as a mechanism for retaining nutrients on harvested sites at LEF and HBEF, 2) to compare the response of cation exchange capacity to disturbance at LEF and HBEF, and 3) to determine how spatial variability in soil drainage, morphology, and nutrient pools (C, N, exchangeable bases, pH) on the watersheds at LEF compares to the spatial variability observed at HBEF. Support for this project comes from a separate grant to Dr. Johnson.

III.C.2.c. Soil organic matter formation - (Parton, Berish)

Soil nutrient levels at the start of recovery will depend on the extent of soil removal or deposition by the disturbance and the labile organic matter remaining or transported on-site that is liable to decomposition. The impact on post-disturbance soil nutrient levels can be ranked from high to low in the following classes of disturbance severity: landslides, harvest, hurricanes, and tree falls. The impact of these disturbances can vary considerably, once again depending on their scale. During recovery, soil nutrients will increase slowly in landslides, but increase and then decrease in clear-cut and hurricane-disturbed areas (cf. Bormann and Likens 1979a). Tree falls may not produce a local nutrient pulse (Vitousek and Denslow 1987, Uhl in MS). One of the critical factors in understanding fluctuations of soil nutrients after disturbance is a comprehension of the dynamics of soil organic matter.

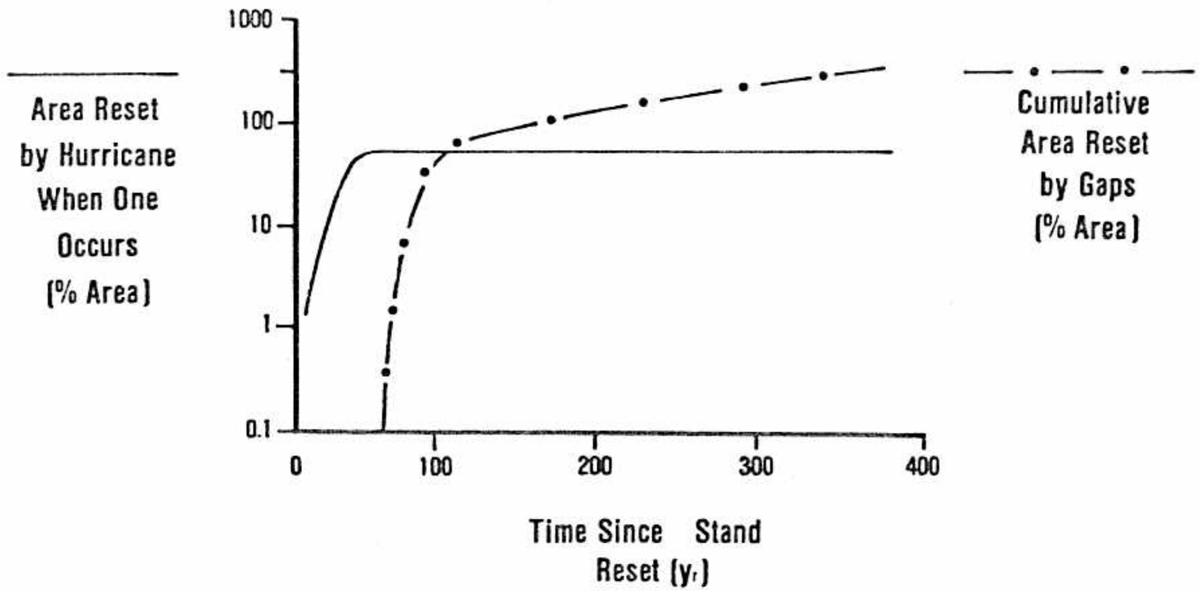

Figure 18. Area reset by hurricanes and small gap formation, assuming 1) small gap formation processes affect 1% of area per year after the stand reaches the age of 60 yrs, and 2) a hurricane making a direct hit on the LEF would reset 60% of the area in forest older than 60 yrs of age.

H.3: Recovery of soil organic matter (SOM) is controlled by soil organic P, soil properties (i. e. clay content), and carbon input.

Soil organic matter is a key constituent of terrestrial ecosystems. It is both a reserve of, and a source for, plant-available nutrients. By acting as a "big, slow" nutrient buffer, it plays an important role in ecosystem response to disturbance and reflects past productivity and disturbance regime. Neither the factors that result in variation in SOM levels from site to site, nor those that control losses and recovery following perturbations are well known (Lugo et al. 1986). Factors that govern attainment of "steady state" levels and those that govern response to disturbance are not independent (Vitousek and Melillo 1979; Schimel et al. 1985) and must be related to concepts of nutrient cycling.

The soils of the LEF are frequently perturbed by disturbances occurring at several frequencies and scales. Establishing the rates at which soil organic C, N, and P accumulate is a key question. Fig. 19 shows a hypothetical time series of soil organic C and P, as they accumulate and are lost due to disturbance. The actual rates of recovery and loss are not known, but the rate of recovery for organic C is hypothesized to be higher than the recovery rate for organic P. This low recovery rate for P occurs because P, once mineralized, is converted to unavailable mineral forms and can only very slowly be converted back to organic forms. The rate at which the system can recover organic matter and organically-bound nutrients relative to the frequency of disturbance should be a major determinant of a long-term system trajectory.

Jenny (1941) and others have suggested that the major factors that control SOM dynamics include climate (temperature and water), parent material (soil texture, base status, total sulphur, and phosphorus), topography, plant production, and site history. Recent modeling work by Parton et al. (1987) and Pastor and Post (1986) shows that regional patterns of plant production and soil organic matter can be simulated for temperate grasslands and forests in the U.S. using models where the major driving factors are climate, soil texture, plant lignin content, and land use history. We are using the conceptual SOM model developed by Parton et al. (1987) to help formulate our SOM research plan (see Fig. 14). The flow diagram shows that SOM is divided into three fractions: 1) an active fraction consisting of live microbes and microbial products with a short turnover time (< 1 to 5 years), 2) a slow SOM pool that is physically protected or biologically resistant to decomposition, with an intermediate turnover time (20 to 50 years), and 3) a slow SOM pool that is chemically recalcitrant or physically protected with a long turnover time (200 to 2000 years). The major factors that control the model include climatic decomposition parameters, lignin content of the vegetation, and soil texture.

We have proposed a series of experiments that will test the major hypotheses that are embodied in the SOM model. Specifically, we propose to evaluate the effect of litter quality, source (root vs. leaf litter), and soil texture on SOM formation. Data from these experiments should be sufficient to quantify the SOM model and test its ability to simulate SOM dynamics in tropical soils. Root and leaf litter decomposition data will also be collected and used for the modeling work. Four operational hypotheses have been proposed to organize the SOM experiments.

H.4: The stabilization of C, N, and P in soil organic matter will increase as the clay content of the soil increases.

This hypothesis reflects data on SOM from second growth forests and pasture in Puerto Rico (Lugo et al. 1986) that show that soil C levels increased more rapidly in secondary growth forest that had higher soil clay content. Their data are consistent with data from grassland soils in the South Central part of the U.S. where the soil C levels were positively correlated to the soil clay content (Nichols 1984). The hypothesis will be tested by comparing the rate at which SOM is formed in parent material that has a high clay content and a low clay content. We will place high (soil from the C horizon) and low (obtained from another site on the island) clay soil into 1 m^2 plots at the Bisley site where the top 20 cm of soil has been removed. The plots will be placed near tabonuco trees and the leaf litter from the tabonuco trees will be added to the plots at a annual rate that is equal to the typical leaf litter fall rate (500 $g\text{-}m^{-2}$; Zucca et al. in prep.). Natural litter fall will be excluded from the plots by using screens that will be cleaned on a two week basis. Changes in total soil C and N, organic N mineralization rates, and microbial biomass C and N will be monitored twice a year. Soil development will result from the addition of the controlled amount of leaf litter and roots that grow into the soil.

H.5: Belowground soil C inputs (i.e., roots) make a larger contribution to SOM formation than do aboveground C sources, and SOM formation will increase as the C input from plant material increases.

Long-term site productivity is directly coupled to SOM which is maintained from both litterfall and root turnover. Results from many grassland, shrub and forest ecosystems suggest that processes associated with roots constitute 40-80% of net primary production (Parton et al. 1978, Schubauer and Hopkinson 1984, Morris et al. 1984, Fogel 1985). In general, then, root turnover contributes as much, or more, C, N, and possibly cations to forest soil as does aboveground litterfall throughout a number of ecosystems (Vogt et al. 1986). We will test the relative importance of root inputs by comparing SOM development in 1 m^2 plots (see previous paragraph) where roots are allowed to invade and differing amounts of leaf litter are applied to the soil surface (0, 500, 1000 $g\text{-}m^{-2}$) annually. The plots will be established near tabonuco trees, and tabonuco leaf litter will be applied annually. The plots will be maintained and monitored in a similar manner as are the other soil development plots. The changes in SOM, C, N, and P with time will allow us to determine the relative role of root vs. leaf litter on SOM formation and the impact of different leaf litter application rates on SOM formation.

H.6: The amount of SOM in tabonuco forest will temporarily increase following a disturbance such as a hurricane or harvest because of the decay of dead roots.

The influence of different types of disturbance and time since disturbance on SOM formation will be determined by monitoring changes in soil organic C, N, and P with time for different types of disturbances (e.g., hurricanes, landslides and treefalls). The different disturbance sites will be selected from sites identified in a recent survey of disturbance sites in the Bisley and Sonadora watersheds (see III.C.1.) and will be sampled at two year intervals following the identification of the sites. Soil samples from each of the identified disturbed areas will be analyzed for total C, N, and P, C and N mineralization potential, and P fractionation for various labile and stable P pools (Tiessen et al., 1984). Analysis for soil physical (e.g., bulk density, waterholding capacity, and texture) and chemical properties (e.g., exchangeable cation, exchange capacity, base saturation, pH, point of zero net change, and P absorption) will be conducted.

H.7: Decomposition rates of plant material will decrease as the lignin:nitrogen ratio of plant material increases, while the stabilization of C, N and P in soil organic matter will be higher for soil where the lignin:nitrogen ratio of the plant material is higher.

The lignin to nitrogen ratio (L:N) affects both the rate of litter decomposition and the amount of soil C, N, and P stabilized. Plant material with high L:N ratios tend to decompose more slowly (Melillo et al. 1984, Parton et al. 1987). The effect of the L:N ratio will be determined by adding leaf litter from Dacryodes (high L:N ratios) and Cecropia (low L:N ratio) to 1 m^2 soil plots where the soil has been removed to the 20 cm depth and replaced with B horizon soil from the Bisley site. Controlled amounts of leaf litter (300 $g\text{-}m^{-2}$) will be added to the plots and root growth will be excluded by running a machete around the plots on a monthly basis (approach used by Dr. Buck Sanford in La Selva, Costa Rica). Screens will be used to exclude plant litter from surrounding trees and the plots will be maintained and monitored in a similar way as the soil texture plots (see previous paragraph). We will monitor changes in soil C, N, and organic P using the same approach used for the soil texture experiments and thus be able to determine the impact of litter quality on organic matter stabilization in the soil. The effect of litter quality on decomposition rate will be determined by litter bag experiments for five different litter types (see below).

III.C.2.d. Litter breakdown - (Berish, Covich, Walker)

In order to determine rates of nutrient input into the soil, we propose to conduct a decomposition study. The study will investigate the role of litter quality and soil moisture (e.g., distance from stream course) on nutrient inputs into the tabonuco forest at Bisley before and after harvest. We propose as a working hypothesis:

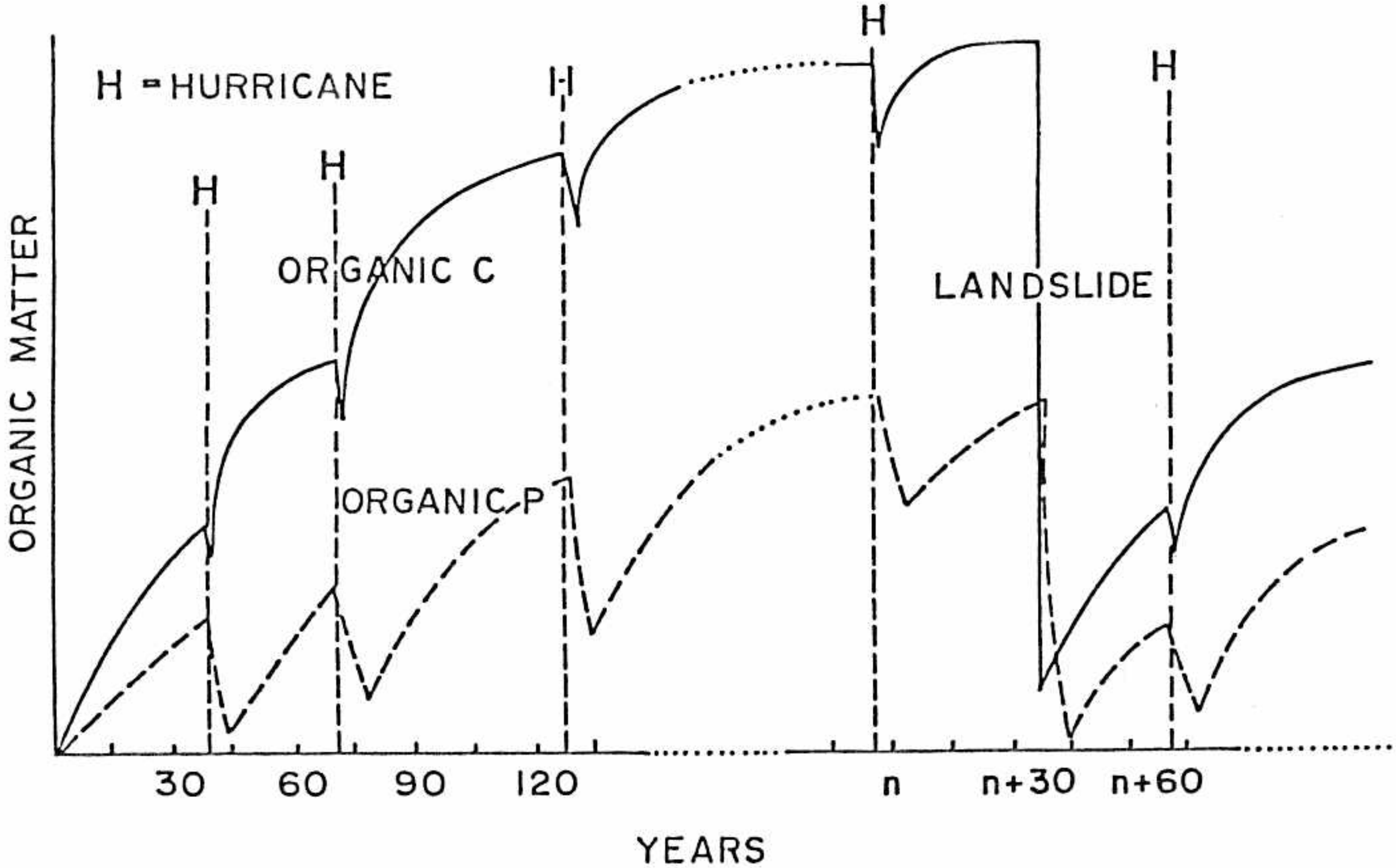

Figure 19. Hypothetical time series of soil organic C and P as they accumulate and are lost due to disturbance.

H.8: Rates of leaf decomposition will decrease as distance from stream increases; after a severe disturbance (harvest) absolute rates of decomposition will decrease throughout the terrestrial-aquatic interface.

Approach - Litter decomposition will be measured along a gradient of moisture from within streams through the stream boundary and into adjacent forest at Bisley 1 and 3. Leaf and fine root material from D. excelsa, Prestoea montana, Cecropia peltata, Manilkara bidentata, and Buchenavia capitata will be put into large-meshed leaf (Zucca et al. in prep.) or soil-inoculated root litter (Harker and Berish in prep.) bags. In the streams, both large- and small-meshed bags will be used to determine the role of stream invertebrate shredders and scrapers in processing leaf litter (Webster et al. 1983, 1987; Webster and Benfield 1986; Fisher 1987; Wallace 1987). The importance of leaf detrital breakdown products as a resource base for aquatic food webs is well established for temperate zone watersheds, but only a few studies (e.g., Bishop 1973, Stout 1980) have focused on these dynamics in tropical streams, and only one previous study (Padgett 1976) has been done in Puerto Rico.

Five samples will be collected at increasing intervals (Berish and Harker in prep.; Zucca et al. in prep.). We will measure mean mass loss and changes in N, P, Ca, K, Mg and lignin contents. Litter invertebrates will be extracted from the terrestrial samples and identified for food web studies (see Section III.C.2.f). Results of these decomposition studies will be comparable with those now being obtained at other LTER sites, especially where comparable streams are located (e.g., Andrews and Coweeta, see Table 3).

Data on wood decomposition are being collected by Ariel Lugo in long-term plots of the U. S. Forest Service. Measurements include changes in wood density and chemical composition of logs of known age (1-40 yrs old). This information will be used to plan cooperative experiments with the H. J. Andrews LTER program.

III.C.2.e. Gap revegetation

Revegetation after disturbance alters abiotic and biotic variables with the amplitude and direction of change strongly dependent on the severity and scale of the initial disturbance. Disturbance within the LEF can be categorized along a continuum of area from small to large gaps, and along a continuum of severity from tree falls to hurricanes and landslides. Within a matrix of these disturbance categories, we hypothesize that the post-disturbance abiotic and biotic components of the ecosystem will change in predictable ways. We have conceptualized these changes along a temporal gradient in Figure 20, which represents our best estimate of the effect of initial disturbance on selected variables and their subsequent behavior during recovery. Our basic operating hypothesis is:

H.9: Disturbances of forests create temporal gradients of resource availability (e.g., light, nutrients, and water). These gradients favor a succession of plant species, each adapted to exploit a particular range of resource concentrations, along the gradient (Tilman 1982).

Table 3. Comparison of stream sites at LTER locations and the Luquillo Experimental Forest[1]

PARAMETER	NORTH INLET	COWEETA	LAKES	HUBBARD BROOK	H J ANDREWS	LUQUILLO
LOCATION	South Carolina	North Carolina	Wisconsin	New Hampshire	Oregon	Puerto Rico
BIOME	Coastal Marine	Southern Decidiuous Forest	Mixed Conifer-Deciduous Forest	Northern Hardwood Forest	Coniferous Forest	Tropical Rain Forest
LATITUDE	33° 30'N	35° N	46° N	43° 60' N	44° 14' N	19° 19' N
LONGITUDE	79_{o} 13' W	83o 30' W	89° 40' W	71° 40' W	122° 11'W	69° 49' W
ELEVATION	Sea Level to 4m	679 to 1592m	500m	200 to 1015m	445 to 1620m	100 to 1075m
AREA	7082ha	2185ha		3300ha	6400ha	11,330ha
CLIMATE	Maritime	Maritime	Continental	Humid Continental	Maritime	Tropical
AIR TEMPERATURE	-4 to 36°C	13 to 21°C	-6 to 26°C	-12 to 20°C	2 to 20°C	18 to 29°C
STREAM TYPE	Intermittent Blackwater	Perennial Clear	Lake Outlet and Perennial Clear and Blackwater	Perennial Clear	Perennial Clear	Perennial Clear
STREAM ORDER	1	1 to 5	1 to 3	1 to 5	1 to 5	1 to 4
CHANNEL SLOPE	< 1%	15 to 30%	5 to 10%	5 to 30%	30 to 45%	20 to 45%
RIPARIAN VEGETATION	Pine, Cypress, Water Oak Sweet Gum	Oak, Hickory, Poplar	Pine, Aspen, Birch	Beech, Sugar Maple, Yellow Birch, Hemlock	Douglas Fir, Hemlock, Alder, Maple	Tabonuco, Sierra Palm, Palo Colorado
FLOW RATE (1/sec)	0 to 278	3 to 20	963 to 3313	0 to 3000	20 to 3600	10 to 14100
ANNUAL PEAK DISCHARGE	Sept-Jan	Mar-May	Apr-May	Mar-May	Nov-Feb	May-Oct
PARENT ROCK	Sand	Granite, Gneiss, Schist	Glacial Till Over Granite	Gneiss, Schist, Granite	Volcanic	Volcanic, Limestone
STREAM SUBSTRATUM	Sand and Humic Organics	Boulder, Cobble, Gravel, Sand	Gravel, Sand, Peat	Boulder, Cobble, Gravel, Sand	Boulders, Cobble	Boulders, Cobble, Gravel, Sand
ALKALINITY (mg/l $CaCO_3$)	10 to 120		25 to 47		14	
pH	6.5 to 7.5	6.6 to 6.7	6.7 to 7.7	4.9	6.4 to 7.4	6.8 to 8.6
NO_3-N (ug/l)	6.6	3 to 4	3 to 20	390	6	18 to 220
NH_4-N (ug/l)	90	4	1 to 38	21		1 to 32
PO_4-P (ug/l)	39	2	2 to 9	1.9	42	<2
Ca (mg/l)		0.5 to 0.6		1.3	3.2	0.7 to 4.3
Mg (mg/l)		0.3	2.3 to 3.5	0.3	0.8	0.6 to 2.2
Na (mg/1)		0.7 to 0.9		0.8	1.9	2.0 to 7.1
K (mg/l)		0.3 to 0.5	0.5 to 0.8	0.2	0.3	0.1 to 0.4
SO_4-S (mg/l)		0.4 to 0.3	2.6 to 4.4	2.0		1.5 to 4.0
Cl (mg/l)		0.5	0.3 to 1.3	0.5		3.3 to 9.3
DOC (mg/l)	10 to 40	<1.5		2.0	2.3	0.8 to 10.9

[1]Data compiled for LTER sites from a variety of published and unpublished sources by C.M. Tate, Kansas State Univ. Chemical data for Luquillo refer to Quebrada Sonadora as compiled by the Center for Energy and Environment Research. Note that several LTER sites have streams similar to the Sonadora except for discharge, which is much higher in Puerto Rican and tropical streams in general.

Specifically, we expect light to be the major factor controlling revegetation in tree falls and other small gaps whereas nutrients, water, and mycorrhizal inoculum control revegetation in large gaps or landslides. The nine specific hypotheses below address the biotic response to disturbance at organismal, population, and community levels.

Organismal level

1. Roots (Fig. 20-A; Berish)

H.10: In a severely disturbed environment, fine root growth is opportunistic, responding to optimum soil moisture and temperature. In a less severely disturbed mature forest, fine root growth is relatively constant, less responsive to environmental changes, and more fixed in proportion to above ground growth.

Root growth, as measured by seasonal changes in fine live and dead root mass, is modified by a complex interaction of the shoot and root environment. However, root growth is strongly affected by environmental conditions of soil temperature and moisture (Larson and Palashev 1973; Kaufmann 1977; Teskey and Hinckley 1981; Tryon and Chapin 1983). Below 17°C, root growth for some species in warm temperate environments is primarily controlled by temperature, but at higher temperatures may be more related to soil water potential (Teskey and Hinckley 1981). Many studies have found a modal pattern of root growth with a peak occurring early in the growing season (Lyr and Hoffman 1967, Ovington and Murray 1968, Roberts 1976, Ford and Deans 1977), whereas others have reported a bimodal pattern, with both early and late growing season peaks (Edwards and Harris 1977). These data suggest that fine root growth is opportunistic: root growth is rapid with favorable soil moisture and temperature conditions.

To date, most belowground root production estimates have been based on incremental changes in fine root live and dead standing stocks (Edwards and Harris 1977, Santantonio et al. 1977, Grier et al. 1981, Keyes and Grier 1981, McClaugherty et al. 1982). Estimates of root production based on sequential core sampling can have large error terms (Singh et al. 1984), and harvest methods cannot account for root turnover between sampling dates.

Approach - We will examine root demography, production, and decomposition (see above) for a mature forest and for an associated harvested site utilizing a combination of the root harvest method and direct observation from a mini-rhizotron (Huck and Taylor 1982, Atkinson 1985, Carpenter et al. 1985). These studies are closely coordinated with those on root decomposition described above.

Rhizotron study - The rhizotron will be used to investigate the synchrony of root growth, soil nutrient availability, soil moisture, and temperature. We will endeavor to develop predictive relationships between root growth as measured on rhizotron plates, soil coring, and soil environmental conditions.

Six rhizotrons will be constructed on the mature forest sites at Bisley and used to establish baseline conditions before forest felling operations. After developing a baseline of data during year 1, the forest around the rhizotrons will be selectively harvested (discussed above) and root dynamics behind rhizotron plates followed for subsequent years.

Root mass from soil cores - We will determine fine (< 2 mm) root live and dead mass by sequential root coring, using a 5 cm diameter stainless steel corer. We will determine the core sampling schedule according to changes in root growth as observed in the rhizotrons. Root mass data from our sequential coring will represent the second tier in our determination of root production, combining coring and rhizotron measurements.

Coarse root mass - Coarse (> 2 mm) root live and dead mass will be measured by the soil monolith technique (Bohm 1979) during the second year. We will excavate pits on the downhill side of each plot and collect all roots > 2 mm diameter.

2. Nutrients, light, and water. (Fig. 20-D-G; Haines, Fetcher, Lawrence, Lodge, Walker).

H.11: Low nutrients limit plant growth after severe disturbances that remove soil. Low light levels limit plant carbon gain and subsequent growth in less severe disturbances such as tree fall gaps, whereas high light environments reduce carbon fixation by inhibiting foliar photosynthetic processes.

Disturbance severity determines the manner in which resources such as nutrients, light, and water are altered. Nutrient availability generally increases due to mineralization following disturbances that do not remove the soil (Bormann and Likens 1979a, Matson and Vitousek 1981) such as tree fall gaps (but see Vitousek and Denslow 1986) or harvesting. Less is known about nutrient availability and mycorrhizal colonization (Garwood et al. 1979) following landslides that involve partial or total soil removal (Miles and Swanson 1986). However, low nutrient availability is characteristic of other severely disturbed areas such as floodplains (Van Cleve et al. 1971, Walker 1985), glacial moraines (Crocker and Major 1955), or volcanic substrates (Vitousek et al. 1987).

In low light environments such as tree fall gaps, plant growth is linearly related to integrated total available light (Chazdon 1986, Fetcher 1986, Fetcher in prep.). Above a certain level, photosynthesis is saturated and further increments in availability of light will not result in increased growth (Fetcher et al. 1983, Fetcher et al. 1987). In very open environments, high photon fluxes may produce chronic photoinhibition of photosystem II (Bjorkman et al. in press).

Approach - We will test nutrient, light and water limitation of plant growth in three habitats representing a hypothetical low nutrient-high light to high nutrient-low light gradient: open landslides, recently colonized landslide edges dominated by Cecropia peltata, and tree fall gaps in the tabonuco forest. We will study responses of three plant life forms; an early successional tree (Cecropia), a late successional tree (Manilkara bidentata), a shrub (Palicourea riparia), and an herb (Phytolacca decandra) to these post-disturbance regimes using a field transplant experiment, a field fertilization experiment, and a greenhouse pot experiment.

a. Field Transplant Experiment. The first field experiment will use individuals from three life forms grown in pots at each of the three sites. This design will eliminate the effects of competition on plant growth and facilitate the measurement of root biomass by confining the root growth within the pots. Plants will be established from cuttings or seeds in 5 liter pots containing native soils and vesicular-arbuscular endomycorrhizal (VAM) inoculum. Fertilization treatments will consist of nitrogen, phosphorus, and both nitrogen and phosphorus. Ten plants per species per site per treatment will be set out in a randomized block design (16 plots per block). In summary, this design will use 3 sites (center and edge of landslides, treefall gaps) times four nutrient treatments (Control, N, P, N+P) on four species (herb, shrub, 2 trees) with 10 replicates for a total of 480 plants. The experiment will be set out in groups of 16 pots per block times 10 blocks at 3 sites.

After planting we will follow plant growth by measuring height and stem diameter at monthly intervals. The plants will be harvested after 6 months (herb) to one year (trees). We will measure total biomass in roots, leaves, and stems as well as nutrient concentration of N, P, K, Ca, Mg, Fe, and Mo. In order to assess plant carbon fixation and stress at the different sites we will measure xylem pressure potential, light saturated photosynthetic rate, and stomatal conductance using a portable photosynthetic system (LI-COR LI-6000) at three month intervals after planting and immediately prior to harvesting. Photoinhibition will be assayed by measurements of initial and variable chlorophyll florescence with a portable fluorometer (Walz Regel- und Massteknik).

b. Field plot fertilization-inoculation experiment. We will establish 2 m^2 plots in each of the three disturbance sites listed above with buffers of at least 1 m between plots. Plots will be selected from homogeneous areas within post-disturbance vegetation type. This plot size will easily accommodate many individuals of the post-disturbance vegetation. Treatments will be the nutrient applications as detailed above plus the addition of VAM inoculation and VAM inoculation plus phosphorus treatments. Each set of treatments will be replicated three times per site. After three years, we will harvest 0.5-1 m^2 areas within each plot and determine aboveground biomass by species and pooled nutrient concentrations for each plot. The remainder of each plot will be reserved for long-term studies of treatment effects on plant succession.

c. Greenhouse nutrient/mycorrhizal experiment. This experiment is designed to test the effect of mycorrhizal infection on the growth, phosphorus uptake efficiency, and carbon balance

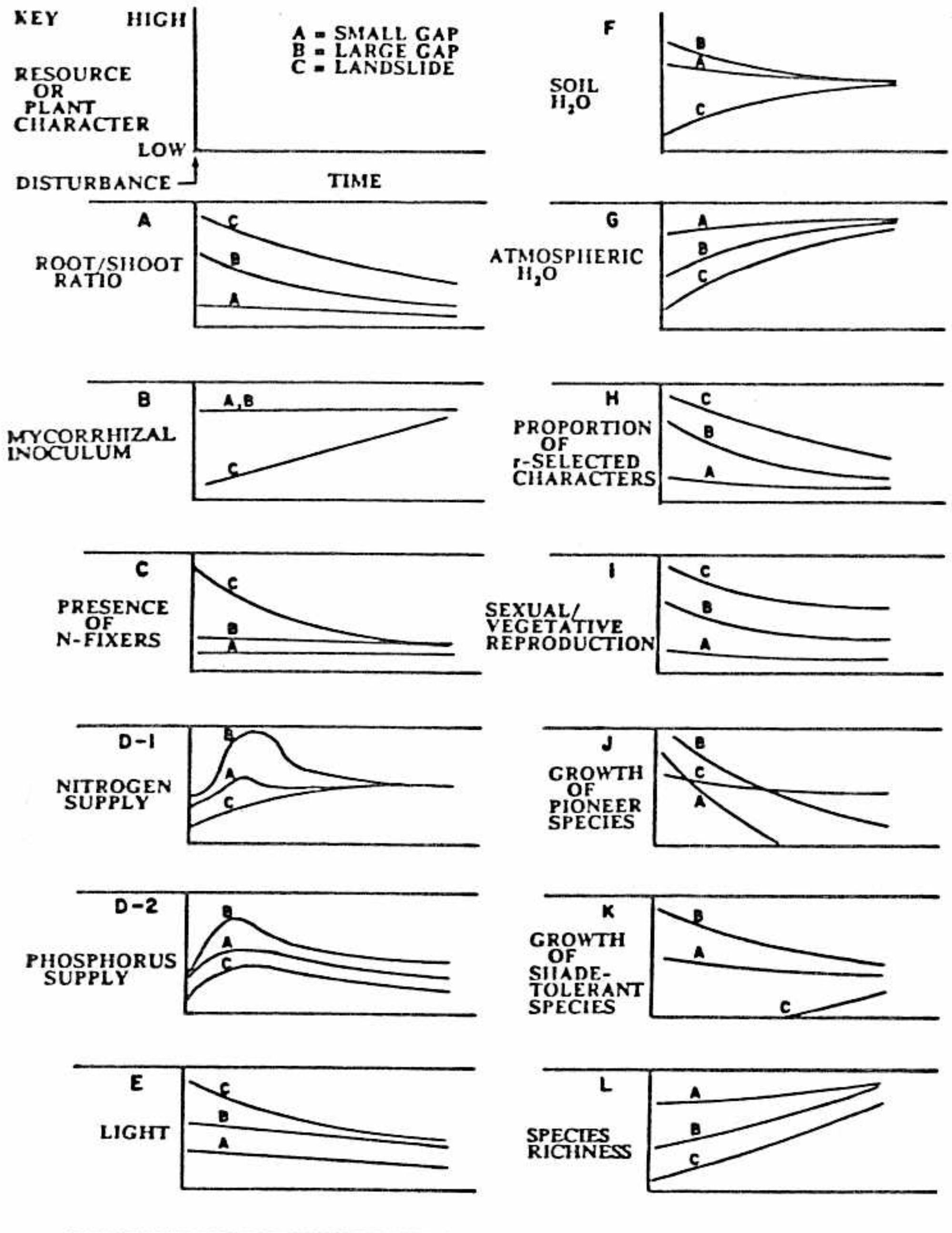

Figure 20. Conception of effects of disturbance on abiotic and biotic variables (A-L) and their subsequent behavior over time. Different severities of disturbance are represented by separate curves on each graph (see key): A = small gaps, B= large gaps, and C = landslides. These figures illustrate the hypothesis that temporal resource gradients favor a succession of species adapted to exploit particular ranges of resource concentrations along these gradients. This hypothesis guides the development of experiments on the revegetation of gaps (Section III.C.2.e).

of shrub, tree, and palm life forms. The experiment will use periodic growth analysis and carbon flux measurements to gage the effects of the treatments prior to final harvest. This series of experiments will be carried out over the long term and will first emphasize those species being used in the field pot/plot experiments described above (sections a. and b.) and then extend to other species that are important in disturbed and mature secondary forest. A rotating cultivation plan will be used which will support the study of 8 species simultaneously on a 1.5 year rotation. This includes approximately 6 months for setup, germination, and establishment, plus a 12 month growth period under treatment before final harvest. A minimum of six surviving plants at final harvest will be assured by growing extra plants. Tree ferns and climbing ferns will also be included among the priority species because they are primary colonizers of landslides.

1. Mycorrhizae X phosphorus. The growth measurements to be made are individual height, total number of leaves, stem diameter at base, and foliar gas exchange. Final preharvest measurements will include the previous list plus total biomass of all plant components, leaf area, leaf specific weight, and root respiration. The final harvest and measurements will be made after final cotyledon abscission and a minimum 2 month waiting period to assure utilization of all seed-related P reserves.

The nutrient protocol will include 3 levels of phosphorus, with the mid-concentration level being equivalent to field P availability in the tabonuco zone. The mycorrhizal treatment will be added inoculum and no inoculum. VAM inoculum will be acquired from commercially available stocks (<u>Glomulus</u>) while the no-inoculum treatment will be initiated by starting with sterilized potting media (coarse sand or other quick draining inert material). All other major and trace nutrients will be supplied by twice-weekly addition of Hoagland's-type nutrient solution to the individual pots. Plants will be kept at field capacity with drip irrigation in San Juan greenhouses.

2. Carbon flux. Infrared gas analysis will be used to measure the root respiration, foliar gas exchange, and potential carbon cost of mycorrhizal infection on the species studied. These measurements will be made to coincide with harvests at 2 and 6 months in addition to the 12 month harvest. The earlier harvests will allow the analysis of root respiration of a smaller range of root size classes to further refine our carbon cost estimates for small roots. Temperature controlled cuvettes (Oechel and Lawrence 1979) will be used to measure foliar gas exchange under a range of light and vapor pressure deficits. Root respiration will be measured on the "whole pot" basis (Lawrence and Oechel 1983 a,b), with an estimate of microbial biomass (Anderson and Ingram 1987) made to subtract from the pot respiration to estimate root-only respiration.

<u>d. Future experimental directions</u>. By year three of the project we will have results from all of these experiments which will be used to guide us in planning subsequent experiments or

extending experiments to include additional species or habitats (e.g., the experimental watersheds), more complete gradients of nutrient levels, a finer resolution of tissue analyses to determine energy and nutrient acquisition, allocation, and uptake kinetics, or measurements of the influence of nitrogen fixers in early succession.

3. Nitrogen-fixation in plants (Fig. 20-C; Walker).

H.12: Plants with symbiotic nitrogen fixers are more common in regeneration after severe disturbance than after less severe disturbance.

Species able to supply their own nitrogen often colonize severely disturbed nitrogen poor soils (Leisman 1957, Stevens and Walker 1970, Vitousek and Walker 1987) where their rapid growth rates may give them a competitive advantage (Walker and Chapin 1986). The resulting increases in soil nitrogen may affect mycorrhizal development, soil organic matter formation, and nutrient cycling as well as alter successional pathways. Although nitrogen is generally less limiting in tropical systems than phosphorus (McGill and Cole 1981, Vitousek and Sanford 1987), it is likely to limit revegetation in early succession following severe disturbances such as landslides.

Approach - Plants with nitrogen-fixing symbionts will be identified and their cover, abundance, and densities will be compared across the disturbance gradients. These data will be used to generate further hypotheses about the role of N-fixers in soil development and interactions among successional guilds.

Population level

4. Populations (Fig 20-H; McCormick).

H.13: Alterations of resource availability resulting from a variety of disturbances change population demography, energetics, nutrient cycling, and successional replacement of species from different successional guilds.

Population responses, and population models, often provide the most sensitive and predictive measures of ecosystem disturbance. Age-specific distribution, abundance, mortality, reproduction, growth, and biomass of plant populations vary considerably along the environmental gradients included in the LEF (McCormick 1983). For example, population behavior of "gap" species such as Cecropia peltata (Silander 1979) and Palicourea riparia (Lebron 1977) can be considered "r"-selected (Fig. 20-H) and are considerably different from "K"-selected climax canopy species such as Buchenavia capitata (Muñiz-Melendez 1978) and Inga vera (De Sastre 1979) or mid-successional species such as Prestoea montana (Bannister 1967). As disturbance initiates changes in plant population behavior or replacement of species, the entire trophic system responds accordingly. Age-specific plant population models provide source terms for those investigating food web structure and function (see Section III.C.2.f).

Approach - Concepts and methods developed by Sharitz and McCormick (1973) have been used to describe ecological life histories of several tree species which represent different successional guilds in the LEF. Population matrix models (Caswell 1978) will be constructed based upon demographic, reproduction, growth and biomass data for previously studied species. Caloric and nutrient equivalents of biomass will be determined in order to convert biomass dynamics to models of nutrient and energy dynamics. Current studies of Manilkara bidentata will be completed in the same manner. Selection of additional species for analysis will be guided by the needs of those studying herbivore trophic levels and the need to include species representing the entire environmental continuum of natural forest, gaps, landslides, and hurricanes. Candidate species include the tree fern (Cyathea arborea), Dacryodes or Didymopanax morototoni.

Community Level

5. Sources of regeneration. (Fig. 20-I; Brokaw, Fetcher, Walker)

H.14: A gradient of relative importance of regrowth from different sources, in the order: advance regeneration, sprouting, seeds, should correlate with the severity of disturbance, in the order: treefall, hurricane, harvest, and landslide.

In the least severe disturbances, treefalls and distant hurricanes (Fig. 17), one to many trees are snapped off or uprooted, but much undamaged vegetation remains. Harvesting removes trees and damages the understory. Direct hits by hurricanes flatten large areas of forest and cause landslides. Landslides, the most severe disturbance (Fig. 4), result in locally complete removal of vegetation. Thus as the severity of disturbance increases, less preexisting vegetation remains on the disturbed site, eliminating the sources of advance regeneration (juvenile plants in the understory of intact forest) and sprouting (snapped or upturned stems). Consequently, regeneration from seed becomes proportionately more important (see Fig. 20-I) (Bazzaz 1984); it may be the only source in large areas of exposed soil in landslides. In this way the severity of disturbance has a profound effect on the effect on the source of biotic response and on the time and pathway to recovery, through biotic regulation, to the steady state.

6. Species composition and growth rate. (Fig. 20-I, J, K; Brokaw)

H.15: Pioneer abundance and growth rates will increase with disturbance size up to a certain point.

Many pioneers have seeds that are abundant in soil prior to disturbance (Whitmore 1983) and that germinate when cued by a direct indicator of disturbance, for example: high light level or fluctuating soil temperature (Vazquez-Yanes and Orozco-Segovia 1984). Bell (1970) showed this to be the case in the tabonuco forest. Pioneers are generally light demanding, and their growth rates can depend on light levels. Thus, because the intensity of disturbance indicators and light availability tend to increase with disturbance size (up to a point), pioneer density and growth do also (Bazzaz 1979, Brokaw 1985). In this manner biotic response is scaled to disturbance size.

Approach - There are long-term studies of regrowth following hurricanes in the Luquillo forest (Crow 1980) and some features of recovery can be studied retrospectively (Foster 1988 a and b; see above). In artificially-created gaps, natural gaps, and landslides, regrowth will be studied directly and compared with features of undisturbed stands.

At Bisley in 1988, approximately two yr before the harvest, we will establish 2 x 2 m grid systems in the intact forest where 15-20 small and 10-15 large gaps will be created. In each site we will map, tag, measure height and dbh, and identify all canopy, or potential canopy, trees > 1 m tall. In stratified, randomly located quadrats in the grid (c. 10 - 30 % sample, depending on overall grid area) we will measure (or estimate cover where appropriate) smaller individuals of canopy trees and plants of other life forms that are important in the food web. Along transects formed by the grid lines we will estimate cover and leaf area index of all plants (Shimwell 1971) and record presence of species not recorded otherwise. To determine productivity and growth efficiency (Waring and Schlesinger 1985), biomass and wood production will be estimated from lab analysis of biomass removed at stratified, randomly selected places in the grids (Moore and Chapman 1986). The proportions of different sources of regrowth (advance regeneration, sprout, seed) will be recorded. Prior to, and for about five yr after, gap creation, these procedures will be carried out annually in all 25-30 study sites (recording recruitment, growth, mortality, leaf area, biomass) before and after gap creation. After five yr from gap creation data will be taken at supra-annual intervals, in pace with decelerating changes in regrowth (Brokaw 1985a).

The same methods will be employed in about 10 sites under intact canopy in the reference watershed at Bisley, where there will be no harvest, and in natural gaps. Landslides, including several created in December 1987 in the Sonadora watershed, will be sampled using transects connecting permanent points in adjacent intact forest and extending across the slides at regular intervals from top to bottom. Sampling will be done at randomly selected points along the transects, stratified so that all microhabitats are included.

Microenvironmental measurements (Section III.C.3) at grid points will be made in a subset of small and large gap sites, and systematically within large gap sites, before and after gap creation, so that we will be able to characterize sites not simply as large or small treefall gaps, or intact vs. disturbed forest, but with quantitative, objective descriptors. Although the variability of conditions and regrowth among and within gaps will be great, our experience indicates that these methods will provide robust, useful generalizations about dominant species and important processes (Chazdon and Fetcher 1984, Brokaw 1985, 1987).

7. Patchiness of regrowth in landslides. (Brokaw, Walker, Swanson)

H.16: Patterns of regeneration vary across landslide scars in relation to a) recovery of physical stability of the slide scar surface, b) the magnitude of biotic and abiotic influences of adjacent non-slide areas, and c) the "legacy" of pre-slide soil and biota.

Despite a first impression, landslides simply do not strip all soil and leave a clean slate for ecosystem recovery. Miles and Swanson (1986), in a study of revegetation of slide scars in western Oregon, observed great variability in microsite characteristics - wet to dry and very stable to persistently subject to surface erosion. They distinguished six microsites within slide scars. Species composition and rate of revegetation varied among the sites. Areas with slide-transported soil that did not leave the slide scar contained a legacy of plants, soil, and soil microorganisms so recovery was most rapid. Smaller slide scars may recover more rapidly because there is a greater influence of propagules and soil sloughing onto the scar surface from the edge of slide scars with high perimeter:area ratios. Consequently, compositional pattern and rate of revegetation may be very complex across a scar surface; revegetation is most clearly interpreted in light of primary (slide) and secondary (surface erosion) disturbance processes and some aspects of slide geometry.

Approach - This hypothesis will be examined by sampling a subset of the slide scars inventoried from written records and interpretation of aerial photographs. Slide scars will be stratified by microsites delineated on the basis of presence-absence of residual soil and vegetation, continued physical instability, water regime, etc. Both large and small slide scars will be sampled to examine size effects.

Slide areas remain unstable for several years after regrowth begins. Therefore we will not attempt to place permanent quadrats on slides. Instead, in undisturbed forest adjacent to the slides we will mark permanent endpoints for transects that will extend across the slides. The transects will cross the slides at regular intervals from slide top to bottom. Sampling will be done at randomly selected points along the transects, stratified such that all major microhabitat types are included. Observations and sampling will be made once per year during the first five years of study and at longer intervals thereafter if the pace of change appears slow enough that supra-annual intervals are sufficient to detect trends. Data to be collected are plant species composition, plant size, biomass (dry weight after harvest), and leaf area. Attention will focus on the regeneration of important canopy trees and plants important in the food web. Environmental variables will be measured in important microhabitats on the slides (see Section III.C.3).

8. Mycorrhizal colonization after disturbance (Fig. 20-B; Lodge).

H.17: Succession following harvesting and gap formation will favor plant species which are facultatively mycotrophic if nutrient availability increases, whereas succession following landslide will favor obligate mycotrophic or non-mycotrophic species, depending on inoculum availability.

Janos (1980, 1983) summarized theoretical considerations and experimental results suggesting that plant community composition is influenced by the availability of mycorrhizal fungi and nutrients. He suggested that at relatively high levels of nutrient availability facultatively mycorrhizal species will be favored, whereas low nutrient availability will favor non-mycorrhizal and obligate mycotrophic plant species at low and high fungal inoculum densities, respectively.

Removal of vegetation, litter, and surface soil by landslide leaves subsoil with relatively poor nutrient availability. Landslides also remove mycorrhizal inoculum (Garwood et al. 1979), but the fungi subsequently disperse into the slip zone from intact vegetation above. This process is suggested in the LEF by the decreasing gradient of infection in young Cecropia peltata trees with distance from the top of a small landslide (Lodge unpubl.). Low availability of inoculum and nutrients in large landslides is likely to favor species with a non-mycotrophic strategy (Janos 1980, 1983). Colonization by non-mycotrophic species can then retard succession toward the more productive climax community which is predominantly mycotrophic (Janse 1896, Johnston 1949, Redhead 1968, 1980, Edmisten 1970, Janos 1975, St. John 1980, Trappe 1981) by keeping inoculum densities low (Reeves et al. 1979, Janos 1980, 1983, Miller et al. 1983, 1985). Additions of mycorrhizal inoculum to plots in a large landslide should favor higher proportions of obligately mycotrophic plants than in untreated control plots.

Phosphorus additions should increase the frequency of facultatively mycotrophic plants and decrease mycorrhizal formation in those species, regardless of inoculum density. Facultatively mycotrophic plants can reduce carbon costs when nutrients are readily available by excluding fungal symbionts (Janos 1980, 1983). Phosphorus additions are expected therefore to have similar effects in plots in a large landslide with or without inoculum additions. Greater nutrient availability due to mineralization following harvesting or hurricanes (Bormann and Likens 1979b, Matson et al. 1987) may also favor facultatively mycotrophic plant species. Subsequent decreases in nutrient availability over time will cause facultatively mycotrophic plants to form mycorrhizae and are likely to favor colonization by obligate mycotrophs which are more efficient in nutrient uptake (Janos 1980). Less severe disturbances such as single tree fall gaps should have a high proportion of obligately mycotrophic trees if nutrient levels remain low (Vitousek and Denslow 1987) because inoculum is available from neighboring trees (Janos 1980, 1983; Harvey et al. 1980). Additions of nutrients to such sites, however, should favor an increase in facultative mycotrophs and a decrease in mycorrhizal density.

Approach - Densities of mycorrhizal inoculum (most probable number technique) and mycorrhizae (coring) will be determined during the initial stages of recolonization following disturbance. The degree of dependence of the principal colonizing plant species on VAM fungi for nutrient uptake and their responsiveness to fertilization will be established through greenhouse tests (see Hyp. 11c above). Nutrient availability will be determined for disturbed (tree falls, man-made gaps, and landslides) versus undisturbed sites and followed through time. The VAM, VAM plus P, and P alone treatments and the control plots (see above) will be sampled to determine the densities of plant species, and these data together with the greenhouse results will be used to determine the percentage that are non-mycotrophic, obligately mycotrophic, and facultatively mycotrophic. Densities of mycorrhizae and non-mycotrophic roots will also be compared among plots. Half of twenty treefall gaps will also be fertilized and compared to the unfertilized gaps. Plots will be sampled once per year for three years. Long-term changes in plant species composition and mycorrhizal densities will then be followed through time in the treefall gaps and fertilization-inoculation plots to determine the validity of Janos' (1980) predictions for changes in nutrient-absorbing strategies during succession.

9. Species richness. (Fig 20L; Brokaw)

H.18: Plant species richness will be greatest in those areas subjected to a disturbance regime of intermediate frequency and severity.

Where disturbances are too frequent or severe only pioneers survive. Where disturbances are too infrequent or mild, only "climax" species survive (Connell 1978; Fig. 20-L). Stated differently, richness is expected to peak at an intermediate point during succession when the community contains both early and late successional species (Bormann and Likens 1979a). Doyle's (1982) tabonuco forest model (Fig. 3) suggests that maximum species richness in the LEF is sustained by the historical frequency of hurricanes, while natural treefalls alone are too mild and landslides too severe to sustain maximum species richness. In the LEF the richest stands may be the oldest extant, if devastating hurricanes generally forestall maturation and interrupt competitive exclusion.

Approach - We will examine this hypothesis both retrospectively, by comparing disturbance frequency with stand composition (Doyle 1982), and directly, by observing species composition during regeneration (see above).

Section Integration

Experiments to examine the nine hypotheses in this revegetation section will be closely integrated. Berish and Lodge will cooperate on root sampling in landslides, and Brokaw and Lodge will cooperate on determining plants species composition in landslides and gaps. McCormick's data will provide the basis for choice of species representing each successional guild. Brokaw's transects will identify frequency and size characteristics of slides and gaps that will direct where we do our more intensive sampling and experiments and how we interpret the results in the context of the whole landscape. The CEER/UPR team (Fetcher, Lawrence, Lodge, Walker) and Haines will interact closely on three experiments that will provide ecophysiological data for Fetcher, Haines, and Lawrence, growth data for Walker, and mycorrhizal data for Lodge - all from the same plots or pots. Our three levels of hypotheses all focus on predicted effects of disturbance severity and successional time on plant characteristics or environmental resources.

III.C.2.f. Spatial and temporal distribution of populations - (Covich, Pfeiffer, Reagan, McCormick, Waide, Willig, Woolbright)

Population measurements - Long-term measurements are required to examine cyclical, directional, episodic, or catastrophic changes in plant and animal populations. Such long-term studies exist for some groups (principally birds; Lack 1966, Holmes et al. 1986) in temperate ecosystems, but long-term population studies are notably lacking for all taxa in the tropics (but see Stewart and Pough 1983, Faaborg et al. 1984, and Snyder et al. 1987). Moreover, simultaneous long-term studies of different tropical taxa at the same site are rare (but see Leigh et al. 1982 and Janzen 1983) and often not coordinated into an ecosystem approach.

We propose to continue population studies of frogs begun in 1978 at El Verde and to initiate parallel investigations of key mammal, bird, reptile, invertebrate, and plant species in both disturbed and control plots. Long-term investigations of key species (Table 4) will provide information on patterns of population changes and serve as a baseline to catastrophic disturbances (e.g., the numerous large landslides associated with heavy rains in December 1987) that are characteristic of forests in the Caribbean and elsewhere. Knowledge of the magnitude of changes in populations as a result of disturbance and the rate and trajectory of recovery will permit us to evaluate both the resistance of populations to disturbance and their resilience after disturbance.

An important measure of the severity of a disturbance is the extent to which the animal community changes following the disturbance. Especially intense or widespread disturbances may substantially alter species composition, whereas smaller disturbances may affect only relative abundance or population demography. Responses will also vary through time depending on the severity, scale, and frequency of disturbance. Because the responses of particular species may differ with disturbance type, alternative general patterns of response are presented (Fig. 21) rather than specific hypotheses.

Approach - Long-term monitoring of populations and measurement of the effects of disturbance will be conducted simultaneously in the same plots used for revegetation and microenvironmental measurements. Previous work in mature tabonuco forest has identified various species of importance (key species; Table 4) defined in terms of biomass, abundance, and position in the food web (Odum and Pigeon 1970; Reagan et al. 1982). We will follow changes in abundance of these key species in undisturbed forest and in naturally-created and artificial gaps. Censuses of each animal species will be conducted twice annually along transects at Bisley and Sonadora, using methods specific for the taxa involved. Plant species will be monitored as part of the investigation of revegetation (Section II.C.2.e) and in an ongoing experimental study of tree regeneration (Devoe; Section III.A.5).

Table 4. Key species selected for intensive study, details about life histories of the species, and predictions about response to disturbance. Four kinds of responses are considered: positive (+), negative (-), neutral (0), and ecotonal (E). Descriptions of these responses are given in Fig. 21.

SPECIES	LIFE FORM	TROPHIC LEVEL*	SUCCESSIONAL STAGE**	PREDICTED RESPONSE TO: SMALL GAP	LARGE GAP
Phytolacca decandra	shrub	P	E	+	+
Piper treleaseanum	shrub	P	E-L	+	+
Palicourea riparia	shrub	P	E-L	-	-
Cecropia peltata	tree	P	E	+	+
Prestoea montana	tree	P	E-L	-	-
Buchenavia capitata	tree	P	L	-	-
Manilkara bidentata	tree	P	L	-	-
Dacryodes excelsa	tree	P	L	-	-
Atya lanipes	shrimp	D	E-L	0	-
Lamponius portoricensis	insect	H	E	+	-
Caracolla caracollus	snail	H-D	E-L	+	-
Epilobocera sinuatifrons	crab	H-C	E-L	0	-
Geotrygon montana	bird	G	L	-	-
Coereba flaveola	bird	F-I	E-L	+	+
Rattus rattus	mammal	H-I	E-L	+	-
Eleutherodactylus coqui	frog	I	E-L	0	-
Anolis stratulus	lizard	I	E-L	+	-
Anolis gundlachi	lizard	I	L	0	-
Leucauge regnyi	spider	I	E-L	+	-
Modisimus signatus	spider	I	E-L	+	-
Todus mexicanus	bird	I-C	E-L	E	-
Stasina portoricensis	spider	I-C	E-L	+	-
Otus nudipes	bird	C-I	L	E	E

*P = producer
D = detritivore
H = herbivore
G = granivore
F = frugivore
I = insectivore
C = carnivore

**E = early successional
L = late successional

Figure 21 presents the idealized form of responses which are expected to result from disturbance within the forest. We expect that some species will shift their response pattern as gap size increases. Transects will be arranged as four radii from the center of each gap and will extend 25 m into adjacent forest in order to sample the spatial range of population responses. Sampling will be continued seasonally (wet and dry) for at least five years in order to quantify responses to succession.

Analysis of the food web - The relatively low diversity of the fauna allows a comprehensive description of the food web and trophic structure at comparatively small effort. Since most of the vertebrate biomass is contained within a few species (see above), detailed study of these species yields relatively complete information on trophic dynamics. An advanced knowledge of the taxonomy of the roughly 2100 species of invertebrates in tabonuco forest (Estrada Pinto et al. 1983) allows much more elaborately detailed treatment than is normally accorded to these groups in other tropical sites. A food web analysis comparable to that which has been conducted in tabonuco forest would be impossible in a mainland tropical site because of the complexity of the continental fauna.

Intensive studies of plant and animal populations in the tabonuco forest of the LEF have led to a detailed understanding of the relationships among key species in the terrestrial food web (Reagan et al. 1982; Reagan and Waide 1989). The principal vertebrate predators in terms of their effect on lower trophic levels are lizards and frogs. There are no native mammals except bats, which are principally frugivores, although an introduced species, Rattus rattus, is a common terrestrial omnivore throughout the forest. More than half of the bird species are omnivores, and in general there is a marked preponderance of species that take prey from two or more trophic levels. Large invertebrates play an important role as predators of vertebrates and other invertebrates. The occurrence of "food loops" (reciprocal predation by two species) is a marked feature of the system (Reagan and Garrison 1983). Vertical stratification is clearly present at all trophic levels, but vertical movement of key species (Stewart 1985) may result in considerable transfer of energy and nutrients between the canopy and the ground. The food web is partitioned into nocturnal and diurnal as well as terrestrial and aquatic sub-webs. Connections between these different sub-webs are limited, and the sub-webs may act to canalize nutrient movement within the ecosystem.

Studies of the spatial and temporal distribution of populations will be augmented by experiments designed to examine controls of food web structure and complexity. Feeding relationships among species also vary both spatially and temporally according to the disturbance regime. Although several factors have been hypothesized to control the length of food chains (i. e.- primary productivity, environmental variability, habitat structure), recent work indicates that

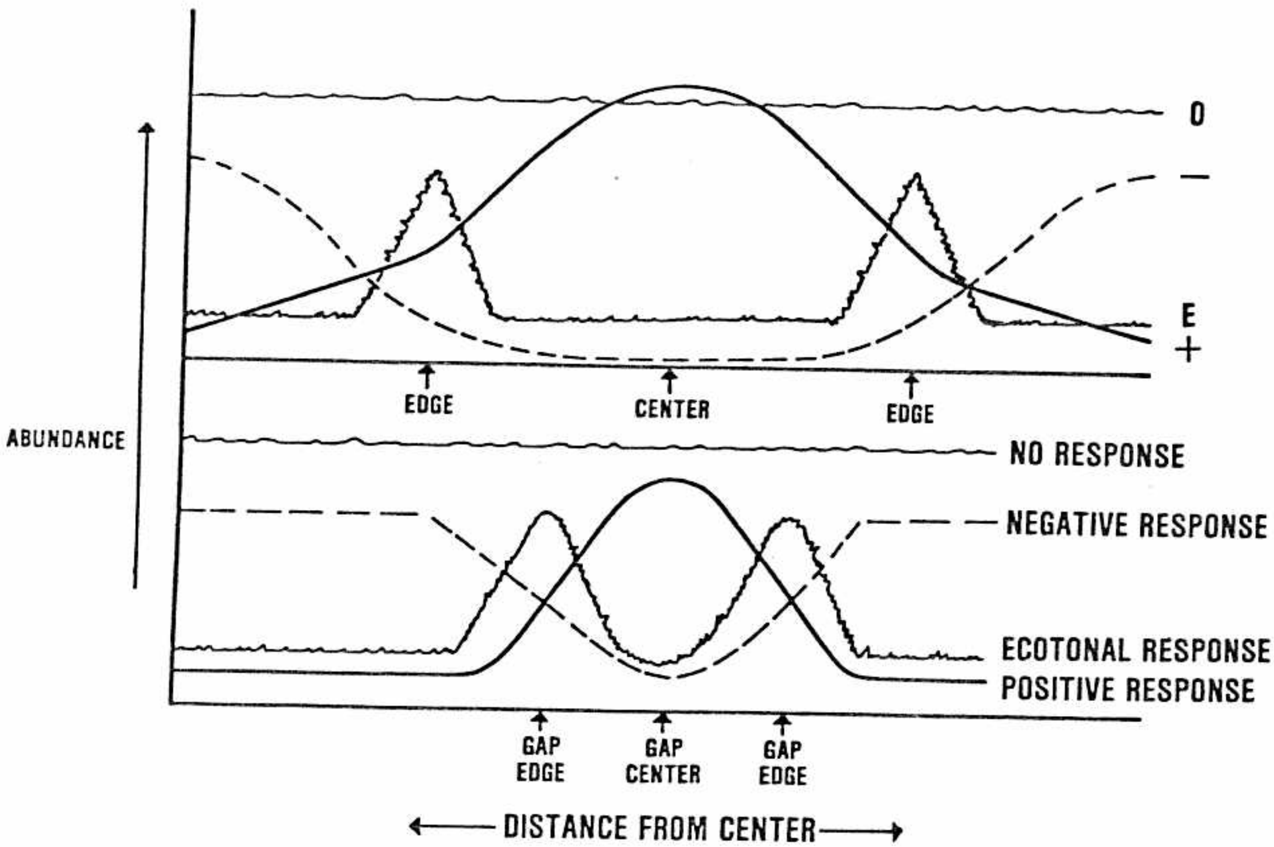

Figure 21. Patterns of possible responses of plant and animal populations to large and small gaps caused by disturbance occurring within mature forest.

only structure is correlated with food chain length in 113 terrestrial and aquatic webs (Briand and Cohen 1987). Based on this finding, we offer the following hypothesis:

H.19: The regeneration of the food web after disturbance proceeds in discrete steps associated with 1) canopy closure, 2) regeneration of the litter layer, and 3) addition of succeeding "layers" of vegetation.

The dynamic aspect of trophic structure in both space and time is the key to understanding how food webs are structured and what role they play in the control of ecosystem processes. At present, we know that temporal changes in the distribution of populations occur on daily, seasonal, and annual scales within mature tabonuco forest, but despite these changes, the basic components of the food web remain intact. We further know that the trophic position of individuals in some species changes as they mature, and that this shift may cause cyclical changes in food web structure related to periods of population recruitment. Superimposed on these changes are fluctuations in population size related to wet and dry season as well as seasonal dietary shifts. What we do not as yet understand is how these complex patterns are formed and how they regenerate after they are disturbed. We hypothesize, however, that the regulating factors in food web regeneration depend on changes in both microenvironment and vegetation structure during regeneration after disturbance.

Disturbance generally creates an opening in the canopy, which increases light intensity, wind, and air temperature and reduces relative humidity (Smith 1970, Odum et al. 1970). The primary modification of the gap microenvironment during regeneration occurs when increasing leaf area index (LAI) moderates understory conditions (Fetcher et al. 1985). The resulting decrease in temperature and wind speed and increase in humidity in the understory permit the simultaneous establishment of a number of species. As understory litter begins to accumulate, litter species are added to the system. As the vertical structure of vegetation increases, faunal species richness and food chain length should also increase (Briand and Cohen 1987). As the forest matures, a decrease in plant species diversity may lead to a less complex food web than occurred in earlier successional stages.

Approach - Plant, vertebrate, and invertebrate populations will be followed through succession in the sites disturbed by landslides, treefalls, and harvest and in reference sites (see above). Key species will be selected for more intensive study (Table 4). Detailed observations and non-destructive sampling of stomach contents will establish feeding relationships. We will relate changes in species richness or food web complexity to changes in structural (LAI, biomass, vegetation height, litter storage; Sect. III.C.2.e) and microenvironmental parameters (light intensity, relative humidity, temperature, soil moisture, litter moisture, wind speed; section III.B.2.a). We anticipate the major change in food web structure to occur after the transition from a two-dimensional to a three-dimensional habitat (Briand and Cohen 1987). This transition will occur at lengthening times after disturbance in the order: treefall < harvest < landslides.

We also will examine the fundamental processes determining linkages within the food web under the disturbance regime prevalent in the LEF:

H.20: Parallel, host-restricted food webs (Gilbert 1980) do not develop in the LEF where forest structure and composition are affected by frequent, large-scale disturbance.

Previous examinations of faunal species richness in the tropics have assumed that tropical forests are stable and unchanging on a medium-to-large scale over the length of time required for evolution to build up trophic structure. This large scale homogeneity coupled with small scale habitat variability resulting from mortality of individual or small groups of trees is thought to provide the conditions necessary for high species richness developing through the co-evolution of parallel, host-restricted food webs (Gilbert 1980). This view has resulted in an emphasis on biotic factors (competition, predation, pollination, seed dispersal) as the dominant forces in determining the interactions among species and the structure of the food web. Hence, Gilbert (1980) attempted to provide guidelines for the management of tropical species on the sole basis of four biotic factors: 1) the chemical mosaic and coevolved food webs; 2) mobile links; 3) keystone mutualists; and 4) the ant mosaic.

While such an approach may have validity for areas of lowland forest such as La Selva, which represent an extreme case in the frequency of occurrence of small scale gaps (Hartshorn 1983), many other tropical forests are subject to large-scale, recurrent natural and anthropogenic disturbances such as fire, floods, hurricanes, landslides, volcanic eruptions, earthquakes, or harvesting activities. As these large scale disturbances tend to be more severe and harder to escape than small scale disturbances, it is reasonable to expect that faunal response will be different. As previously discussed, hurricanes periodically reset the successional process to an early stage in large sections of the LEF. Since extinction and recolonization after succession is not a viable alternative under large scale disturbance regimes (e.g., hurricanes), as it is under small-scale disturbance, species must be able to survive and reproduce under the range of abiotic and biotic conditions that occur during succession. Such conditions are not optimal for the development of food sub-webs dependent on a single species or taxon of plant for their resource base. If parallel, host-restricted food webs are not important in the tabonuco forest, different source webs will show large overlap in the species that constitute them.

Approach - We will make detailed observations of two types of source food webs (a source food web is one defined by one or more kinds of organisms that supply energy plus all the higher trophic-level organisms that live off that energy; Cohen 1977). Live leaves of five dominant canopy and three understory species (Table 4) will be used to define eight different source food webs. Wet and dry season surveys of insects (both day and night) will be made for each plant species each year by counting individual insects along transects. Access to canopy foliage will be gained through the tower at Bisley and the canopy walkway in the Sonadora watershed. Actual feeding relationships will be established by 1) long-term observations, 2) feeding choice experiments for numerically dominant insect species (Willig et al. 1986), and 3) published information (Martorell 1976).

The second type of source web will be dead leaves of the same five canopy tree species and the litter detritivores that depend on this resource. Large litter bags will be filled with new-fallen leaves of a single tree species and used as microcosms to establish the overlap between detritivores feeding on litter from different tree species. Invertebrates will be extracted from the litter bags used in the decomposition experiment (III.C.2.d). Replicate bags will be placed randomly within a homogeneous area of the forest floor in both wet and dry seasons, and five bags per species will be harvested at two week intervals for three months and at increasing intervals thereafter. A pilot study will be performed from Feb-Apr 1988 to measure variability. If variability is high, a larger number of bags will be used in subsequent experiments. Tullgren funnels will be used to extract the litter invertebrates, which will be identified to the lowest possible taxonomic level (usually species).

H.21: Food web complexity is directly correlated with nutrient use efficiency.

An inverse theoretical relationship has been postulated between ecosystem resilience (the speed with which a system returns to equilibrium state following a perturbation; DeAngelis 1980) and food web complexity (Pimm 1982). Resilience has also been shown theoretically to be inversely related to the tightness of nutrient cycling (DeAngelis 1980), raising the possibility of a direct relationship between food web complexity and the tightness of nutrient cycling (Pimm 1982). This hypothesized relationship could be the result of a shift from herbivory to detritivory as food webs develop through successional time (Odum 1969). We will use measures of nutrient use efficiency collected by collaborators (Section III.C.2.g) to examine the relationship between the tightness of nutrient cycling and food web complexity.

III.C.2.g. System properties - (Lugo, Asbury, Scatena, Waide)

Vitousek (1985) discussed details of successive structural and functional phases in ecosystem recovery following clearcutting in a temperate forest. The phases, based on the model presented by Bormann and Likens (1979a), are reorganization, aggrading, transition and steady-state, during which vegetation, nutrient dynamics, and water budgets are closely linked.

Vitousek and Reiners (1975) advanced a hypothesis that explained changes in nutrient cycling and export associated with these phases of recovery. This hypothesis suggests that, because of linkage between nutrient and carbon cycles, nutrient accumulation is a direct, and nutrient export an inverse, function of net ecosystem production. Thus, nutrient availability was hypothesized to be lowest during the aggrading phase of rapid vegetation growth. Implicit in this hypothesis was the idea that geochemical processes (e.g., mineral soil sorption) are in balance or unimportant relative to changes in the stock of organic matter. Predictions based on this hypothesis have been supported in several studies (e.g., Vitousek 1977, Bormann and Likens 1979a, Vitousek and Matson 1984).

Biotic mechanisms are believed to be important in acting to retain and recycle nutrients in tropical forests, particularly in high-rainfall areas (Jordan and Herrera 1981, Jordan 1985). However, the degree of linkage between carbon and nutrient cycles in tropical forests has been disputed. For example, in recent a review, Jordan (1985) argued against the view (e.g., Richards 1952) that most of the nutrient capital in tropical forests is in the biomass. In the tabonuco forest, there is evidence that, in addition to organic matter, geochemical factors may be important influences on nutrient cycling and export: 1) high weathering rates (McDowell et al. in prep.) and high rates of erosion (Curtis et al. 1984) suggest high rates of soil formation; 2) soil in the LEF has high cation exchange capacity and high rates of P and S sorption relative to most temperate and many tropical soils (Fox 1982); 3) soil in the LEF is nutrient-rich relative to many tropical high-rainfall areas (Jordan 1985), and nutrient-use efficiency of the vegetation appears to be in the low range of tropical sites (Zucca et al. in prep.; new data suggest that the high value calculated by Vitousek [1984] from limited previous data for the El Verde site was erroneous), so that the relative importance of geochemical regulation may be greater than at sites with lower nutrient availability.

We propose to test the application of models based on strong linkage between carbon and nutrient cycling to prediction of system properties in tabonuco forest during recovery from disturbance. Our hypotheses specifically address the Bormann and Likens (1979a)/Vitousek and Reiners (1975) model of recovery phases:

H.22: Phases of recovery will be evident in vegetation and internal cycling, but will be less evident for nutrient exports because geochemical regulation of nutrient concentrations will dominate below the rooting zone.

H.23: Phases of recovery will be more evident in regeneration from larger and more severe disturbances than in regeneration from small or less severe disturbances.

H.24: Rates of recovery will vary inversely with disturbance size and severity because of a direct relationship between disturbance size or severity and soil nutrient loss and propagule destruction.

H.25: Increasing intensity of disturbance results, during the aggrading phase, in an increase in nutrient-use efficiency by plants, a reduction in litter quality, and a slower rate of litter mineralization, and nutrient accumulation. This is because litter quality (Melillo et al. 1982) and thus mineralization rates will depend on soil nutrient availability (Vitousek 1982; 1984), which is predicted to be lowest in the aggrading phase.

H.26: Nutrient-use efficiency will decrease when nutrient mineralization and nutrient pools in soil and litter return to near pre-disturbance levels.

Approach - Phases of ecosystem recovery are delimited by points of inflection in the rates of change of vegetation parameters (e.g., biomass, leaf-area index), nutrient-use efficiency (using the index of Vitousek 1982), soil total and available nutrient concentrations, nutrient exports, water runoff, and soil organic matter. Bormann and Likens (1979) give detailed examples of these inflection points. By applying their criteria to data gathered in appropriate components of this study, we will seek to identify significant inflection points in ecosystem processes in order to determine the existence and duration of distinct phases of recovery.

To evaluate the relationship between phases of recovery in nutrient exports and phases in vegetation recovery, we will examine data on N, P, Ca, and K concentrations from lysimeters placed below the rooting zone in replicated treefall gap, harvest, and landslide plots in the Bisley watersheds, and also data for runoff chemistry for landslide and harvested plots. Changes in these data will be compared to changes in vegetation parameters for the same plots. The vegetation parameters to be tested have been described in previous sections of this proposal but include nutrient use efficiencies associated with biomass accumulation, senescence of tissue, litter fall, and response to high rainfall (leaching). These processes are summarized in Fig. 12 and 15.

III.C.3. Environmental monitoring - (Fetcher, Lawrence)

This section of the LEF LTER project has three main objectives: 1) the collection of long-term meteorological data for the characterization of forest ecosystems at different elevations and the comparison of these data with those of other LTER sites; 2) the analysis of historical meteorological data for the LEF and its integration into the LTER database; and 3) the acquisition of meteorological data to support experiments described in this proposal.

The first objective will be met using Level 2 (Greenland 1986) LTER standard meteorological stations at two sites within subtropical wet forest (El Verde and Bisley), and single sites in the subtropical rain forest (Rio Blanco landslide) and lower montane rain forest (East Peak) life zones in the LEF (Ewel and Whitmore 1973). A multi-site approach is being taken due to the wide range of environments and community types found within the LEF. This will increase effort involved but will yield significant information on the range of meteorological conditions across the LEF elevational gradient and serve later LTER efforts in different community types.

The installation of fixed meteorological stations in three distinct life zones of a highly dissected topographic area such as the LEF can yield only localized information. The range and variability of the climatic parameters at each site can be gaged, but the range and variability of conditions across the same life zones in the rest of the forest can only be estimated. To collect the detailed measurements necessary for typifying other areas within the forest, short term installation of a Level 3 station will be rotated between many sites within each life zone. This will help broaden our knowledge of meteorological and microclimatic variability.

To broaden the scope and the simultaneity of our observations across the whole of the LEF, we will routinely use large scale remotely-sensed spectral information (Greegor 1986) from both NOAA and EOSAT satellite instruments, as well aircraft-borne packages (when available). Imagery is available in a variety of resolutions that have individual picture elements that range in size from rather coarse to fine (ca. 4 km and 1 km for Advanced Very High Resolution Radiometer (AVHRR) data, to 30 m for Landsat-TM, 10 m for SPOT, and 5 m or less with aircraft). This information, besides its utility in mapping, contains canopy and ground temperature data and other spectral signatures that can be used to infer many ecosystem level processes, as well as detect change (Waring et al. 1986) and forest damage (Rock et al 1986). The imagery will be acquired in conjunction with two on-going collaborative projects between NASA and CEER scientists and analyzed with the LTER GIS. LTER-oriented meteorological data will be used as corroborative ground observations.

The availability of data for three tropical life zones will add considerable range to the existing suite of LTER sites (Swift and Ragsdale 1985). Published meteorological measurements along elevational gradients are rare in the tropics (but see Holben et al. 1979) as are long-term, continuous meteorological records (see Section V and Briscoe 1966 for existing Luquillo data). Data collected in this study will be useful in future efforts under the LTER program to discern the basis for the differentiation of vegetative communities in the LEF across a limited gradient of temperature, substrate, and slope. The data collected will be placed on the LEF LTER network for computer-based access, summarization, and reporting as requested (see section III.C.4.).

The second objective, the integration of historical meteorological data, will help establish the temporal variability of environmental conditions in the LEF. The several data sets in existence for the LEF will be added to the LEF database.

Meeting the meteorological data acquisition needs of the individual research projects is the third objective of this section. This work will be carried out on investigator request and will primarily be dedicated to measuring the effects of disturbance and recovery on local microclimates. An intensive instrumentation approach will be used with one portable Level 3 (Swift and Ragsdale 1985) station available to measure light, temperature, and humidity gradients across disturbed patches and during the regeneration of the biota. The Level 2 stations at El Verde, Bisley, and the Rio Blanco landslide are also being used in direct support of the extensive experimentation and observation to be underway at these sites.

III.C.4. Data management

The principal goal of the data management section is to design, implement and oversee the storage, retrieval, and analysis of data from the different components of the LEF LTER program. A secondary goal will be to merge existing LEF data sets into the LEF LTER database. To facilitate both the sharing of data among the LEF LTER collaborators and the comparison of data between LTER sites (Swift and Ragsdale 1985), data will be available on a local area computer network (LAN) at CEER. A network with more than 20 nodes has be functioning at CEER for more than 3 years and is being expanded to accommodate more on-site users and the enhanced LTER data input and archiving capabilities. A port will be added to allow telephone access for off-site collaborators. The individual components of the data management plan are discussed below.

III.C.4.a. Data storage - Before any data acquisition begins, each investigator will submit an abstract to the LEF LTER Data Coordinator. This abstract will be a concise description of the planned experimental design, the data to be acquired, and the proposed analyses. A more detailed section will describe each variable and the methodology used in sampling and all analysis. Precision and proposed quality control for each variable will be specified by the investigator. The number of samples and/or eventual size of the data set will be specified so that data storage needs can be determined. This extensive documentation will insure future utility of the data. Our data management will generally follow the lead set by other LTER sites (Swift and Ragsdale 1985, Greenland 1986). Their experience, when adapted to our site and experimental design, will not only save us considerable design work, but will also make intersite data comparisons much easier. Dr. William Michener from the Baruch Institute spent two days with us in November 1987 helping to plan our data management protocols and select appropriate hardware and software.

Raw data will be input to the LTER LAN at CEER according to the specifications previously agreed to by the investigator and the Data Manager. The data will be entered using a full-screen editor capable of initial quality control testing for out-of-range or wrong data type inputs. After input and initial quality control the data will be returned to the investigator in printed form for verification. Corrections will be made by direct comparison to the original data sheet, and a second verification copy sent to the investigator. Once data is approved, a final printout will go to the investigator, and backup protocols will be initiated.

Backup and archiving are a critical part of this operation. From the approved data set (resident on LTER LAN hard disk) a file floppy will be made, and a permanent master made on a WORM (write once, read mostly) optical disk drive. Archive backups will also be made on 9 track magnetic tape of each verified and corrected data and documentation file. The hardcopy of original data sheets and the clean data file printout will both be xeroxed in duplicate, as will field notebooks and any comment sheets. One of these sets of hard copy and the archive tape will be stored at the USFS Institute of Tropical Forestry, and the other at CEER, both in fire-resistant cabinets. Magnetic tapes will be copied at 2-3 year intervals to insure their integrity.

The existing historical data for the LEF is in a variety of formats. The bulk is on handwritten data sheets, some on punched cards, and a small amount on tape of several densities. A few historical data sets, selected for their relevance to present research, will be put on the LEF LTER network by a data entry person specifically assigned to this task. A digest of these data is in preparation and will be circulated to the collaborators of the LEF LTER for inputs as to prioritization of data entry on the network.

III.C.4.b. Data retrieval - The retrieval and use of data will be facilitated by the use of a text-oriented data base manager. This DBM will be used on the LEF LTER computer network to search the data abstracts for key words or phrases of interest to the searcher. A query type system will allow the use of Boolean arguments to subset and extract the data as required. Once needed data sets are located by this query system, the master data ID can then be used on-line to acquire all or part of a data set in printed or magnetic media format. Both data and data description abstracts can be obtained in this manner. As new data sets are acquired, they will be announced in a LEF LTER newsletter. The Data Manager will have primary responsibility for data access and distribution. Data will be considered the personal property of the investigator until their general release to the network.

It is anticipated that the initial on-line data level at the LEF LTER network will be less than 1000 Mbytes. Until this level is passed, the 2 WORM drives and the system hard disks will be capable of handling the load. Using the dual WORM drives, more than 1000 megabytes of data can be on the network at any time (more than 2700 IBM PC floppy disks). This capacity will be sufficient to keep all current and historical data available on-line. As the WORM drives reach their capacity, their media can be changed and seldom-used datasets stored off-line.

III.C.4.c. Data analysis - The analytical treatment of any data set collected will be the primary responsibility of the investigator that planned its acquisition. However, the data, once verified by the investigator can be made "public domain" upon his request, which will make it searchable by other LTER collaborators. The data set will be accompanied by an abstract that defines the basic experimental rationale, the methods used in sample collection and preparation, and a description of the data file itself. Any or all of these levels of description can be requested by data users. As a precaution, data sets will be available in 'read only' form on the LEF LTER network to assure their integrity. The investigator will also be provided a log of data distribution for his information.

The use of appropriate statistical techniques are an important part of any data analysis scheme. Dr. Michael Willig has agreed to act as statistical consultant to the LEF LTER team. Dr. Willig will help design experiments and statistical analyses for any investigator that requests such assistance.

Our analytical scheme includes three levels of power. The first is a 'spread sheet' type environment on the local LTER LAN, and the second, also on the LAN, are versions of SPSS-PC and SYSTAT for statistical analyses. The third level consists of the SAS, SAS-graph, and SPSS-X statistical packages on the Medical Sciences campus IBM 4361 mainframe. These three levels provide ascending user capabilities, with the first two levels using the data directly from the LEF LTER network and the third requiring data transfer. This transfer will be quite easy, using one of the LTER LAN nodes as a hard-wired IBM 3278/79 emulator on the IBM 4361. The three levels allow anything from a quick look and graphics to full-blown statistical analyses of the acquired data sets. Within the next 6 months the hard-wire connection to the IBM 4361 will allow us to communicate with the UPR-NET which will connect via satellite to mainland networks (NSF-NET, BITNET, TYMNET, etc.).

As a first step in implementing this system, four PC-AT clones have been acquired by ITF and CEER to access the existing LAN. Three have been implemented as work stations for the LTER network, and the fourth resides at ITF (with future modem access to LAN). A PC-XT with software functionally equivalent to the LAN has assigned to the El Verde Field Station for data analysis and entry. An IBM 3278/79 emulator card has been acquired for full graphics capability on the mainframe via a coaxial cable connection which is being installed. An XY plotter and high speed printer have also been acquired for data presentation and high volume hard copy. A 230Mb hard disk and a 800 Mb WORM drive are now being ordered for installation in the LTER LAN.

Future acquisitions will include a PC with a Intel 80386 processor for modeling and data analysis on the LAN, and a portable, battery operated computer that will serve for field programming and data downloading from "smart" instruments.

III.C.4.d. Analytical Quality Control - Many of the samples of water, vegetation and soil will be chemically analyzed in the laboratories at ITF and CEER. Active quality assurance programs are present in both laboratories. EPA-approved procedures are followed where applicable, and in other cases standard methods for vegetation and soil analysis are used. Blind analyses of EPA check samples or other standards (e.g., standard orchard leaves) are made frequently, and analytic results are cross-checked with other laboratories.

To insure comparability of results, we will survey analytical methods used by other LTER sites and adopt applicable methods in our laboratory. Also, LTER sites will be included in the cross-checking program. We are currently a participating lab in the Tropical Soil Biology and Fertility program and will follow their "MINPAC and MAXPAC" protocols in soils analyses (Anderson and Ingram 1987).

III.D. Summary and Relationship to NSF Core Research Areas

The five core areas of research that are common to existing LTER sites (p. 2) are embodied in the research work proposed for the LEF. One of the core areas, patterns and frequency of disturbance to the research site, comprises the central focus of the research activity in the LEF proposal. Tree fall gaps, land slides, and hurricanes are the major natural disturbances to be considered. Research in progress at the LEF also includes other disturbances that supplement the main focus of the LTER work. Examples of those other disturbances under study are: gamma radiation (Odum and Pigeon 1970; Silander 1985); recovery of sites from accidental disturbances such as an airplane crash (Byer and Weaver 1977); and recovery of vegetation from experimental cuts and silvicultural treatments (Brown et al. 1983). The history of disturbance of the LEF is well documented (Brown et al. 1983).

The proposed research work integrates the remaining four core research areas to the disturbance theme by examining in detail how ecosystem biotic structure reorganizes following a perturbation and how the reorganization of ecosystem structure and function affects site quality or its capacity to support biotic activity. The model of nutrient cycling used to guide the collection of nutrient data and for estimating use efficiencies (Fig. 15) embodies the core area on "patterns of inorganic inputs and movements of nutrients through soils, groundwater, and surface waters". The coupling to disturbance is illustrated by the external forces acting on the nutrient cycles of the forest (also illustrated in Fig. 15).

"Patterns and control of organic matter accumulation in surface layers and sediments" are embodied in the model that addresses SOM (Fig. 14 and 19). The focus of our research in this core area is on surface soil layers and sediment export, as sediment accumulation is not an important process in the steep mountain terrain of the LEF.

"Pattern and control of primary productivity" will be addressed with particular emphasis on the effects of nutrient availability, severity of disturbance, and climatic factors (rainfall, temperature, saturation deficit, and light intensity). Rates of primary productivity drive ecosystem recovery after disturbance and place nutrient demands on the system that can be met from soil storage or through biotic recycling. The quality of the products of primary productivity (such as roots or litter) in turn may affect the rate of nutrient mineralization. All models presented in this proposal require an understanding of how rates of primary productivity respond to autochthonous and allochthonous factors. Continuous assessment of forest primary productivity is thus an important aspect of our long-term measurement routines (Table 2).

Trophic structure will be addressed in both spatial and temporal scales and will comprise a wide array of populations believed to be representative of the complex aquatic and terrestrial food webs found in the LEF. The process of the restructuring of food webs following perturbation and the potential effects of this process on such ecosystem functions as nutrient cycling efficiency provides another example of the integrated approach used in this proposal. We address the five core research areas within the context of unifying hypotheses that help explain whole ecosystem response to periodic perturbations at different scales.

IV. ADVANTAGES OF THE LEF AS AN LTER SITE

The advantages of the LEF as a Long-Term Ecological Research site are grouped into six categories: 1) tradition in long-term ecological research, 2) scientific opportunities, 3) excellence of current programs and facilities, 4) simplicity of logistics, 5) security and continuity of management, and 6) institutional commitment.

IV.A. Research tradition. Research at the site began over 100 yr ago with a series of botanical explorations (e.g., Eggers 1883). Over 300 publications record the results of this activity (Mosquera and Feheley 1984; Appendix 1). Portions of the LEF were protected by the Spanish Crown as early as 1860 and transferred to the U.S. government in 1898. Since then the area of the protected forest has increased to 11,231 ha. In 1939 the U.S. Forest Service established a research station whose mission was to study and manage the LEF. Facilities for this research included a new building in Rio Piedras, field stations, and permanent personnel. Today, the Institute of Tropical Forestry is among the oldest tropical forestry research institutions in the hemisphere and is the oldest among U.S. government facilities, including those in Panama and Hawaii. The Institute published 24 volumes of the Caribbean Forester when regional research journals were not available. The rich research tradition in the site is documented in Odum and Pigeon (1970), Brown et al. (1983), Mosquera and Feheley (1984), and elsewhere.

IV.B. Research opportunities. Unique scientific opportunities result from the size of the island of Puerto Rico, its mountainous topography, and its location relative to the trade wind belt and hurricane trajectories. For example, rainfall ranges from 500 to 5,000 mm in ecosystems separated by a three hour drive; within the LEF rainfall ranges from about 2,000 mm to 5,000 mm along a 1,000 m elevational transect. The diversity of rainfall conditions, complex topography, and variety of soil types in the LEF support a rich array of ecosystems with contrasting diversity of species and functional attributes that cannot be matched in continental sites where distance and access limit comparative research. The range of mature vegetation available for research in Puerto Rico is representative of many environments in tropical America. Using the life zone system of Holdridge as a guide, the six life zones in Puerto Rico (4 in the LEF) represent 40% of the land area in Central America (Budowski 1965).

Periodic visits by hurricanes and tropical depressions in the Caribbean and their interaction with steep topography offer an opportunity to study long-term responses of complex ecosystems to natural disturbance, which is greatly enhanced in the LEF by the existence of long-term observation plots established by the Forest Service in the 1940's. These plots have changed dramatically in species composition and growth rates during the 30-40 yr since the last major disturbance (Crow 1980, Brown et al. 1983, Weaver 1986).

Scientific opportunities are enhanced by the fact that the island of Puerto Rico as a whole (including much of the lowlands of the LEF but not its uplands) was deforested early in this century (to about 10% forest cover) and has since recovered naturally to about 35% forest cover (Birdsey and Weaver 1982). Critical questions about succession, ecosystem recovery from human devastation, and the issues of how tropical diversity responds to human disturbance and management can be addressed in an island where research sites can be protected over long time periods.

The intensive management of lands by the U.S. Forest Service in the LEF adds another dimension to the scientific opportunity at the site. Beginning in 1933 over 2,300 ha of plantations of dozens of exotic and native tree species were established in the LEF. Today the LEF has some of the oldest research plantations in the American tropics as well as an arboretum with over 100 tree species planted. Twenty mahogany provenances from central America (NW Mexico to Panama) and the West Indies are preserved in the arboretum. Seed collections are available and knowledge of tree establishment is much more advanced in Puerto Rico than in any other tropical research site (e.g., 412 tree species, including 100 native ones, have been tested; Marrero 1947).

In the LEF, the availability of long-term weather and growth records, an understanding of land use change, and a complex mix of ecosystems provide unique opportunities to study tropical moist forests under natural conditions, disturbed by periodic hurricanes, responding to previous human impacts, and managed with the purpose of restoring the land to production. Nowhere else under the U. S. flag is there such a mix of opportunity and background understanding for long-term ecological research. Furthermore, forest lands such as those in the LEF are the ones that are most likely to be deforested and used for agricultural production. Understanding montane moist tropical ecosystems should have priority if ecological research is to be of relevance to resolving the fiber and water needs of the growing human populations in the tropics.

IV.C. Excellence of programs and facilities. Previous studies in the LEF provide essential information to support ecosystem-oriented long-term ecological research (Table 5). The completeness of this background information is demonstrated by the fact that many other tropical sites are only now beginning to collect information that has been collected for years in the LEF. Few sites, for example, have comparable understanding of the hydrologic system, soils, geology, vegetation, life histories of tree species, systematics of all groups, food webs, climatic factors, and ecosystem response to radiation, cutting, herbicides, human management, and other controlled treatments. The LEF has strength in all of these important subjects because its research has always been oriented to understanding ecosystems and has benefited from strong institutional support. The long list of active investigators and programs is another measure of the excellence

Table 5. Data sets available for locations within the Luquillo Experimental Forest. Data currently being collected are indicated by -->.

Data category	Tabonuco	Colorado	Palm	Dwarf	Plantation
Maps and remote sensing					
Detailed topography	1964, 1986				
Landslide mapping	1980	1980	1980	1980	1980
Aerial photos	7x since 1936	6x since 1936	same	same	same
Landsat TM, TMS, TIMS	1983 -->	1983 -->	1983 -->	1983 -->	1983 -->
Climatology					
Air temperature	since 1909		1980-81	since 1909	
Daily precipitation	since 1909		1980-81	since 1909	
Instant. precipitation (NADP standard gauge)	1984 -->				
Solar radiation	1958-62,63-66	1965-66		1958-62	
Wind speed, direction	1958-62,63-66	1965-66		1958-62	
Relative humidity	1958-62,63-66	1965-66	1980-81	1958-62	
Chemical composition					
Precipitation (bulk)	1964-69,83-85			1964-69,83-85	
Precipitation (NADP)	1984 -->				
Dryfall (NADP)	1984 -->				
Cloudwater				1984-86	
Bulk soil	1965-69		1980-81		1982-85
Soil solution	1965-69,83-84		1980-81		
Throughfall	1966-69,83-84		1980-81		
Stemflow	1966-69		1980-81		
Streamwater	1966-69,83 -->		1980-81		
Plant. tissue	1966-69		1980-81		1982-85
Animal tissue	1979-82				
Fungal tissue	1983-86				
Vegetation					
Composition	1965-69	1984-85	1980-81	Howard (1968)	1982-85
Biomass	1957-62,66-67	1984-85	1980-81	Dugger (1977)	1982-85
Tree growth/mortality	since 1943	since 1943	since 1943	since 1943	since 1943
Litterfall	1964-66,70-73, 81	1984-85	1980-81		1982-85
Litter decomposition	1964-65,68-71, 81-82		1980-81		
Wood decomposition	1940 -->				
Mycorrhizal associations	1983-86				
Fauna					
Composition	1958-59,64-66, 81 -->				
Biomass	1958-59,81 -->				
Microflora					
Composition	1960-69,80-83				
Biomass	1984-85				
Watershed					
Streamflow	1940-53,76 -->				

and continuity of the ecological research activity in the LEF.

The facilities available to support research in the LEF are excellent and provide the needed conditions for a vigorous long-term ecological research program. There is institutional commitment for continued upgrading and maintenance of these facilities.

The Institute of Tropical Forestry (ITF) is a research branch of the USDA Forest Service's Southern Forest Experiment Station. It is housed in San Juan and in the LEF where it shares facilities with the U. S. Forest Service, Caribbean National Forest. Among the resources available through ITF are:

- Headquarters building with all expected facilities (xeroxing, office and audiovisual equipment, etc.)
- Woodshop, fully equipped
- All apparatus needed to measure photosynthesis, respiration, transpiration, and stomatal resistance in the field
- Solar drying oven and several other large convection ovens, programmable
- Analytical laboratory for soils and vegetation (over $200,000 in equipment)
- Research nursery with automatic watering system
- Tropical forestry library with 55,000 documents, 10,000 bound volumes. 100 journal subscriptions, map, film, and slide collection, microfilm of the entire Oxford forestry collection, FAO documents and journal listings from larger libraries (e.g., Oxford, University of Georgia, University of Florida, National Agricultural Library) in microfiche, and computerized literature searching facilities.
- Walk-in refrigerator
- Eleven micro computers with printers, hard disks, and modems
- A Data General MV-6000 computer with a 354 megabite disk, capacity for 24 terminals, and hook-up with U.S. Forest Service FLIPS system
- Federal telecommunication system (FTS) facilities
- Access to GSA vehicles plus three 1/2 ton trucks
- Research herbarium with over 95% of the 700+ tree species in Puerto Rico, and access to more extensive herbaria in the same campus location
- Tropical wood collection

The Center for Energy and Environment Research (CEER) is a research organization with facilities located on the Medical Science (San Juan) and Mayaguez campuses of the University of Puerto Rico. The Terrestrial Ecology Division of CEER is primarily dedicated to tropical forest research at the El Verde field site in the LEF. A core of seven staff scientists direct ecosystem-level research with the assistance of field and laboratory technicians and graduate students. Adjunct scientists from Puerto Rico and the mainland also carry out research related to the main CEER program under individual grants or through Oak Ridge Associated University Fellowships. Resources available to CEER scientists include:

- The El Verde Field Station with living and laboratory facilities for up to 15 scientists.
- A library at the field station containing publications relevant to the LEF and access through the CEER main library to all holdings on the island.

- Comprehensive collections of local flora and fauna that are more than 80% complete for the following groups: fungi, ferns, dicotyledons, myriapods, arachnids, insects, amphibians, and reptiles. Extensive reference collections of invertebrates are also accessible at the USDA Experimental Station (San Juan) and Biology Departments on the Rio Piedras and Mayaguez campuses of the University of Puerto Rico.
- Three permanent walk-up towers offering access to the canopy and a 25 m canopy walkway constructed from scaffolding from which even non-athletic researchers can take canopy measurements.
- A 300 m power cable providing electricity at one of the walk-up towers.
- Radio and telephone communication from the field station to San Juan and off-island plus mobile units.
- An NADP wet-dry deposition station.
- ERDAS remote image analysis system with table digitizer
- IBM PC-AT (5), IBM PC (5), and Apple IIe (3) computers plus access to University mainframe computers.
- A Li-Cor portable photosynthesis system
- A Li-Cor leaf area meter
- A complete nutrient analysis laboratory in San Juan including an Erba C-H-N analyzer, pressure bombs, a calorimeter, a Waters ion chromatograph, a Technicon Auto Analyzer II, gas chromatographs, spectrophotometers, a Perkin Elmer atomic absorption spectrophotometer, and other associated equipment.
- A field laboratory at El Verde that has light meters, balances, microscopes, pH meters, hoods, etc., line power backed up by a generator, and gas, air, and vacuum lines.
- Outdoor and indoor animal-holding facilities with light and temperature control and one-way observation windows.
- Equipped electrical and carpentry shops at the field station.
- Facilities for field-drying of specimens.

An upgrade of communications facilities and an increase in both laboratory and living space at the El Verde Field Station are planned for the near future. A proposal for funds for these improvements will be submitted to NSF in February, 1988. Matching support has already been requested from UPR.

IV.D. Simplicity of logistics. U.S. citizens require no passport to visit Puerto Rico as the island is a Commonwealth of the United States and all Puerto Ricans are American citizens. U.S. mail and U.S. currency are used in Puerto Rico. Communication with the mainland U.S. is routine with all major services such as overnight delivery, scientific supply houses, direct dialing telephone system, etc. available on the island. U. S. federal agencies operate in Puerto Rico as they do in the mainland. Researchers arriving on the island find their research areas within an easy drive and yet not subject to vandalism. Work in the forest offers no hazards from animals or poisonous plants. Electricity, walk-up towers, canopy walkways, and field laboratories have been available at the El Verde site since the early 1960's. No country in the American tropics offers the logistic simplicity and convenience for ecological research that Puerto Rico offers.

Nine of the investigators contributing to this proposal are permanent residents of Puerto Rico. Their full-time presence on site will greatly facilitate long-term studies that require frequent measurements and will enhance the possibility of studying infrequent but important natural events (e.g., hurricanes, landslides). Researchers at many sites in the tropics are prevented from spending long periods in the field by commitments to their home institutions. These commitments added to the high cost of transportation often result in studies that emphasize short-term intensive measurements for logistic rather than scientific reasons. The high proportion of resident scientists involved in this proposal minimizes these logistic problems. Even our off-island collaborators will be able to visit the field easily and frequently. Air fares from mainland cities are reasonable, and direct flights are available from many places. Travel from any site in the continental U.S. to the LEF requires less than a day and no stopovers.

Dealing with foreign customs, foreign currency, government instability, long drives on poor roads, isolation, disease and public health hazards, poor medical facilities, dangerous animals, uncertainty about equipment transport and maintenance, 50 cycle and 220 volt electrical systems, and transportation of food supplies and equipment to sites are normal logistic difficulties in most tropical countries but not in Puerto Rico. For these reasons, cost-effectiveness of research is much greater in Puerto Rico.

IV.E. Security and continuity of management. The Luquillo Experimental Forest is an administrative division of the U. S. National Forest System. In addition to its status as a National Forest, the LEF is a Biosphere Reserve and contains several research natural areas. The LEF is managed for research by the Forest Service under a 50-yr management plan that covers until the year 2030. Hence, future management plans for the forest are known well in advance.

Research areas within the forest are under the control of the Institute of Tropical Forestry. The El Verde research site is occupied by CEER under a use agreement with the Forest Service. All of these administrative arrangements have been in force for many years and are contained in the management plan for the LEF.

Procedures for the approval of research projects are already established by the Forest Service. No other manipulations can be performed in the LEF without Forest Service approval. Projects proposed for the LTER sites under this proposal have been endorsed by the Forest Service (Appendix 2). The approval of future projects will take advantage of the established review system with additional input from LTER investigators.

The principal investigators both have full-time positions in Puerto Rico. Lugo is a native of Puerto Rico and Waide has been a resident for eight years. Both plan to make Puerto Rico their permanent home and are committed to continuing ecosystem research regardless of the fate of this proposal. Each PI has commitments outside of the LTER program. Should this proposal be successful, Waide will continue his responsibilities as Head of CEER's Terrestrial Ecology Division, but 80% of his time will be devoted to the LTER program. Lugo will continue to perform his duties as Project Leader of ITF, but his research will focus on the goals of the current proposal.

IV.F. Institutional commitment. The Center for Energy and Environment Research and the Institute of Tropical Forestry have demonstrated their commitment to the LTER concept by donating salary support for seven scientists as a shared cost in the proposal. The value of this support exceeds $270K annually. In addition, the President of the University of Puerto Rico has shown his support for our effort to establish an LTER site in Puerto Rico by pledging matching funds of $150K annually for the first five year LTER period. An allocation of $58K has already been made by the University to match the $150K we received from NSF in October, 1987. Further support for the LTER program comes in the form of donated facilities, equipment, technician time, and student support. The total value of shared costs surpasses the annual request to NSF contained in this proposal.

V. SITE DESCRIPTION

The program of research proposed herein will be conducted on the Luquillo Experimental Forest, which is congruent with the Caribbean National Forest. A detailed description of the site is contained in Brown et al. (1983) and is summarized here.

V.A. Location and facilities

The LEF is located in the Luquillo Mountains in eastern Puerto Rico (Fig. 2) and is administered from the Rio Piedras offices of the U. S. Forest Service, located 25 km west of the field site. Local headquarters for the Forest Service is in a new facility at Catalina on the NE slope of the Luquillo Mountains.

Research facilities on the LEF include field stations at El Verde in the tabonuco zone and at East Peak in the colorado forest (see below), both maintained by the University of Puerto Rico. In addition, the Forest Service has office and housing space in the towns of Sabana and El Verde on the east and west slopes of the mountains, respectively. Housing for 25 scientists is available in these various facilities. Laboratory space is available at the two field stations.

V.B. Physical and biological features

The LEF occupies 11,231 ha of land in the Luquillo Mountains of eastern Puerto Rico and encompasses elevations ranging from 100-1070 m above sea level (Table 1). Increasing elevation is accompanied by changes in climate, soils, and vegetation structure (Brown et al. 1983). Data from weather stations distributed around the Luquillo Mountains indicate a general increase in rainfall with elevation except at the highest station (Fig. 22; Brown et al. 1983). Rainfall records from an intensive one-year study of precipitation distribution along the elevational gradient indicate a fairly regular increase in rainfall from a low of 287 cm/yr at 540 m elevation to a high of 429 cm/yr at El Yunque peak (1000 m elevation; Holben et al. 1979). Rainfall is more evenly distributed throughout the year at lower elevations than at higher elevations (Brown et al. 1983).

Mean annual temperature decreases with elevation in the LEF (Fig. 22). The range of temperatures in a given month is smaller at low elevation stations, while the annual variation in mean monthly temperatures is the same for low and high elevations (3.5 and 3.0 degrees C, respectively; Brown et al. 1983). Average absolute humidity is higher and varies less at high elevations than at lower elevations. Wind velocity is higher and more constant at higher elevations. While the annual pattern of incoming solar radiation is the same at sea level and the top of the Luquillo Mountains, the absolute amount of radiation measured is half as great at high elevation due to cloud cover (Briscoe 1966).

Although a variety of soil types occur at lower altitudes in the Luquillo Mountains, the most frequently encountered soil is Humatas clay, a deep, well-drained soil overlying volcanic-clastic rocks. Soil at slightly higher elevations on the western slopes of the mountains is a Los Guineos clay and silty loam, also deep and well-drained. Soils at higher elevations are continuously wet and unstable, with low permeability and high susceptibility to slippage. As much as 20% of higher elevations are stony and lack soil cover.

Tree height, number of species, basal area, average tree dbh, and complexity index decrease with elevation and only stem density increases (Fig. 22). Vines and lianas become less common and epiphytes more common with increasing elevation (White 1963). Impeded soil drainage has been suggested as a factor in determining the distribution of tabonuco and colorado forest types (Wadsworth and Bonnet 1951). As soil becomes wetter, drainage poorer, and organic matter content greater with increasing elevation, surface roots arranged in a mat become more common. Odum (1970) suggests that this surficial root structure and the presence of many epiphytes may be important in maintaining tight nutrient cycles in colorado and dwarf forest where evapotranspiration is low and precipitation and run-off are high.

V.C. Site history

The LEF has been the site of research activity conducted by the ITF, CEER, the University of Puerto Rico, and a large number of investigators from mainland universities. The scale of research has varied from the study of individual species to long-term studies of whole ecosys-

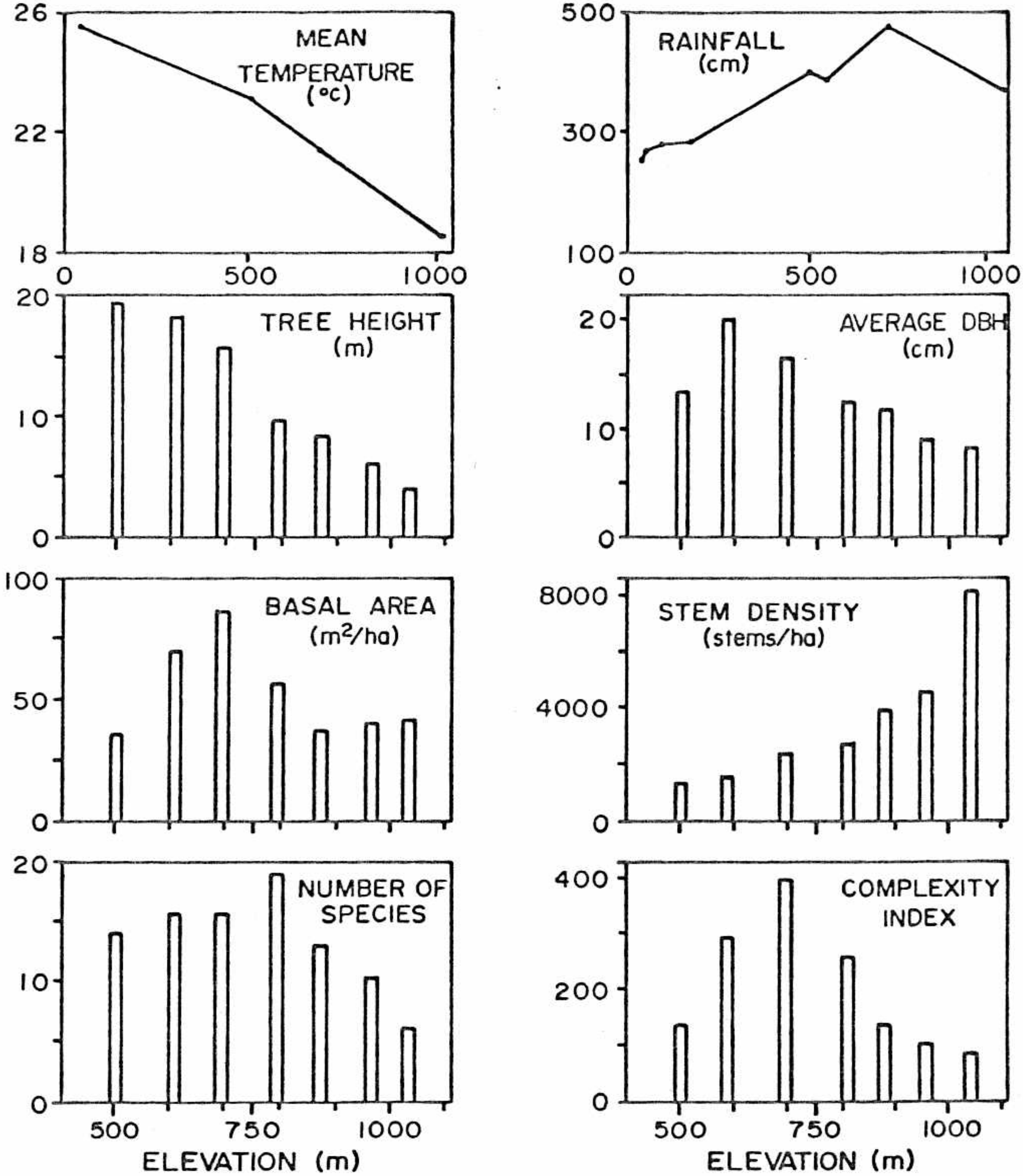

Figure 22. Variation of rainfall, temperature, stand structure, diversity, and complexity index with elevation in the Luquillo Mountains (adapted from Brown and Lugo 1983).

tems. Forest growth and regeneration have been the principal focus of studies conducted by ITF with the goal of improving forest management practices. CEER has conducted studies of nutrient cycling and transport under the auspices of the U. S. Department of Energy.

In addition to studies of tabonuco forest mentioned above (Section III.A.1), researchers have conducted detailed investigations of the other LEF forest types. The dwarf forest has been the subject of a number of studies including a series of floristic surveys by the Arnold Arboretum (Howard 1968, 1969, 1970 and others). Studies of plant physiology (Weaver 1972, 1975), photosynthesis (Odum and Cintron 1970), secondary succession (Byer and Weaver 1977), nutrient cycling (Weaver et al. 1986), and rain and cloud chemistry (McDowell and Trinidad 1985, Trinidad 1986) have also been conducted in dwarf forest. The carbon, phosphorus, and water cycles of a palm stand were studied by Frangi and Lugo (1985), and the long-term growth and stand dynamics of palm were investigated by Lugo and Rivera-Battle (in press) and Lugo and Bokkestijn (in prep.). The colorado forest has been the subject of an intensive study (Weaver 1985, 1986) that examined 40 years of growth records as well as succession and ecosystem net above-ground primary productivity.

V.D. Permanent research and monitoring programs

Past research accomplishments on the LEF are reflected in the over 350 publications and 65 dissertations from the forest. The principal research sponsors continue to be the Forest Service, the U. S. Department of Energy, and the University of Puerto Rico, although DOE's involvement in directed research is decreasing. NASA has recently initiated support of research in the LEF, and a variety of other agencies provide funds through grants to individual investigators. The expenditures on these research projects in FY-1987 totaled $2 million.

Current research directions emphasize the use of long-term research plots and experimental manipulations of gaged watersheds to examine ecosystem processes. ITF maintains over 20 permanent plots throughout the LEF (Fig. 2) that cover the full range of natural and introduced forest types. Some of these plots have continuous data sets stretching back for over 40 yrs. In addition, sites used in the AEC irradiation project in the 1960's continue to be monitored for long-term changes and successional trends (Silander 1985, Silander and Waide, in prep). The data sets currently available from the LEF are shown in Table 5.

VI. SITE AND PROGRAM MANAGEMENT

VI.A. Site Administration - The LEF is administered by the U. S. Forest Service with ITF having primary responsibility for research programs. The working relationship between CEER and ITF/USFS has existed for over 25 years and is embodied by a Memorandum of Understanding between CEER and USFS.

VI.B. Program Management - The proposed management structure of the LEF LTER program is shown in Figure 23. A. E. Lugo and R. B. Waide are the program co-directors and will have responsibility for developing and guiding the proposed research. Waide and Lugo will supervise a site manager, who will have responsibility for the day-to-day operation of the program, and a data manager, who will be responsible for data entry and retrieval. Waide will have administrative responsibility for the grant.

The Program Policy Committee is an advisory body composed of collaborating scientists and representatives of CEER, ITF, and USFS. The members of the committee in residence will meet monthly, and the full committee will meet at least once a year. This committee has the responsibility to review new research proposals and changes to the stated program plan. It will be the policy of the LEF LTER program to accommodate all research proposals compatible with the objective of this proposal and to actively seek funds to support such proposals. The committee will make annual reviews of the five-year research schedules submitted by individual collaborators. The Program Policy Committee has the responsibility to review program direction in the light of emerging research results.

An annual review of program direction will also be conducted by the National Advisory Committee, whose members are H. Mooney, H. T. Odum, W. Swank, P. Risser, and R. Wiegert. Management of individual LTER components will be the responsibility of the scientists collaborating in each component. Leadership responsibility will be exercised by a full-time resident scientist within each group whenever possible, or by a designated non-resident scientist. The co-directors and site manager will be responsible for on-site supervision and control of each research component.

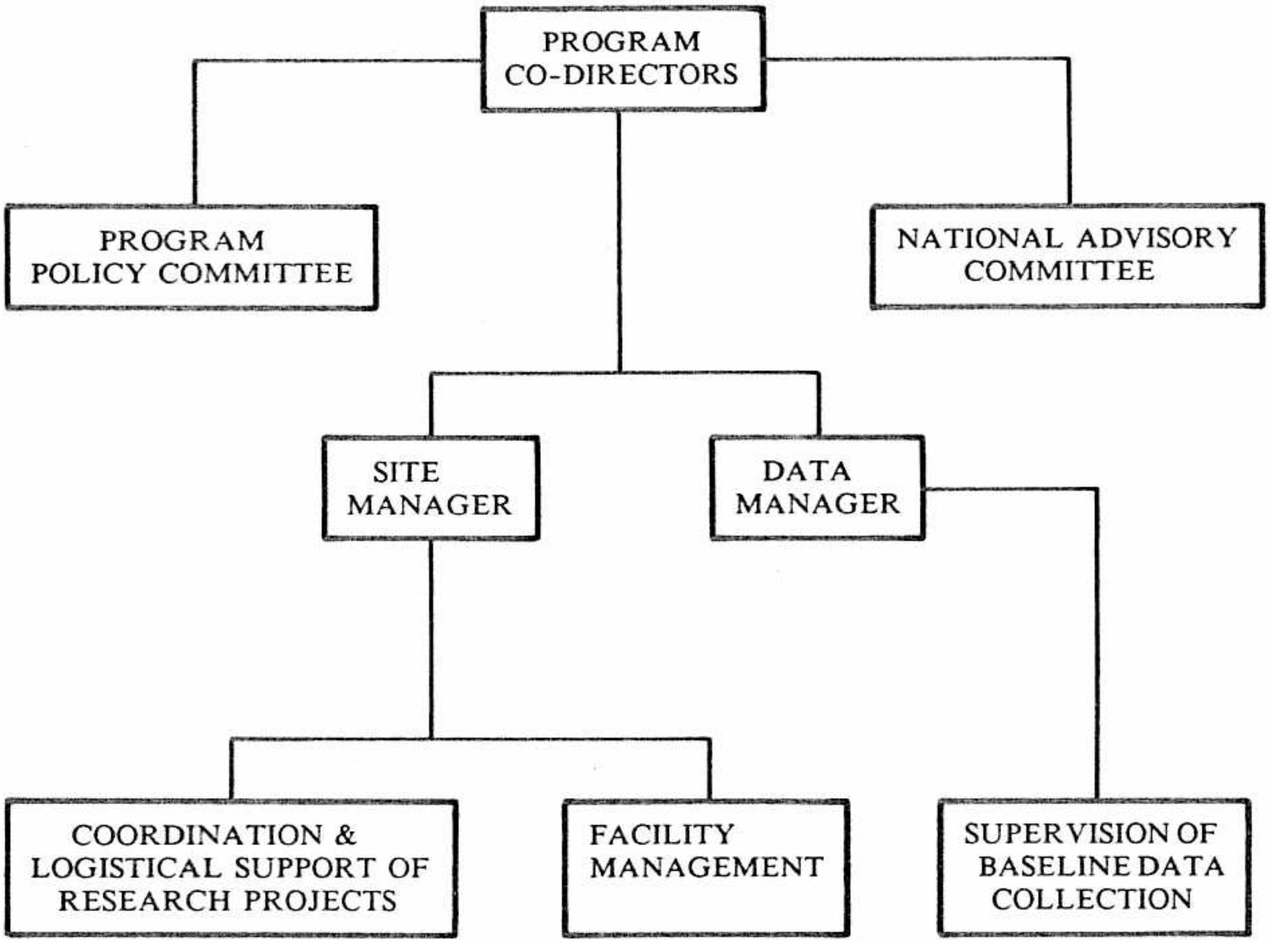

Figure 23. Administrative structure of the LEF LTER Program.

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APPENDIX 1. CURRICULUM VITAE OF COLLABORATORS

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Scientific advisor to the CO_2 Program of the Institute of Energy Analysis in Oak Ridge, Tennessee - 1982-1984; Executive Committee of U.S. Man and the Biosphere program - 1981-1984; Senior Advisory Committee to the President of the University of Puerto Rico - 1982-present (Chairman, 1985-present); National Research Council Committee on EcologicalProblems Associated with Development of the Humid Tropics - 1980-1982; General Scientific Advisory Panel of the UNESCO Man and the Biosphere Program in Paris - 1985-1986; Advisory Committee, Yale Tropical Resources Institute - 1985-present; Advisor to Rhode Island University Coastal Zone Program for tropical countries - 1985-present.

PUBLICATIONS (5 YEARS)

Lugo, A. E. 1988. Estimating reductions in the diversity of tropical forest species. Chapter 6 in F. M. peter and E. O. Wilson (editors). Biodiversity. National Academy Press, Washington, D. C. (in press).

Lugo, A. E., S. Brown, and J. Chapman. 1987. An analytical review of production rates and stemwood biomass of tropical forest plantations. Forest Ecology and Management (in press).

Lugo, A. E., M. M. Brinson, and S. Brown (editors). 1987. Forested wetlands. Ecosystems of the world Vol. 15. Elsevier, Amsterdam, The Netherlands (in press).

Weaver, P. L., R. A. Birdsey and A. E. Lugo. 1987. Soil organic matter in secondary forests in Puerto Rico. Biotropica 19(1):17-23.

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Murphy, P. G. and A. E. Lugo. 1986. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17:67-88.

Lugo, A. E. 1986. Water and the ecosystems of the Luquillo Experimental Forest. U.S.D.A. Forest Service, Southern Forest Expriment Station General Technical Report SO-63, New Orleans, LA. 17 p.

Brown, S., A. E. Lugo, and J. Chapman. 1986. Biomass of tropical tree plantations and its implications for the global carbon budget. Canadian Journal of Forest Research 16(2):390-394.

Twilley, R., A. E. Lugo, and C. Patterson-Zucca. 1986. Litter production and turnover in basin mangrove forests in southwest Florida. Ecology 67(3):670-683.

Lugo, A. E., M. J. Sanchez, and S. Brown. 1986. Land use and organic carbon content of some subtropical soils. Plant and Soil 96:185-196.

Lugo, A. E. and P. G. Murphy. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. Journal of Tropical Ecology 2:55-76.

Murphy, P. G. and A. E. Lugo. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18(2):89-96.

Lugo, A. E. 1986. mangrove understory: an expensive luxury? Journal of Tropical Ecology 2:287-288.

Lugo, A. E. and S. Brown. 1986. Steady state ecosystems and the global carbon cycle. Vegetatio 68(2):83-90.

Lugo, A. E. and J. Figueroa. 1985. Performance of Anthocephalus chinensis in Puerto Rico. Canadian Journal of Forest Research 15:577-585.

Jimenez, J. A., A. E. Lugo, and G. Cintron. 1985. Tree mortality in mangrove forests. Biotropica 17(3):177-185.

Frangi, J. L. and A. E. Lugo. 1985. Ecosystem dynamics of a subtropical floodplain forest. Ecological Monographs 55(3):351-369.

Brown, S. and A. E. Lugo. 1984. Biomass of tropical forests: a new estimate based on forest volumes. Science 223:1290-1293.

Lugo, A. E. and F. Quinones-Marquez. 1983. Organic carbon expoert from intensively used watersheds in Puerto Rico. Pages 237-242 in E. T. Degens (editor). Transport of carbon and minerals in major world rivers. Part 2. SCOPE/UNEP Sonderband, Heft 5S Hamburg, Germany.

Lugo, A. E., M. Applefield, D. J. Pool, and R. B. McDonald. 1983. The impact of hurricane David on the forests of Dominica. Canadian Journal of Forest Research 13(2):201-211.

Brown, S., A. E. Lugo, S. Silander, and L. Liegel. 1983. Research history and opportunities in the Luquillo Experimental Forest. U.S.D.A. Forest Service, Southern Forest Experiment Station, General Technical Report SO-44. 128 p.

Brown, S. and A. E. Lugo. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14(3):161-187.

Lugo, A. E. and S. Brown. 1982. Conversion of tropical moist forests: a critique. Interciencia 7(2):89-93.

Lugo, A. E. 1982. Some aspects of the interaction among nutrient cycling, hydrology, and soils in wetlands. Water International 7(4):178-184.

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CURRENT POSITION

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EDUCATION

1978 - Ph.D. in Zoology, University of Wisconsin - Madison
Dissertation: Interactions between tropical resident and north temperate migrant birds in southern Campeche, Mexico.

1973 - M.S. in Zoology, University of Wisconsin - Madison
Thesis: Seasonal changes in the avifauna of a tropical wet forest.

AWARDS AND GRANTS

1987 - Principal investigator since 1982 on U. S. DOE grant no. HA-0203020 to conduct studies of cycling and transport processes in a subtropical wet forest. The annual award has varied between $150,000-359,000.

1986 - Co-principal investigator for grant titled "Joint NASA/University of Puerto Rico Research Program". NASA, $250,000/year for five years.

1985 - Principal investigator for grant entitled "Biomass Accumulation in Secondary Tropical Forest in Early Successional Stages". NASA, $217,000.

SELECTED PUBLICATIONS

Waide, R. B. and P. M. Narins. 1988. Tropical forest bird counts and the effect of sound attenuation. Auk (in press).

Sader, S. A., A. T. Joyce, R. B. Waide, and W. T. Lawrence. 1986. Monitoring tropical forests from satellite and aircraft platforms: some limitations and new approaches. Tenth William T. Pecora Memorial Remote Sensing Symposium. pp. 473-482.

Brower, L. P., L. S. Fink, R. B. Waide, and P. R. Spitzer. 1983. Overwintering Monarch butterflies as food for insectivorous birds in Mexico. Biotropica 15:151-153.

Waide, R. B. and D. P. Reagan. 1983. Competition between West Indian anoles and birds. An. Nat. 121:133-138.

Reagan, D. P., R. W. Garrison, and R. B. Waide. 1982. Preliminary evaluation of trophic structure in a Puerto Rican rain forest. pp. 78-99 in Octavo Simposio de Recursos Naturales. Departamento de Recursos Naturales. San Juan,PR.

Waide, R. B. 1981. Interactions between resident and migrant birds in southern Campeche, Mexico. Tropical Ecology 22:134-154.

Waide, R. B. 1980. Resource partitioning between migrant and resident birds: the use of irregular resources. pp. 337-352 in Migrant birds in the American Tropics: Distribution, Ecology, Behavior, and Conservation. E. S. Morton and A. Keast, eds. Smithsonian Institution Press.

Waide, R. B., J. T. Emlen, and E. J. Tramer. 1980. The distribution of migrant birds in the Yucatan Peninsula: a survey. pp. 165-172 in Migrant Birds in the American Tropics: Distribution, Ecology, Behavior, and Conservation. E. S. Morton and A. Keast, eds. Smithsonian Institution Press.

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EDUCATION

Ph.D. Ecology and Evolutionary Biology, Cornell University, expected 5/88. Thesis title: Groundwater seepage and its relationship to nutrient budgets and sediment chemistry in Mirror Lake, New Hampshire.
M.S. Environmental Science, University of Massachusetts, 1979
B.S. Pre-medical Studies, Davidson College, 1972

EXPERIENCE

Research Scientist I, Center for Energy and Environment Research, Univ. of Puerto Rico, February, 1986 to present.
Graduate Research Assistant, Cornell University, 1982 - 1985.
Teaching Assistant, Cornell University, 1980 - 1982.
Smithsonian-Peace Corps Environmental Program volunteer, Brazil, 1977 - 1980.
Graduate Research Assistant, University of Massachusetts, 1975 - 1977.

PUBLICATIONS

Hartman, E., C.E. Asbury and R.A. Coler. Seasonal variations of primary productivity in Lake Tapacurá, a tropical reservoir. J. Freshwater Ecol. 1 (2): 203-213. 1981.
Asbury, C.E., F. Vertucci, M. Mattson and G.E. Likens. Comparing historic and modern data to detect acidification of Adirondack lakes. Submitted to Environmental Science and Technology.
Lodge, D.J. and Clyde Asbury. Rhizomorph fungi retard downhill export of fallen leaves in a tropical montane rain forest. Submitted to Mycologia.

CONTRIBUTED PAPERS AND NATIONALLY ABSTRACTED PROCEEDINGS

Asbury, C.E. Effects of seepage on the exchange of nutrients between littoral sediments and the epilimnion of an oligotrophic lake. Presented at Ecological Society of America, Fort Collins, Colo. 8/84.
Asbury, C.E. The effects of groundwater seepage on the nutrient content of sediments in an oligotrophic lake. Presented at American Society of Limnology and Oceanography, Minneapolis, Minn. 6/85.
Asbury, C.E., F. Vertucci, M. Mattson, and G.E. Likens. Comparison of historic and modern data to detect acidification of lakes in the Adirondack Mountain region of New York. Presented at Ecological Society of America, Syracuse, NY. 8/86.
Asbury, C.E. and D.J. Lodge. Rhizomorph fungi retard downhill export of fallen leaves in a tropical montane rain forest. Presented at Ecological Society of America, Columbus, OH. 8/87.

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Ph.D. Botany (Ecology). University of Florida, 1983.
Organization for Tropical Studies, Inc. Summer Course in the Fundamentals of Tropical Biology: An Ecological Approach. Costa Rica, 1977.
M.F.S. Forest Science. Yale, School of Forestry and Environmental Sciences, 1976.
B.S. Biology. Western Michigan University, 1974.

PROFESSIONAL POSITION:

Assistant Professor of Biology, Emory University, 1985-present.

LANGUAGES:

Read and speak Spanish.

SELECTED PUBLICATIONS:

Ewel, J., C. Berish, B. Brown, N. Price, and J. Raich. 1981. Slash and burn impacts on Costa Rican wet forest site. Ecology 62:816-829.
Berish, C.W. 1982. Comparison of root biomass and surface area in three successional tropical forests. Can. J. For. Res. 12:699-704.
Berish, C.W. and H.L. Ragsdale. 1985. Chronological sequence of element concentrations in wood of *Carya* spp. in the southern Appalachian Mountains. Can. J. For. Res. 15:477-483.
Berish, C.W. and H.L. Ragsdale. 1986. Chemical partitioning of metals in southern Appalachian forest soils. Journal of Environmental Quality 15:183-187.
Berish, C.W. and J.J. Ewel. Roots in tropical succession. Plant and Soil. (In press).
Harker, A.C. and C.W. Berish. Fine root dynamics of regenerating southern Appalachian forests: the influence of black locust. Can. J. For. Res. (Submitted).

SELECTED SUPPORT:

Principal investigator.
Fine root growth in a loblolly pine plantation at the B.F. Grant Forest. 1987-1989. Award amount: $29,924. Georgia Power Company.

Co-Principal investigator.
Co-Principal investigator with others from a multi-institutional consortium. Long-term ecological research in forested watersheds at Coweeta. 1986-1990 Award amount: $186,000. NSF.

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RESEARCH EXPERIENCE:

1974: Population ecology of a terrestrial bromeliad, Panama
1975 - continuing: Treefalls, gap-phase regeneration, and tree community structure, Barro Colorado Island, Panama
1977,78: Revegetation of landslides, Panama
1977: Bird community ecology, Panama
1982 - continuing: experimental demography of tropical forest trees, Panama
1987: Biological survey of wildlands in Belize
1987: Treefalls and forest dynamics, Borneo

RELEVANT PUBLICATIONS:

Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica 14:158-160.

Brokaw, N. V. L. 1982. Treefalls: frequency, timing, and consequences. Pages 101-108 in E. G. Leigh, A. S. Rand, and D. M. Windsor (eds.). The Ecology of a Tropical Forest. Smithsonian Institution Press, Washington DC.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682-687.

Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. Pages 53-69 in S. T. A. Pickett and P. S. White (eds.). The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Brokaw, N. V. L. 1986. Seed dispersal, gap colonization, and the case of *Cecropia insignis*. Pages 323-331 in A. Estrada and T. H. Fleming (eds.). Frugivory and Seed Dispersal. Dr W Junk, The Hague.

Brokaw, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. Journal of Ecology 75:9-19.

Brokaw, N. V. L., and S. M. Scheiner. 1988. Gap processes and forest characteristics. Ecology (Special Feature), to appear.

Garwood, N. C., D. P. Janos, and N. Brokaw. 1979. Earthquake-caused landslides: a major disturbance to tropical forests. Science 140: 997-999.

Schemske, D. W. and N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. Ecology 62:938-945.

GRANTS:

National Geographic Society, 1982
Charles A. Lindbergh Fund, 1983
National Geographic Society, 1984
National Science Foundation (BSR 8516633), 1986
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Yale University; Ph.D., 1970; M.S., 1966.
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FELLOWSHIPS:

University of Oklahoma Associate's Distinguished Lectureship, 1984-85.
NSF Post-doctoral Fellowship, University of California, Santa Barbara, 1970-71.
NSF Traineeship, Yale University, 1968-89.
NDEA Title IV Fellowships, Yale University, 1965-67.

RECENT PUBLICATIONS (26 publications in total):

Covich, A.P. 1987. On contrasts in tropical stream communities. Oikos (in review).

Covich, A.P. 1987. Atyid shrimp in the headwaters of the Luquillo Mountains, Puerto Rico: filter feeding in natural and artificial streams. Verhanlungen Internationale Vereinigung fur Theoretische und Augewardte Limnologie (In review)

Bradbury, J.P., R.M. Forester, and A.P. Covich. 1987. Paleolimnology of Laguna de Cocos, Albion Island, Rio Hondo, Belize. In: Paleoecology of the Maya Lowlands (M. Pohl, ed.). University of Minnesota Publications in Archeology. (In press)

Covich, A.P. 1987. Optimal use of space by neighboring central-place foragers. Advances in Behavioral Economics (1):249-294.

Lodge, D.S., K.M. Brown, S.P. Klosiewski, R.A. Stein, A.P. Covich, B. Leathers, and C. Bronmark. 1986. Distribution of freshwater snails: spatial scale and the relative importance of physicochemical and biotic factors. Am. Malacological Bulletin 5:73-84.

Corr, M., A.P. Covich and T. Yoshino. 1984. Vertical migration and time allocation of a freshwater snail. Hydrobiologia 112:69-72.

Covich, A.P. 1983. A contrast in species diversity: Three molluscan assemblages from aquatic and terrestrial habitats. Pp. 120-139 In: Pulltrouser Swamp: A preliminary study of habitat, land use, and settlement of the prehistoric Maya (B.L. Turner II and P.D. Harrison, eds.). University of Texas Press, Austin.

Bloom, P.R., M. Pohl, C. Buttleman, F. Wiseman, A.P. Covich, and C. Miksicek, J. Ball and Julie Stein. 1983. Prehistoric Maya agriculture and the development of alluvial deposits near San Antonio, Rio Hondo, Belize. Nature 301:417-419.

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EDUCATION

B.A.	Harvard College	Major - German	1967
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Ph.D.	Colorado State University	Major - Range Science	1977

PUBLICATIONS (LAST 5 YEARS)

Fetcher, N., S. F. Oberbauer, G. rojas, and B. R. Strain. 1987. Efectos del régimen de luz sobre la fotosíntesis y el crecimiento en plantulas de árboles de un bosque lluvioso tropical de Costa Rica. Revista de Biología Tropical.

Clark, D. A., R. Dirzo, and N. Fetcher. (eds.). 1987. Ecología y ecofisiología de plantas en los bosques Mesoamericanos. Revista de Biología Tropical.

Shaver, G. R., N. Fetcher, and F. S. Chapin III. 1986. Growth and flowering in Eriophorum vaginatum: Annual and latitudinal variation. Ecology 67:1524-1535.

Wunderle, J. M., Jr., M. S. Castro, and N. Fetcher. Risk averse foraging by bananaquits on negative energy budgets. Behavioral Ecology and Sociobiology (in press).

Chapin, F. S., III, N. Fetcher, and K. Kielland, J. R. Everett, and A. E. Linkins. Enhancement of productivity and nutrient cycling by flowing ground water in Alaskan tussock tundra. Ecology (in press).

Oberbauer, S. F., B. R. Strain, and N. Fetcher. 1985. Effect of CO_2-enrichment on seedling physiology and growth of two tropical tree species. Physiol. Plantarum 65:352-356.

Fetcher, N. 1985. Effects of removal of neighboring species on growth, nutrients, and microclimate of Eriophorum vaginatum. Arctic and Alpine Research 17:7-17.

Fetcher, N. S. F. Oberbauer, and B. R. Strain. 1985. Vegetation effects on microclimate in lowland rain forest in Costa Rica. International Journal of Biometeorology 29:145-155.

Chazdon, R. and N. Fetcher. 1984. Light environments of tropical forests. In Physiological Ecology of Plants of the Wet Tropics. E. Medina, H. A. Mooney, and C. Vazquez-Hanes (eds.). Dr. W. Junk, The Hague, p. 27-36.

Chazdon, R. L. and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. Journal of Ecology 72:553-564.

Fetcher, N., T. F. Beatty, B. Mullinax, and D. S. Winkler. 1984. Changes in arctic tussock tundra thirteen years after fire. Ecology 65:1332-1333.

Fetcher, N., B. R. Strain, and S. F. Oberbauer. 1983. Effects of light regime on the physiology and growth of seedlings of tropical trees: A comparison of gap and pioneer species. Oecologia 58:314-319.

Fetcher, N. and G. R. Shaver. 1983. Life histories of tillers of Eriophorum vaginatum in relation to tundra disturbance. Journal of Ecology 71:131-148.

Fetcher, N. 1983. Optimal life history characteristics and vegetative demography in Eriophorum vaginatum. Journal of Ecology 71:561-570.

Linkins, A. E. and N. Fetcher. 1983. Effects of surface-applied Phrudhoe Bay crude oil on vegetation and soil processes in tussock tundra. Pages 723-728 in Permafrost: 4th International Conference, Proceedings. National Academy Press. Washington, DC.

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Research interests explore long-term changes in vegetation composition and structure, especially those resulting from natural disturbance regimes and vegetation development. In the boreal region of Canada research on the history and pattern of lightning-ignited fires has shown regional variations in the fire regime that are controlled by physiography, climate and the distribution of fire breaks. The recent history of disturbance and geomorphology characteristics of the region are used to explain current landscape-level patterns of vegetation distribution. Comparative stratigraphic investigations of northern peatlands in North America and Scandinavia have focussed on the relative importance of autogenous development and allogenic factors in controlling mire formation. The effect of broad-scale mire development on upland disturbance processes such as fire connects these two areas of interest.

Current research involves the study of wind damage to forests on a variety of spatial scales ranging from differences in species susceptibility to landscape level patterns of damage. Geographically this work is centered on hurricane change to New England forests. Comparative studies on tornado damage to forests in western Pennsylvania recently initiated in collaboration with S. Pickett.

RELEVANT BIBLIOGRAPHY

Foster, D. R. 1983. Fire history and landscape patterns in southeastern Labrador. Canadian Journal of Botany 61: 2459-2471.

Foster, D. R. and G. A. King. 1984. Landscape features and developmental history of a patterned mire complex on the Eagle Plateau, southeastern Labrador. Journal of Ecology 72: 115-143.

Foster, D. R. 1985. Vegetation development following fire in the Picea mariana (black spruce)-Pleurozium forests of southeastern Labrador. Journal of Ecology 73: 517-534.

Foster, D. R. and G. A. King. 1986. Vegetation pattern and diversity in S. E. Labrador, Canada: Betula papyrifera (birch) forest development in relation to fire history and physiography. Journal of Ecology 74: 465-483.

Foster, D. R. and S. C. Fritz. 1987. Mire development, pool formation, and landscape processes of patterned fens in Dalarna, central Sweden. Journal of Ecology 75: 409-437.

Foster, D. R. 1987. Disturbance history, vegetation dynamics, and community organization of the old-growth Pisgah Forest, southern New Hampshire. Journal of Ecology 75: In press.

Foster, D. R. 1987. Species and stand response to catastrophic wind in Central New England. Journal of Ecology 75: In press.

Foster, D. R., H. E. Wright, M. Thelaus and G. A. King. 1987. Bog development and the dynamics of bog landforms in central Sweden and eastern Canada. Journal of Ecology 75: In Press.

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B. A	University of California, Santa Barbara, with honors, Field Biology	1964
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Ph.D.	Duke University, Botany	1971

SELECTED PUBLICATIONS (5 YEARS)

Montagnini, F., B. Haines, and W. T. Swank. 1988 (in press). Factors controlling nitrification in soils of early successional and oak-hickory forests in the southern Appalachians. Forest Ecology and Management.

White, D. L., B. L. Haines, and L. R. Boring. 1988- in press. Litter decomposition in southern Appalachian black locust and pine-hardwood stands: litter quality and nitrogen dynamics. Canadian Journal of Forest Research.

Haines, B. L. and W. T. Swank. 1988. Acid precipitation effects on forest processes. pp 359-366. In: Swank, W. T. and D. Crossley (eds). Forest hydrology and ecology at Coweeta. Springer-Verlag, New York.

White, D. L., B. L. Haines, and L. R. Boring. 1988- in press. Litter decomposition in southern Appalachian black locust and pine-hardwood stands: litter quality and nitrogen dynamics. Canadian Journal of Forest Research.

Haines, B. L., M. Black, J. Fail, Jr., L. McHargue, G. Howell. 1987. Potential sulfur gas emissions from a tropical rainforest and a southern Appalachian deciduous forest. pp 559-610. In Hutchinson, T. C. and K. M. Meema (eds) "Effects of Atmosphric Pollutants on Forests, Wetlands, and Agricultural Ecosystems", Series G. Ecological Sciences 16. Springer-Verlag, New York.

Haines, B. L. 1987. Research interests in tropical soil biology. Intecol Bulletin 14: 7-9

Boring, L. R., D. L. White, and B. L. Haines. 1987. Litterfall and throughfall nitrogen transfers in black locust (Robinia pseudoacacia L.) and pine-hardwood stands. Nitrogen Fixing Tree Research Reports 5:54-56

Montagnini, F., B. Haines, L. Boring, and W. Swank. 1986. Nitrification potentials in successional black locust mixed hardwood forest stands in the southern Appalachians, USA. Biogeochemistry 2:197-210.

Fail, J. L. Jr., M. B. Hamazh, B. L. Haines and R. L. Todd. 1986. Above and below ground biomass, production, and element accumulation in riparian forests of an Agricultural Watershed in Correll, D. L. (ed) Watershed Research Perspectives. Smithsonian Environmental Research Center. Edgewater, Md.

Neufeld, H. S., J. A. Jernstedt, and B. L. Haines. 1985. Direct foliar effects of simulated acid rain. I. Damage, Growth and gas exchange. New Phytologist 99:389-405.

Haines, B. L., J. A. Jernstedt, and H. S. Neufeld. 1985. Direct foliar effects of simulated rain. II. Leaf surface characteristics. New Phytologist 99:407-416.

Haines, B. L., C. F. Jordan, H. Clark, and K. Clark. 1983. Acid rain in an Amazon rainforest. Tellus 35B, 77-80.

Haines, B. L. 1983. Forest ecosystem SO4-S input-output discrepancies and acid rain: are they related? Oikos 41, 139-143.

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EDUCATION

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Ph.D.	University of North Carolina, Chapel Hill	Zoology 1970

SELECTED PUBLICATIONS (FROM A TOTAL OF 75)

Hall, C.A.S. 1986. The changing intellectual climate of fisheries management. Environ. Mgmt. 10:331-334.

Detwiler, P., and C.A.S. Hall. Tropical forests and the global carbon cycle. Science. 239:42-47.

Bogdonoff, P., R. P. Detwiler and C. A. S. Hall. 1984. Land use change and carbon exchange in the tropics: III. Structure, dynamics and sensitivity analysis of the model. Environ. Mgmt. 9:345-354.

Hall, C. A. S. and D. DeAngelis. Models in ecology: Paradigms found or paradigms lost? Ecological Bulletin. 66(3):339-346.

Detwiler, R. P., C. A. S. hall and P. Bodgonoff. 1984. Land use change and carbon exchange in the tropics: II. Preliminary simulations for the tropics as a whole. Environ. Mgmt. 9:335-344.

Hall, C.A.S., R. P. Detwiler, and P. Bodnofoff and S. Underhill. 1984. Land use change and carbon exchange in the tropics: I. Detailed assessment for Costa Rica, Panama, peru and Bolivia. Cover article, Environ. Mgmt. 9:313-334.

Cleveland, C., R. Costanza, C. Hall and R. Kaufmann. 1984. Energy and the U.S. Economy: A Biophysical Perspective. Cover article, Science. 225:890-897.

Woodwell, G. M., C. A. S. Hall, D. E. Whitney, R. A. Houghton and R. A. Moll. 1979. The Flax Pond ecosystem study: The annual metabolism and nutrient budget of a salt marsh. pp. 491-511. IN: R. L. Jefferies and A. J. Davy (eds.). Ecological processes in Coastal Environments. Blackwell Scientific Publications.

Woodwell, G. M., C. a. S. Hall, D. E. Whitney and R. A. Houghton. 1979. The Flax Pond ecosystem study; Exchanges of inorganic nitrogen between an estuarine marsh and Long Island Sound. Ecology. 60:695-702.

Hall, C. A. S., C. Ekdahl and D. Wartenberg. 1975. A fifteen-year record of biotic metabolism in the northern hemisphere. Nature. 255:136-138.

BOOKS

Day, J. W., C. A. S. Hall, A. Yanez, and M. Kemp. 1988. Estuarine Ecology. Wiley Interscience, New York. In press.

Hall, C. A. S., C. Cleveland and R. Kaufmann. 1986. Energy and Resource Quality: The Ecology of the Economic Process. Wiley Interscience, New York. 577 pp.

Hall, C. A. S. and J. Day (eds.). 1977. Ecosystem Modeling in Theory and Practice. Wiley Interscience, New York. 684 pp.

CURRICULUM VITAE

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Education

Ph.D., Ecology, Joint-University of California, Davis and San Diego State University Doctoral Program, 1983.

M.Sc., Biology, San Diego State University, 1975.

B.A., Environmental Biology, Univ. California, Santa Barbara, 1970.

Publications

Lawrence, W.T. 1987. Gas exchange characteristics of representative species from the scrub vegetation of Chile. p. 279-394 In J.D. Tenhunen, F.M. Catarino, O.L. Lange, and W.C. Oechel (eds) Plant Response to Stress - Functional Analysis in Mediterranean Ecosystems. NATO Advanced Science Institute Series. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.

Waide, R.B., S.A. Sader, W.T. Lawrence, and A.T. Joyce. 1987. Estimation of tropical forest biomass using Landsat-TM data. p. 103-108 In Third Annual Landsat TM Workshop, September 1-3 1987, Univ. of California, Santa Barbara. Laboratory for Terrestrial Physics, National Aeronautics and Space Administration, Landsat Data Applications Code 620, Goddard Space Flight Center, Greenbelt, MD 20771.

Lawrence, W.T. 1987 (in review). The use of satellite-based remote sensing to detect drought stress in vegetation canopies. Proceedings of the 5th MEDECOS meeting, International Society of Mediterranean Ecologists, Montpellier, France, 1987.

Chapin, F.S., W.C. Oechel, K. Van Cleve, and W.T. Lawrence. 1987 (accepted for publication). The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. Oecologia.

Lawrence, W.T. 1985. Gas exchange and water relations of cultivars of pigeon pea (Cajanus cajan) in Puerto Rico. Proc 21st Annual meeting Caribbean Food Crops Society, Trinidad.

Oechel, W.C. and W.T. Lawrence. 1985. Physiological Ecology of the Taiga. p. 66-94 In Mooney, H.A. and B. Chabot (eds) Physiological Ecology of the Vegetation of North America. Chapman & Hall, London.

Cox, G.W. and W.T. Lawrence. 1984. Cemented horizon in arctic Alaskan sand dunes. Amer. J. Sci. 283:369-373.

Lawrence, W.T. 1984. Gas exchange characteristics of mango (Mangifera indica) in Puerto Rico: Field measurements with a portable photosynthesis system. Tech. Rpt. CEER T-183, Center for Energy and Environment Research, San Juan, P. R., 25 p.

Lawrence, W.T. and W.C. Oechel. 1984. Soil temperature effects on carbon exchange in taiga trees. p. 127-136 In N.S. Margaris, M. Arianoustou-Farragitaki, and W.C. Oechel (eds) Being alive on land. T.VS, vol. 13, Dr. W. Junk Publishers, The Hague.

Lawrence, W.T. 1983. Soil temperature effects on carbon exchange in taiga species of interior Alaska, Ph.D. Dissertation, University of California, Davis, 131 p.

Lawrence, W.T. and W.C. Oechel. 1983. Soil temperature effects on the carbon exchange of taiga seedlings. I. Root respiration. Can. J. For. Res. 13: 840-849.

Lawrence, W.T. and W.C. Oechel. 1983. Soil temperature effects on the carbon exchange of taiga seedlings. II. Photosynthesis, respiration, and conductance. Can. J. For. Res. 13: 850-859.

Oechel, W.C. and W.T. Lawrence. 1981. Carbon allocation and utilization. pp. 185-235 In P.C. Miller (ed), Resource Use by Chaparral and Matorral. A comparison of vegetation and function in two Mediterranean type ecosystems. Vol. 39, Ecological Studies. Springer-Verlag, New York.

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EDUCATION

Ph.D. Botany/Ecology, North Carolina State University, 1985
Thesis title: Ecollgy of ectomycorrhizal and endomycorrhizal fungi associated with eastern cottonwood.

M.S. Plant Pathology/Entomology, N. Carolina State Univ., 1979
Thesis title: Genetic diversity in populations of Helminthosporium carbonum pathogenic to corn in N. Carolina.

B.S. Botany, Kent State University, 1976.

PROFESSIONAL EXPERIENCE:

Current position:
Research Scientist I, Center for Energy & Environment Research. Beginning date: July, 1985.
Previous Positions:
Senior Associate, Center for Energy & Environment Research. October, 1983 to July, 1985.
Laboratory Technician, North Carolina Agricultural Extension Service, Plant Disease and Insect Diagnostic Clinic. 1979-1982.
Research Assistant, Department of Plant Pathology, North Carolina State University, 1976-1978.
Assistant Greenhouse Manager, Kent State University, 1974-1976.

PUBLICATIONS IN PEER REVIEW JOURNALS (1980-PRESENT):

Lodge, D. J. 1988. Three new species of Mycena from Puerto Rico. Transactions of the British Mycological Society. In Press.

Lodge, D. J. 1987. Nutrient concentrations, percentage moisture and density of field-collected fungal mycelia. Soil Biol. & Chem. 19:727-733.

Wunderle, J. M., and D. J. Lodge. 1987. The effect of age and visual cues on floral patch use by bananaquits. Animal Behaviour. In press.

Lodge, D. J. and K. J. Leonard. 1984. A cline and other patterns of genetic variation in Cochliobolus carbonus isolates pathogenic to corn in North Carolina. Can. J. Bot. 62:995-1005.

CONTRIBUTED PAPERS AND NATIONALLY ABSTRACTED PROCEEDINGS (1980-): NINE OTHER PUBLICATIONS AND PROJECT REPORTS

Lodge, D. J., 1986. English translations of Polish and Russian Literature on mycorrhizae. (A bibliography). CEER Pub. No. X-215. Center for Energy and Environment Research, G.P.O. Box 3682, San Juan, P. R. 00936. 5 pages.

Lodge D. J., 1985. The effect of soil water potential on the formation of endo- and ectomycorrhizae in eastern cottonwood. The Sixth N. Am. Conference on Mycorrhizae, June 1984, Bend, Oregon. p. 280. Forest Research Laboratory, Oregon State Univ., Corvallis OR.

Lodge, D. J. and W. J. Pfeiffer. 1985. A comparison of early decomposition rates in bagged versus teathered leaves in a Puerto Rican rainforest. Proceedings of the Association for Tropical Biology, August 1985.

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EDUCATION

Butler University, B.S. in Biology, 1958
Emory University, M.S. in Biology, 1960
Ph.D. in Biology, 1961; major field, Ecology; Minor field, Geology.
Ph.D. dissertation: Effects of Ionizing Radiation on a Natural Plant Community.

SELECTED RELEVANT PUBLICATIONS

Ecosystems Dynamics

Influence of Environmental Stressors Upon Energy Flow in a Natural Terrestrial Ecosystem. In: Stress Effects on Natural Ecosystems. John Wiley and Sons (with A. Lugo). 1981. Chapt. 8. Pp. 79-102.

Influence of nutrient availability upon ecosystem structure. In: Mineral Cycling in Southeastern Ecosystems; ERDA Symposium Series, CONF-740513, 1975. pp. 756-779, with R. Meyer and C. G. Wells.

Tropical Ecology

Ecological Guidelines for Development of Tropical Mountain Regions. In: Proceedings of the International Symposium on Ecology of the Development of Tropical and Subtropical Mountain Areas. Oct. 1985, pp. 185-187. China Academic Publishers.

Growth and Survival of the Sierra Palm under Radiation Stress in Natural and Simulated Environments. In: A Tropical Rain Forest. Ed. H. T. Odum. Chapter 9, 12 pp.

Direct and Indirect Effects of Radiation on Seedling Diversity and Abundance in a Tropical Rain Forest. In: A Tropical Rain Forest. Ed. H. T. Odum. Chapter D10. 32 pp.

Radiation Ecology

Long Term effects of ionizing radiation on a pine forest. (With K. Dyer). 1985. Bull. ASB. Vol. 31, No. 2, pp. 57.

Pattern of Radiation Exposure in the Tropical Rain Forest. In: A tropical Rain Forest. Ed. H. T. Odum, Chapter C4. 12 pp.

Effects of Gamma Irradiation of the Forest at El Verde. In: A Tropical Rain Forest. Ed. h. T. Odum, Chapter D1.

WILLIAM J. PARTON, JR.

ACADEMIC TRAINING

B.S.	1966	Pennsylvania State Univ.	Meteorology
M.S.	1968	University of Oklahoma	Meteorology
Ph.D.	1972	University of Oklahoma	Meteorology

PROFESSIONAL EXPERIENCE

1971-1974	Postdoctoral Fellowship	Natural Resource Ecology Laboratory
1974-1975	Postdoctoral Fellowship	National Center for Atmospheric Research
1975-1982	Research Associate	Natural Resource Ecology Laboratory, Colorado State University
1982-present	Senior Research Scientist	Natural Resource Ecology Laboratory, Colorado State University

RECENT PUBLICATIONS (40 SINCE 1979)

Parton, W. J., A. R. Mosier, and D. S. Schimel. Spatial and temporal variability on rates and pathways of nitrous oxide production in a shortgrass teppe. Biogeochemistry (in press).

Parton, W. J., J. W. B. Stewart, and C. V. Cole. 1987. Dynamics of C, N, P and S. in grassland soils: A model. Biogeochemistry.

Schimel, D. S., W. J. Parton, F. J. Adamsen, R. G. Woodmansee, R. L. Senft, and M. A. Stillwell. 1986. The role of cattle in the nitrogen budget of a shortgrass steppe. Biogeochemistry 2:39-52.

Mosier, A. R., and W. J. Parton. 1985. Denitrification in a shortgrass prairie: A modelling approach. Planetary Ecology, pp. 441-452.

Parton, W. J. 1984. Predicting soil temperature in a shortgrass steppe. Soil Sci. 138 (2):93-101.

Peterson, Thomas C., and W. J. Parton. 1983. Diurnal variations of wind speeds at a shortgrass prairie site. A model. Agric. Meteorol. 28:365-374.

Parton, W. J., D. W. Anderson, C. V. Cole, and J. W. B. Stewart. 1983. Simulation of soil organic matter formations and mineralization in semiarid agroecosystems. In: R. Lowrance, R. Todd, L. Asmussen, and R. Leonard (eds.) Nutrient Cycling in Agricultural Ecosystems, pp. 533-550. U. Georgia Press, Athens.

Mosier, A. R., W. J. Parton, and G. L. Hutchinsen. 1983. Modelling nitrous oxide evolution from cropped and natural soil. Environ. Biogeochemistry, Ecol. Bull. (Stockholm) 35:229-241.

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Risser, P. G., and W. J. Parton. 1982. Ecological Analysis of a tallgrass prairie: Nitrogen cycle. Ecology 63(5):1342-1351.

Mosier, A. R., M. Stillwell, W. J. Parton, and R. G. Woodmansee. 1981. Nitrous oxide emissions from a native shortgrass prairie. Soil Sci. Am. J. 45:614-619.

Parton, W. J., and J. A. Logan. 1981. A sample model for diurnal change in soil and air temperature. Agric. Meteorol. 23:205-216.

Parton, W. J., W. K. Lauenroth, and F. M. Smith. 1981. Water loss from a shortgrass steppe. Agric. Meteorol. 24:97-109.

Parton, W. J., W. D. Gould, F. J. Adamsen, S. Torbit, and R. G. Woodmansee. 1980. NH_3 volatilization model. In Behavior in Soil Plant Systems, pp. 233-244. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Parton, W. J., and P. G. Risser. 1980. Impact of management practices on a tallgrass prairie. Oecologia 46:223-234.

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EDUCATIONAL BACKGROUND

BS Bowling Green State University. 1972. Magna cum laude

PhD University of Georgia. 1988 (pending). [Dynamics and energetics of the grazing food web associated with Spartina alterniflora in a Georgia intertidal grassland].

PROFESSIONAL EXPERIENCE

Current Position

Senior Associate, Rank 6
Center for Energy and Environment Research
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April 1983-present.

PUBLICATIONS

Gallagher, J. L., P. L. Wolf, and W. J. Pfeiffer. 1984. Rhizome and root growth rates and cycles in protein and carbohydrate concentrations in Georgia Spartina alterniflora Loisel. plants. American Journal of Botany 71:165-169.

Robertson, J. R. and W. J. Pfeiffer. 1982. Deposit feedinb by the ghost crab Ocypode quadrata. Journal of Experimental Marine Biology and Ecology 56:165-177.

Pfeiffer, W. J. and R. G. Wiegert. 1981. Grazers on Spartina and their predators. Pages 87-112 in L. R. Pomeroy and R. G. Wiegert, editors. The ecology of a salt marsh. Springer Verlag Publishers, New York.

Gallagher, J. L., R. J. Reimold, R. A. Linthurst, and W. J. Pfeiffer. 1980. Aerial production, mortality and mineral accumulation-export dynamics in Spartina alterniflora and Juncus roemerianus plant stands in a Georgia salt marsh. Ecology 61:303-312.

MANUSCRIPTS IN REVIEW/PREPARATION

Pfeiffer, W. J. 1989. Arboreal arachnids. In: D. Reagan and R. Waide, editors. The Food Web of a Tropical Rain Forest. University of Chicago Press.

Pfeiffer, W. J. 1989. Litter anthropods, IBID. [The Food Web of a Tropical Rain Forest, University of Chicago Press].

Pfeiffer, W. J. Dynamics and energetics of a spider assemblage in the litter of a tropical rain forest.

MEMBERSHIPS IN PROFESSIONAL SOCIETIES

Ecological Society of America
Entomological Society of America
American Arachnological Society
Association for Tropical Biology

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Manager, Ecology and Environmental Planning Department, ESE, Denver, Colorado (1982 to Present).
Head, Terrestrial Ecology Division, Center for Energy and Environment Research, San Juan, Puerto Rico (1980 to 1982).
Scientist and Project Manager, NUS Corporation (1974 to 1976, Pittsburgh, Pennsylvania; 1976 to 1979, Denver, Colorado)
Instructor, Zoology Department, University of Arkansas, Fayatteville, Arkansas (1970 to 1973)

EDUCATION

Ph.D.	Zoology (Ecology)	1972	University of Arkansas
M.S.	Biology	1967	University of New Mexico
B.A.	Biology	1964	Hartwick College

PUBLICATIONS (5 YEARS)

Reagan, D. P. 1986. Foraging behavior of Anolis stratulus in the rain forest canopy. Biotropica 18(2):157-160.
Reagan, D. P. 1984. Ecology of the Puerto Rican boa (Epicrates inornatus) in the Luquillo Mountains of Puerto Rico. Caribbean J. Sci. 20:119-128.
Reagan, D. P. 1984. Competitive interactions between rain forest lizards: field observations and experimental evidence. Bull. Ecol. Soc. Amer. 65:233 (abstract).
Reagan, D. P. 1984. Foraging Behavior of Anolis stratulus in the Rain Forest Canopy. Occas. Pap. Center for Energy and Environment Research, San Juan, Puerto Rico (in press).
Reagan, D. P. Species Distribution in Three-dimensional Habitats: the Rain Forest Anoles of Puerto Rico (manuscript submitted to the American Naturalist).
Reagan, D. P. and R. W. Garrison. 1983. Food web organization in a Puerto rican rainforest. Bull. Ecol. Soc. Amer. 64:114 (abstract).
Reagan, D. P. (with R. B. Waide). 1983. Competition between West Indian Anoles and Birds. Amer. Natur. 121:133-138.
Reagan, D. P., R. W. Garrison, and R. B. Waide. 1983. Preliminary Evaluation of Tropic Structure in a Puerto Rican Rain Forest. Proc. octabo Symposio de los Recursos naturales, San Juan, Puerto Rico.
Reagan, D. P. (with A. Estrada-Pinto, R. W. Garrison, R. B. Waide, and C. P. Zucca). 1983. Flora and Fauna of the El Verde Field Station. Center for Energy and Environment Research Publ. CEER-T-159, San Juan, Puerto Rico.
Reagan, D. P. 1982. Aspects of Ecosystem Organization Relevant to the Evaluation of Stress in a Tropical Rain Forest. Proc. DOE Symp. on Energy and Environmental Processes in Terrestrial Systems, Gaithersburg, Maryland.
Reagan, D. P. and C. P. Zucca. 1982. Inventory of the Puerto Rican Boa (Epicrates inornatus) in the Caribbean National Forest. Center for Energy and Environment Research Publ. CEER-T-136, San Juan, Puerto Rico.

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EDUCATION

Johns Hopkins University, Baltimore Maryland — 1983-1987
Doctor of Philosophy, Geog. & Environmental Engineering
Dissertation: "Sediment Budgets and Delivery in Suburban Watersheds", Graduate Fellow, Teaching Assistant

Wesleyan University, Middletown Connecticut — 1980-1982
Master of Arts in Earth & Environmental Science
Thesis:"Patterns of Bedload Transport in the Connecticut River Estuary". Graduate Fellow, Teaching Assistant.

San Francisco State University, San Francisco California — 1972-1977
Bachelors of Arts in Geology, Cum Laude
Thesis, "A Fortran Computer Program for Calculating the CIPW Normative Mineral Suite"

RELEVANT PROFESSIONAL EXPERIENCE

Century Engineering Inc., Towson Maryland — 1985-1987
Consulting Hydrologist and Geomorphologist

Peace Corps Jamaica, Kingston, Jamaica — 1984
Advisor in Hydrology and Program Development

Foster Parents Plan Inc. Colombia, South America — 1983
Advisor in Hydrogeology and Program Development

Peace Corps Malawi, Malawi, Central Africa — 1982
Advisor in Hydrogeology and Program Development

National Institute of Potable Water and Sewage — 1977-1979
Division of Hydrology, Dominican Republic
U.S. Peace Corps Volunteer Hydrogeologist

RELEVANT PUBLICATIONS AND SPECIAL REPORTS

"Physiography and Landuse History of the Bisley Experimental Watersheds" 1988, Twelfth Congress of Scientific Investigation, San Juan P.R.

"Recent Sediment Accumulation in an Urban Tidal Embayment, Anacostia Md." 1987, Amer. Soc. Civil Engineers, Coastal Sediments 87.

"River Flood Routing by Nonlinear Muskingum Method", 1987 Discussion by L. M. Brush and F.N. Scatena, Journal of Hydraulics Division, A.S.C.E.

"Identification and Evaluation of Watershed Sediment Sources", 1986 D.J. Coleman & F.N. Scatena, Inter. Ass. Hydrological Sci., Pub. 159.

"Sediment Delivery Pathways in Agricultural Watersheds", 1986 Trans. A.G.U.

Water Resource Assessments: Stewart Town Jamaica; Tumaco Colombia; Rural Malawi, Rural and Urban Dominican Republic.

"Floodplain Reconnaissance Study, November 1985 Flood, Potomac River" 1986, Interstate Commission on the Potomac River Basin Publication.

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EDUCATION AND DEGREES

University of North Carolina, Chapel Hill. M.A. 1951.
Cornell University, Ithaca, New York. Ph.D. 1956.

RELEVANT PUBLICATIONS

1986. Sexual size dimorphism in Eleutherodactylus coqui: selection pressures and growth rates. (with L. L. Woolbright). Herpetologica. In press.

1986. Courtship and mating behavior of a Puerto Rican frog, Eleutherodactylus coqui (with D. S. Townsend). Herpetologica. 42:165-170.

1986. The effect of temeprature on direct development in a terrestrial-breeding neotropical frog. (with D. S. Townsend). Copeia 1986 (2):520-523.

1985. Arboreal use and parachuting by a subtropical forest frog. Journal of Herpetology. 19(3):391-401.

1985. Direct development in Eleutherodactylus coqui (Anura:leptodactylidae): a staging table. (with D. S. Townsend). Copeia 1985(2)423-436.

1984. A most unforgettable experience. Notes from NOAH XI(4):81-85.

1984. Male parental care and its adaptive significance in a neotropical frog (with D. S. Townsend, F. H. Pough). Animal Behavior 32:421-431.

1984. Water balance of terrestrial anuran (Eleutherodactylus coqui) eggs: importance of parental care. (with T.L. Taigen, F. H. pough). Ecology 65(1):248-255.

1984. Response to simultaneous dehydration and thermal stress in three species of Puerto Rican frogs (with C. A. Beuchat, F. H. Pough). Jour. Comp. Physiology. B 154:579-585.

1983. Behavioural modification of evaporative water loss by a Puerto rican frog (with F. H. Pough, T. L. Taigen, P. F. Brussard). Ecology 64(2):244-252.

1983. Population density of tropical forest frogs: relation to retreat sites. Science 221)4610):570-572 (with F. H. Pough).

1982. Altitudinal and interspecific differences in the rehydration abilities of Puerto Rican frogs (Eleutherodactylus) (with F. H. van Berkum, F. H. Pough, P. F. Brussard). Physiological Zoology 55:130-136.

1981. Predation by giant crab spiders on the Puerto Rican frog, Eleutherodactylus coqui (with D. Formanowicz, K. Townsend, F. H. Pough and P. F. Brussard). J. Herpetologica 37(3):125-129.

1981. Internal fertilization in an oviparous frog (with D. S. Townsend, F. H. Pough and P. F. Brussard). Science 212(4493):469-471.

1979. The role of introduced species in a Jamaican frog community, pp. 113-146. IN H. Wolda, ed. Proceedings IV Symposium Internacional de Ecologia Tropical. Vol. I-III. Panama City, Panama.

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EDUCATION:

B.S.	1966	Pennsylvania State University (Geological Sciences)
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PUBLICATIONS (recent, relevant)

Swanson, F. J., R. J. Janda, T. Dunne, and D. N. Swanson (eds.). 1982. Sediment budgets and routing in forested drainage basins. USDA For. Serv. Gen. Tech. Rep. PNW-141, 165\p.

Miles, D. W. R., F. J. Swanson and C. T. Youngberg. 1984. Effects of landslide erosion on subsequent Douglas-fir growth and stocking levels in the western Cascades, Oregon. Soil Science Society of America Journal 48:667-671.

Franklin, J. F., J. A. MacMahon, F. J. Swanson, and J. R. Sedell. 1985. Ecosystem responses to the eruption of Mount St. Helens. National Geographic Research 1(2): 198-216.

Swanson, F. J.; Graham, R. L.; Grant, G. E. 1985. Some effects of slope movements on river channels. In: Proceedings, 1985 International Symposium on Erosion, Debris Flow and Disaster Prevention; 1985 September 3-5; Tsukuba, Japan. Tsukuba, Japan: Tokyo, Japan; 273-278.

Miles, D. W. R.; Swanson, F. J. 1986. Vegetation composition on recent landslides in the Cascade Mountains of western Oregon. Can. Jour. For. Res. 16: 739-744.

Swanson, F. J.; Kratz, T. K.; Caine, N.; Woodmansee, R. G. accepted. Landforms effects on ecological processes and features. Bioscience.

Swanson, F. J.; Franklin, J. F.; Sedell, J. R. in press. Landscape ecology perspectives from the forests and mountains of the Pacific Northwest,USA. In: I. S. Zonneveld and R. T. T. Forman (eds.). Trends in Landscape Ecology, Springer-Verlag.

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Education: Ph.D. 1985. Ecology. University of Alaska, Fairbanks.
M.S. 1977. Botany. University of Vermont, Burlington.
B.A. 1975. Botany. Goddard College, Plainfield, VT.

Positions Held: 1984-1985. Pre-doctoral Research Associate, Institute of Arctic Biology, University of Alaska, Fairbanks.

1985-1987. Post-doctoral Research Associate, Stanford University, Stanford, CA.

1988- Assistant Professor, University of Puerto Rico, Rio Piedras, PR.

Awards: 1985-1987. The role of the alien Myrica faya in altering primary succession in Hawaii Volcanoes National Park. NSF (Vitousek PI). $114,000/yr.
1984-1985. The role of salt crust formation on floodplain succession. NSF (Van Cleve PI). #58,000/yr.
1981-1984. Alaskan Resource Fellowship, a competitive grant from the University of Alaska. $10,000/yr.

Selected Publications:

Walker, L.R., J.C. Zasada, and F.S. Chapin III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. Ecology 67:1243-1253.

Walker, L.R. and F.S. Chapin III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67:1508-1523.

Vitousek, P.M. and L.R. Walker. 1987. Colonisation, succession, and resource availability: ecosystem-level interactions, in: Colonisation, succession, and stability, A. Gray, M. Crawley, and P.J. Edwards (eds.), Blackwell Scientific, Oxford, pages 207-223.

Walker, L.R. and F.S. Chapin III. 1987. Relative importance and interactions among processes controlling successional change. Oikos 50:131-135.

Vitousek, P.M., L.R. Walker, L.D. Whiteaker, D. Mueller-Dombois, and P.A. Matson. 1987. Biological invasion by Myrica faya alters ecosystem development in Hawaii. Science.

Walker, L.R. Submitted. Soil development and nitrogen availability in primary succession on an Alaskan floodplain.

Walker, L.R., P.M. Vitousek, and L.D. Whiteaker. In prep. Demography and ecosystem effects of an invading shrub, Myrica faya, in Hawaii.

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SELECT PUBLICATION DURING PAST 5 YEARS

1987 Willig, M. R. and R. Hollander. Vampyrops lineatus. Mammalian Species No. 275:1-4.

1987 Willig, M. R. and R. D. Owen. Fluctuating asymmetry in the cheetah: Methodological and interpretive concerns. Evolution, 41:225-227.

1987 Willig, M. R. and R. D. Owen. Univariate analyses of morphometric variation do not emulate the results of multivariate analyses. Syst. Zool. (In Press).

1987 Willig, M. R. and M. A. Mares. A comparison of bat assemblages from phytogeographic zones of Venezuela. Spec. Publ. The Museuem. Texas Tech Univ. (In Press).

1987 Morris, D. W., Z. Abramsky, B. J. Fox, and M. R. Willig (Editors). Patterns in the Structure of Mammalian Communities, Spec. Publ., The Museum, Texas Tech Univ. (In Press).

1987 Willig, M. R., M. R. Gannon, K. B. Willis, J. Arroyo-Cabrales, and T. J. Nicholson. Stenodermatinae, in The Mammals of South America (S. Anderson and A. L. Gardner, Eds.). Univ. of Chicago Press, Chicago (In Press).

1987 Willig, M. R. and E. A. Sandlin. Bat species diversity gradients in the New World: a comparison of "quadrat" and "band" methodologies, in: Latin American Mammals: Their Conservation, Ecology, and Evolution (M.A. Mares and D. J. Schmidly, Eds.) Univ. of Oklahoma Press, Oklahoma (In Press).

1987 Willig, M. R. Mammals, in: A Tropical Food Web (D. P. Reagan and R. B. Waide, Eds.). Univ. of Chicago Press, Chicago, IL (In Press).

1987 Gannon, M. R., M. R. Willig, and J. K. Kones, Jr. Sturnira lilium. Mammalian Species. (In Press).

1987 Willig, M. R. and H. H. Genoways. Geographical ecology of volant vertebrates in the West Indies: a comparison of bats and birds, in: Biogeography of the West Indies (H. H. Genoways and C. Wood, Eds.). Univ. Florida Press, Gainesville, FL (In Press).

1986 Willig, M. R., R. W. Garrison, and A. Bauman. Population dynamics and natural history of a neotropical walking stick, Lamponius portoricensis Rehn (Phasmatodea, Phasmatidae). Texas J. Sci. 38:131-137.

1986 Willig, M. R., R. D. Owen, and R. L. Colbert. Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. Sys. Zool. 35:195-203.

1986 Willig, M. R. Bat community structure in the Neotropics: A tenacious chimera? Rev. Chilena Hist. Natur. 59:151-168.

1985 Mares, M. A., M. R. Willig, and T. E. Lacher, Jr. The role of the Brazilian Caatinga in South American biogeography: Tropical mammals in an arid zone. J. Biogeography 12:57-69.

1985 Willig, M. R. Ecology, reproductive biology, and systematics of Neoplatymops mattogrossensis (Chiroptera, Molossidae). J. Mamm. 66:618-628.

1985 Willig, M. R. Reproductive patterns in bats from Caatingas and Cerrado biomes of Northeast Brazil. J. Mamm. 66:668-681.

1985 Willig, M. R. and J. K. Jones, Jr. Neoplatymops mattogrossensis. Mammalian Species No. 281:1-4.

1985 Willig, M. R. Reproductive activity in female bats from Northeast Brazil. Bat. Res. News 26:17-20.

1984 Willig, M. R. and A. Bauman. Notes on bats from the Luquillo Experimental Forest of Puerto Rico. CEER-T-194.

1983 Willig, M. R. Composition, microgeographic variation, and sexual dimorphism in Caatingas and Cerrado bat communities from Northeast Brazil. Bull. Car. Mus. 23:1-123.

Lawrence L. Woolbright
Assistant Professor of Biology
Siena College
Loudonville, N.Y. 12211
(518) 783-2451

EDUCATION

Ph.D. Ecology and Animal Behavior. 1985. State University of New York at Albany, Albany, N.Y. Dissertation: Sexual dimorphism in body size of the tropical frog, *Eleutherodactylus coqui*.

PUBLICATIONS

Woolbright, L.L. 1983. Sexual selection and size dimorphism in anuran Amphibia. American Naturalist 121:110-119.

Woolbright, L.L. 1985. Patterns of nocturnal movement and calling by the tropical frog, *Eleutherodactylus coqui*. Herpetologica 41:1-9.

Woolbright, L.L. 1985. Anuran size dimorphism: reply to Sullivan. American Naturalist 125:741-743.

Woolbright, L.L. and M.M. Stewart. 1987. Foraging success of the tropical frog, *Eleutherodactylus coqui*: the cost of calling. Copeia 1987:69-75.

Stewart, M.M. and L.L. Woolbright. 1989. The role of amphibians in the food web of an island subtropical forest. Chapt. 7 in Reagan and Waide (eds.) The Food Web of a Tropical Rain Forest. Univ. Chicago Press. In Prep.

RESEARCH EXPERIENCE IN LEF

1973. Feeding biology of *Alsophis portoricensis*. AEC summer undergraduate research program. Field time: 3 mos.

1979-1984. Reproductive success, foraging, time and energy budgets of *Eleutherodactylus coqui*. Dissertation research. Field time: 10 mos.

1986-1987. Variation in demography and behavior of *E. coqui* as a function of structural habitat characteristics. Field time: 3 mos.

(revised 10/7/87)

University of Puerto Rico
G.P.O. Box [illegible]-G
San Juan, Puerto Rico 00936

December 12, 1986

Dr. David T. Kingsbury
Assistant Director
Directorate for Biological,
Behavioral and Social Sciences
Room 506
National Science Foundation
1800 G Street, NW
Washington, D.C.

Dear Dr. Kingsbury:

The University of Puerto Rico recognizes the importance of long-term ecosystem studies in the tropics. The Center for Energy and Environment Research has, through research conducted at the El Verde Field Station, been one of the leaders in ecological research in the tropics for over 20 years. We view the National Science Foundation's Long-Term Ecological Research program as an important step in assuring continuity of ecological programs in the United States. We are particularly pleased by the recomendation that a tropical site be included in the LTER network.

The University of Puerto Rico fully supports the proposal submitted by the Center for Energy and Environment Research to develop an LTER site in the Luquillo Experimental Forest. To this end, the University will assign $150,000 per year in matching funds to this project, should the proposal be approved. This will complement the general operating funds already allocated to the Terrestrial Ecology Division of the CEER by the University of Puerto Rico.

We believe development of an LTER site in Puerto Rico will enhance the strength of the overall network, and look forward to the possibility of close collaboration with other LTER sites in the United States. Such collaboration will be of mutual benefit to both the National Science Foundation, the University of Puerto Rico, and the scientific community as a whole.

Cordially,

Fernando E. Agrait

rrt

United States Department of Agriculture | Forest Service | Institute of Tropical Forestry | Call Box 25000 Rio Piedras, P.R. 00928-250

Reply to: 4070

Date: October 17, 1986

Dr. James T. Callahan
Division of Biotic Systems and Resources
National Science Foundation
1800 G Street, NW
Washington, D.C. 20550

Dear Dr. Callahan:

The U.S. Forest Service enthusiastically endorses the proposal to designate the Luquillo Experimental Forest/Caribbean National Forest a National Science Foundation Long Term Ecological Research Site. This forest has been formally dedicated to tropical forestry research since 1956 when the National Forest was established as an experimental forest. Since 1939 part of the mission of the Forest Service in Puerto Rico has been related to fundamental research to improve management of tropical forest lands. Much of this work has been conducted in cooperation with the University of Puerto Rico and with many other institutions from the United States and throughout tropical America.

Our commitment to research in the Luquillo/Caribbean Forest remains strong particularly in light of the need to understand these ecosystems for the benefit of the millions of landless people in the tropics who require forest products for their day-to-day survival. We believe that the designation of this forest as a long term ecological research site enhances the capability of the U.S. Government to provide leadership in tropical forest management because excellent science is required to support enlightened management.

Because the forest is located in U.S. territory and the Forest Service is in the process of implementing a land management plan for the Caribbean National Forest, increased research activity will be of mutual benefit to our respective agencies. We benefit from better understanding of forest function and cooperating scientists benefit from real-world conditions where research experiments can be conducted.

Sincerely,

Thomas H. Ellis

THOMAS H. ELLIS
Director

Leroy Jones for JOHN E. ALCOCK
Regional Forester

RECEIVED
NOV - 5 1986
USDA FOREST SERVICE

National Aeronautics and
Space Administration

National Space Technology Laboratories
NSTL, Mississippi 39529

NASA

Reply to Attn of: HA10

January 20, 1988

Dr. Robert B. Waide
Head, Terrestrial Ecology
Center for Energy and Env. Research
G.P.O. Box 3682
San Juan, PR 00936

Dear Dr. Waide:

The purpose of this letter is to confirm our intent to collaborate with the Center for Energy and Environment Research and the Institute of Tropical Forestry in any NSF funded research efforts that correspond to the Earth Resources Laboratory's program for tropical forest ecosystem research. Our particular interest is to bring advanced technology in remote sensing and modeling to bear on improving our understanding of tropical forest ecosystems.

The Earth Resources Laboratory (ERL) of the National Space Technology Laboratories (NSTL) has a multidisciplinary staff of ecologists, botanists, foresters, and other disciplinary scientists as well as sensor engineers, computer scientists, etc. who are well versed in remote sensing technology.

We are prepared to support NSF-funded research in the Luquillo Experimental Forest both through making our archived remotely sensed data available, and through planning the future acquisition of remotely sensed data so as to optimize acquisition over LTER or other study sites for NSF-funded research.

Through our past research efforts in the Luquillo Experimental Forest we also have a fairly extensive georeferenced data base including information on topography, soils, climate, etc. that would be made available to support future research efforts.

C.A. Whitehurst
Director, ERL

United States Department of the Interior
GEOLOGICAL SURVEY

Water Resources Division
P.O.Box 4424
San Juan, Puerto Rico 00936

20 January 1988

Dr. Ariel Lugo, Director
Institute of Tropical Forestry
U.S. Dept. of Agriculture
Call Box 25000
Rio Piedras, Puerto Rico
00928-2500

Dear Dr. Lugo,

We are pleased that you are submitting a proposal to the National Science Foundation for the Longterm Ecological Research Program in Luquillo National Forest. The USGS is presently in the first year of a three year, quantitative assessment of landslide hazards in Puerto Rico. The Rio Blanco drainage basin, in the southern half of the Luquillo National Forest, is one of three study areas included in this effort. We are conducting a multidisciplinary study using techniques from the fields of geology, geomorphology, soil mechanics, hydrology, botany, plant ecology and climatolgy. This work is being done in cooperation with the Puerto Rico Planning Board, and in addition to basic research, has the objective of providing the Commonwealth government with information on landslide potential in the interest of public safety.

Potential areas of cooperation between our two research groups would be in the location, mapping, and dating of landslide and other forest-disturbance events, using both aerial photography, and actual field checking of sites. The regeneration of plant species on those sites, including rate, type and sequence, as well as species identification, is also an area of mutual concern. In addition, real-time rainfall data will be useful for both groups.

We look forward to the continuation and expansion of our present sharing of technical, scientific and logistic expertise. Best of luck in securing of funding for your valuable project.

Sincerely,

Allen Zack,
District Chief

UNIVERSITY OF PUERTO RICO
COLLEGE OF NATURAL SCIENCES
BOX AR
RIO PIEDRAS, P.R. 00931

OFFICE OF THE DEAN

January 25, 1988

Dr. Robert Waide
Head
Terrestrial Ecology Division
Center for Energy and Environment
Research
GPO Box 3682
San Juan, PR 00936

Dear Dr. Waide:

As Dean of the Faculty of Natural Sciences of the Río Piedras Campus of University of Puerto Rico, I applaud your efforts to seek funding for Long-Term Ecological Research in the Luquillo Experimental Forest and will strongly encourage participation by our faculty as well as their students. Our Faculty has a strong commitment to research in tropical forest ecosystems and we have recently hired several individuals whose primary focus of interest is in tropical forests.

The University of Puerto Rico recently submitted a proposal to the National Science Foundation to develop a Minority Center of Excellence. One of the principal objectives of this project is the continued development of the program in tropical ecology on the Río Piedras Campus. As a Co-Director of the MRCE, I feel confident that this project will complement the LTER strongly.

If the LTER project is funded, we will take it into account in considering our future needs for personnel. We will endeavor to hire individuals whose interests can be pursued within the framework of the LTER.

Cordially,

Rafael Arce
Dean

lrc

ORGANIZATION	PROPOSAL NO.	DURATION (MONTHS)	
Center for Energy and Environment Research		Proposed	Granted
PRINCIPAL INVESTIGATOR/PROJECT DIRECTOR	AWARD NO.		
Robert B. Waide/Ariel Lugo			

A. SENIOR PERSONNEL: PI/PD, Co PI's, Faculty and Other Senior Associates (List each separately with title, A.6. show number in brackets)	NSF FUNDED PERSON MOS CAL.	ACAD	SUMR	FUNDS REQUESTED BY PROPOSER	FUNDS GRANTED BY NSF (IF DIFFERENT)
1. Co-PI - R. B. Waide - CEER 0.7 FTE				$	$
2. Co-PI - A. E. Lugo - ITF 0.25 FTE					
3. C. Asbury - CEER 0.6 FTE					
4. W. Lawrence - CEER 0.8 FTE					
5. (5) OTHERS (LIST INDIVIDUALLY ON BUDGET EXPLANATION PAGE)					
6. (9) TOTAL SENIOR PERSONNEL (1-5)					
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. ( ) POST DOCTORAL ASSOCIATES					
2. (6) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	68			75,000	
3. (1) GRADUATE STUDENTS				6,500	
4. ( ) UNDERGRADUATE STUDENTS					
5. ( ) SECRETARIAL-CLERICAL					
6. ( ) OTHER					
TOTAL SALARIES AND WAGES (A+B)				81,500	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS) (21.5%)				16,125	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A+B+C)				97,625	
D. PERMANENT EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $1,000:) IBM PC Model 80 or equivalent with hard disk and 4 Mb extended memory				8,000	
TOTAL PERMANENT EQUIPMENT				8,000	
E. TRAVEL 1. DOMESTIC (INCL. CANADA AND U.S. POSSESSIONS)				21,790	
2. FOREIGN					
F. PARTICIPANT SUPPORT COSTS					
1. STIPENDS $					
2. TRAVEL					
3. SUBSISTENCE					
4. OTHER					
TOTAL PARTICIPANT COSTS					
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				21,750	
2. PUBLICATION COSTS/PAGE CHARGES					
3. CONSULTANT SERVICES				8,660	
4. COMPUTER (ADPE) SERVICES					
5. SUBCONTRACTS				176,329	
6. OTHER Aerial Photos				2,000	
TOTAL OTHER DIRECT COSTS				208,739	
H. TOTAL DIRECT COSTS (A THROUGH G)				336,154	
I. INDIRECT COSTS (SPECIFY) 50% TDC less subcontracts, equipment, and student stipends					
TOTAL INDIRECT COSTS				72,663	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				408,817	
K. RESIDUAL FUNDS (IF FOR FURTHER SUPPORT OF CURRENT PROJECTS SEE GPM 252 AND 253)					
L. AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				$408,817	$

PI/PD TYPED NAME & SIGNATURE*	DATE	FOR NSF USE ONLY		
Robert B. Waide	1/29/88	INDIRECT COST RATE VERIFICATION		
INST. REP. TYPED NAME & SIGNATURE*	DATE	Date Checked	Date of Rate Sheet	Initials - DGC
Juan A. Bonnet, Jr. Juan A. Bonnet, Jr.	1/29/88			

NSF Form 1030 (1-87) Supersedes All Previous Editions

*SIGNATURES REQUIRED ONLY FOR REVISED BUDGET (GPM 233)

ORGANIZATION	PROPOSAL NO.	DURATION (MONTHS) Proposed	Granted
Center for Energy and Environment Research			
PRINCIPAL INVESTIGATOR/PROJECT DIRECTOR	AWARD NO.		
Robert B. Waide/Ariel Lugo			

A. SENIOR PERSONNEL: PI/PD, Co-PI's, Faculty and Other Senior Associates (List each separately with title, A.6. show number in brackets)	NSF FUNDED PERSON-MOS CAL.	ACAD	SUMR	FUNDS REQUESTED BY PROPOSER	FUNDS GRANTED BY NSF (IF DIFFERENT)
1. Co-PI - R. B. Waide - CEER 0.7 FTE				$	$
2. Co-PI - A. E. Lugo - ITF 0.25 FTE					
3. C. Asbury - CEER 0.6 FTE					
4. L. Lawrence - CEER 0.8 FTE					
5. (5) OTHERS (LIST INDIVIDUALLY ON BUDGET EXPLANATION PAGE)					
6. (9) TOTAL SENIOR PERSONNEL (1-5)					
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. ( ) POST DOCTORAL ASSOCIATES					
2. (6) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	69			78,750	
3. (3) GRADUATE STUDENTS				19,500	
4. ( ) UNDERGRADUATE STUDENTS					
5. ( ) SECRETARIAL-CLERICAL					
6. ( ) OTHER					
TOTAL SALARIES AND WAGES (A+B)				98,250	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS) 21.5%				16,931	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A+B+C)				115,181	
D. PERMANENT EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $1,000:)					
LI-COR 6200 System upgrade				7,000	
TOTAL PERMANENT EQUIPMENT				7,000	
E. TRAVEL 1. DOMESTIC (INCL. CANADA AND U.S. POSSESSIONS)				21,790	
2. FOREIGN					
F. PARTICIPANT SUPPORT COSTS					
1. STIPENDS $					
2. TRAVEL					
3. SUBSISTENCE					
4. OTHER					
TOTAL PARTICIPANT COSTS					
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				22,000	
2. PUBLICATION COSTS/PAGE CHARGES					
3. CONSULTANT SERVICES				6,885	
4. COMPUTER (ADPE) SERVICES					
5. SUBCONTRACTS				175,937	
6. OTHER Aerial photos ($2,000), electronics maintenance ($6,000)				8,000	
TOTAL OTHER DIRECT COSTS				212,822	
H. TOTAL DIRECT COSTS (A THROUGH G)				356,793	
I. INDIRECT COSTS (SPECIFY) 50% TDC less subcontracts, equipment, and student stipends					
TOTAL INDIRECT COSTS				77,178	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				433,971	
K. RESIDUAL FUNDS (IF FOR FURTHER SUPPORT OF CURRENT PROJECTS SEE GPM 252 AND 253)					
AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				$ 433,971	$

PI/PD TYPED NAME & SIGNATURE*	DATE	FOR NSF USE ONLY		
Robert B. Waide	1/29/88	INDIRECT COST RATE VERIFICATION		
INST. REP. TYPED NAME & SIGNATURE*	DATE	Date Checked	Date of Rate Sheet	Initials - DGC
Juan A. Bonnet, Jr. Juan A. Bonnet, Jr.	1/29/88			Program

NSF Form 1030 (1-87) Supersedes All Previous Editions

*SIGNATURES REQUIRED ONLY FOR REVISED BUDGET (GPM 233)

COMPLETING) PROPOSAL BUDGET FOR NSF USE ONLY

ORGANIZATION	PROPOSAL NO.	DURATION (MONTHS) Proposed	Granted
Center for Energy and Environment Research	AWARD NO.		
PRINCIPAL INVESTIGATOR/PROJECT DIRECTOR: Robert B. Waide/Ariel Lugo			

SENIOR PERSONNEL: PI/PD, Co-PI's, Faculty and Other Senior Associates (List each separately with title, A.6. show number in brackets)	NSF FUNDED PERSON-MOS CAL.	ACAD	SUMR	FUNDS REQUESTED BY PROPOSER	FUNDS GRANTED BY NSF (IF DIFFERENT)
				$	$
1. Co-PI - R. B. Waide - CEER 0.7 FTE					
2. Co-PI - A. E. Lugo - ITF 0.25 FTE					
3. C. Asbury - CEER 0.6 FTE					
4. W. Lawrence - CEER 0.8 FTE					
5. (5) OTHERS (LIST INDIVIDUALLY ON BUDGET EXPLANATION PAGE)					
6. (9) TOTAL SENIOR PERSONNEL (1-5)					
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. ( ) POST DOCTORAL ASSOCIATES					
2. (6) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	69			82,688	
3. (3) GRADUATE STUDENTS				19,500	
4. ( ) UNDERGRADUATE STUDENTS					
5. ( ) SECRETARIAL-CLERICAL					
6. ( ) OTHER					
TOTAL SALARIES AND WAGES (A+B)				102,188	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS) 21.5%				17,778	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A+B+C)				119,965	
D. PERMANENT EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $1,000:)					
TOTAL PERMANENT EQUIPMENT					
E. TRAVEL 1. DOMESTIC (INCL. CANADA AND U.S. POSSESSIONS)				21,790	
2. FOREIGN					
F. PARTICIPANT SUPPORT COSTS					
1. STIPENDS $					
2. TRAVEL					
3. SUBSISTENCE					
4. OTHER					
TOTAL PARTICIPANT COSTS					
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				22,000	
2. PUBLICATION COSTS/PAGE CHARGES				2,000	
3. CONSULTANT SERVICES				6,885	
4. COMPUTER (ADPE) SERVICES					
5. SUBCONTRACTS				175,017	
6. OTHER Aerial photos ($2,000), electronics maintenance ($6,000)				8,000	
TOTAL OTHER DIRECT COSTS				213,902	
H. TOTAL DIRECT COSTS (A THROUGH G)				355,657	
I. INDIRECT COSTS (SPECIFY) 50% TDC less subcontracts, equipment, and student stipends					
TOTAL INDIRECT COSTS				80,570	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				436,227	
K. RESIDUAL FUNDS (IF FOR FURTHER SUPPORT OF CURRENT PROJECTS SEE GPM 252 AND 253)					
L. AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				$ 436,227	$

PI/PD TYPED NAME & SIGNATURE*	DATE	FOR NSF USE ONLY		
Robert B. Waide	1/29/88	INDIRECT COST RATE VERIFICATION		
INST. REP. TYPED NAME & SIGNATURE*	DATE	Date Checked	Date of Rate Sheet	Initials - DGC
Juan A. Bonnet, Jr. Juan A. Bonnet, Jr.	1/29/88			Prog

NSF Form 1030 (1-87) Supersedes All Previous Editions

*SIGNATURES REQUIRED ONLY FOR REVISED BUDGET (GPM 233)

ORGANIZATION	PROPOSAL NO.	DURATION (MONTHS) Proposed	Granted
Center for Energy and Environment Research	AWARD NO.		
PRINCIPAL INVESTIGATOR/PROJECT DIRECTOR: Robert B. Waide/Ariel Lugo			

A. SENIOR PERSONNEL: PI/PD, Co PI's, Faculty and Other Senior Associates (List each separately with title, A.6. show number in brackets)	NSF FUNDED PERSON MOS. CAL.	ACAD	SUMR	FUNDS REQUESTED BY PROPOSER	FUNDS GRANTED BY NSF (IF DIFFERENT)
1 Co-PI - R. B. Waide - CEER 0.7 FTE				$	$
2 Co-PI - A. E. Lugo - ITF 0.25 FTE					
3 C. Asbury - CEER 0.6 FTE					
4 W. Lawrence - CEER 0.8 FTE					
5. (5) OTHERS (LIST INDIVIDUALLY ON BUDGET EXPLANATION PAGE)					
6 (9) TOTAL SENIOR PERSONNEL (1-5)					
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. ( ) POST DOCTORAL ASSOCIATES					
2. (6) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	69			86,822	
3. (3) GRADUATE STUDENTS				19,500	
4. ( ) UNDERGRADUATE STUDENTS					
5. ( ) SECRETARIAL-CLERICAL					
6. ( ) OTHER					
TOTAL SALARIES AND WAGES (A+B)				106,322	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS)				18,667	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A+B+C)				124,989	
D. PERMANENT EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $1,000:)					
TOTAL PERMANENT EQUIPMENT					
E. TRAVEL 1. DOMESTIC (INCL. CANADA AND U.S. POSSESSIONS)				21,790	
2. FOREIGN					
F. PARTICIPANT SUPPORT COSTS					
1. STIPENDS $					
2. TRAVEL					
3. SUBSISTENCE					
4. OTHER					
TOTAL PARTICIPANT COSTS					
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				18,500	
2. PUBLICATION COSTS/PAGE CHARGES				3,000	
3. CONSULTANT SERVICES				6,885	
4. COMPUTER (ADPE) SERVICES					
5. SUBCONTRACTS				157,181	
6. OTHER Aerial photos ($2,000), electronics maintenance ($6,000)				8,000	
TOTAL OTHER DIRECT COSTS				193,566	
H. TOTAL DIRECT COSTS (A THROUGH G)				340,345	
I. INDIRECT COSTS (SPECIFY) 50% TDC less subcontracts, equipment, and student stipends					
TOTAL INDIRECT COSTS				81,832	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				422,176	
K. RESIDUAL FUNDS (IF FOR FURTHER SUPPORT OF CURRENT PROJECTS SEE GPM 252 AND 253)					
L. AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				$ 422,176	$

PI/PD TYPED NAME & SIGNATURE*	DATE	FOR NSF USE ONLY		
Robert B. Waide	1/29/88	INDIRECT COST RATE VERIFICATION		
INST. REP. TYPED NAME & SIGNATURE*	DATE	Date Checked	Date of Rate Sheet	Initials - DGC
Juan A. Bonnet, Jr. Juan A. Bonnet, Jr.	1/29/88			Prog

*SIGNATURES REQUIRED ONLY FOR REVISED BUDGET (GPM 233)

COMPLETING) PROPOSAL BUDGET FOR NSF USE ONLY

ORGANIZATION	PROPOSAL NO.	DURATION (MONTHS) Proposed	Granted
Center for Energy and Environment Research			
PRINCIPAL INVESTIGATOR/PROJECT DIRECTOR	AWARD NO.		
Robert B. Waide/Ariel Lugo			

SENIOR PERSONNEL: PI/PD, Co PI's, Faculty and Other Senior Associates (List each separately with title, A 6. show number in brackets)	NSF FUNDED PERSON-MOS. CAL.	ACAD	SUMR	FUNDS REQUESTED BY PROPOSER	FUNDS GRANTED BY NSF (IF DIFFERENT)
1. Co-PI - R. B. Waide - CEER 0.7 FTE				$	$
2. Co-PI - A. E. Lugo - ITF 0.25 FTE					
3. C. Asbury - CEER 0.6 FTE					
4. W. Lawrence - CEER 0.8 FTE					
5. (5) OTHERS (LIST INDIVIDUALLY ON BUDGET EXPLANATION PAGE)					
6. (9) TOTAL SENIOR PERSONNEL (1-5)					
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. ( ) POST DOCTORAL ASSOCIATES					
2. (6) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	69			91,163	
3. (3) GRADUATE STUDENTS				19,500	
4. ( ) UNDERGRADUATE STUDENTS					
5. ( ) SECRETARIAL-CLERICAL					
6. ( ) OTHER					
TOTAL SALARIES AND WAGES (A+B)				110,663	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS)				19,600	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A+B+C)				130,263	
D. PERMANENT EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $1,000:)					
TOTAL PERMANENT EQUIPMENT					
TRAVEL 1. DOMESTIC (INCL. CANADA AND U.S. POSSESSIONS)				21,790	
2. FOREIGN					
F. PARTICIPANT SUPPORT COSTS					
1. STIPENDS $					
2. TRAVEL					
3. SUBSISTENCE					
4. OTHER					
TOTAL PARTICIPANT COSTS					
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				17,500	
2. PUBLICATION COSTS/PAGE CHARGES				5,000	
3. CONSULTANT SERVICES				6,885	
4. COMPUTER (ADPE) SERVICES					
5. SUBCONTRACTS				113,329	
6. OTHER Aerial photographs ($2,000), electronics maintenance ($6,000)				8,000	
TOTAL OTHER DIRECT COSTS				150,715	
H. TOTAL DIRECT COSTS (A THROUGH G)				302,767	
I. INDIRECT COSTS (SPECIFY) 50% TDC less subcontracts, equipment, and student stipends					
TOTAL INDIRECT COSTS				84,969	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				387,736	
K. RESIDUAL FUNDS (IF FOR FURTHER SUPPORT OF CURRENT PROJECTS SEE GPM 252 AND 253)					
AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				$ 387,736	$

PI/PD TYPED NAME & SIGNATURE*	DATE	FOR NSF USE ONLY		
Robert B. Waide	1/29/88	INDIRECT COST RATE VERIFICATION		
INST. REP. TYPED NAME & SIGNATURE*	DATE	Date Checked	Date of Rate Sheet	Initials - DGC
Juan A. Bonnet, Jr. Juan A. Bonnet, Jr.	1/29/88			Prog

*SIGNATURES REQUIRED ONLY FOR REVISED BUDGET (GPM 233)

COMPLETING | PROPOSAL BUDGET | FOR NSF USE ONLY

ORGANIZATION	PROPOSAL NO.	DURATION (MONTHS) Proposed	Granted
Center for Energy and Environment Research	AWARD NO.		
PRINCIPAL INVESTIGATOR/PROJECT DIRECTOR: Robert B. Waide/Ariel Lugo			

A. SENIOR PERSONNEL: PI/PD, Co-PI's, Faculty and Other Senior Associates (List each separately with title, A.6. show number in brackets)	NSF FUNDED PERSON-MOS. CAL.	ACAD	SUMR	FUNDS REQUESTED BY PROPOSER	FUNDS GRANTED BY NSF (IF DIFFERENT)
1. Co-PI - R. B. Waide - CEER 0.7 FTE				$	$
2. Co-PI - A. E. Lugo - ITF 0.25 FTE					
3. C. Asbury - CEER 0.6 FTE					
4. W. Lawrence - CEER 0.8 FTE					
5. (5) OTHERS (LIST INDIVIDUALLY ON BUDGET EXPLANATION PAGE)					
6. (9) TOTAL SENIOR PERSONNEL (1-5)					
B. OTHER PERSONNEL (SHOW NUMBERS IN BRACKETS)					
1. ( ) POST DOCTORAL ASSOCIATES					
2. (6) OTHER PROFESSIONALS (TECHNICIAN, PROGRAMMER, ETC.)	345			414,422	
3. (3) GRADUATE STUDENTS				84,500	
4. ( ) UNDERGRADUATE STUDENTS					
5. ( ) SECRETARIAL-CLERICAL					
6. ( ) OTHER					
TOTAL SALARIES AND WAGES (A+B)				498,922	
C. FRINGE BENEFITS (IF CHARGED AS DIRECT COSTS)				89,101	
TOTAL SALARIES, WAGES AND FRINGE BENEFITS (A+B+C)				588,023	
D. PERMANENT EQUIPMENT (LIST ITEM AND DOLLAR AMOUNT FOR EACH ITEM EXCEEDING $1,000:) IBM PC Model 80 or equivalent with hard disk and 4 MB extended memory LI-COR 6200 System upgrade					
TOTAL PERMANENT EQUIPMENT				15,000	
E. TRAVEL 1. DOMESTIC (INCL. CANADA AND U.S. POSSESSIONS)				108,950	
2. FOREIGN					
F. PARTICIPANT SUPPORT COSTS 1. STIPENDS $ 2. TRAVEL 3. SUBSISTENCE 4. OTHER					
TOTAL PARTICIPANT COSTS					
G. OTHER DIRECT COSTS					
1. MATERIALS AND SUPPLIES				101,750	
2. PUBLICATION COSTS/PAGE CHARGES				10,000	
3. CONSULTANT SERVICES				36,200	
4. COMPUTER (ADPE) SERVICES					
5. SUBCONTRACTS				797,793	
6. OTHER				34,000	
TOTAL OTHER DIRECT COSTS				979,743	
H. TOTAL DIRECT COSTS (A THROUGH G)				1,691,716	
I. INDIRECT COSTS (SPECIFY) 50% TDC less subcontracts, equipment, and student stipends					
TOTAL INDIRECT COSTS				397,211	
J. TOTAL DIRECT AND INDIRECT COSTS (H + I)				2,088,927	
K. RESIDUAL FUNDS (IF FOR FURTHER SUPPORT OF CURRENT PROJECTS SEE GPM 252 AND 253)					
L. AMOUNT OF THIS REQUEST (J) OR (J MINUS K)				$2,088,927	$

PI/PD TYPED NAME & SIGNATURE*	DATE	FOR NSF USE ONLY		
Robert B. Waide	1/29/88	INDIRECT COST RATE VERIFICATION		
INST. REP. TYPED NAME & SIGNATURE*	DATE	Date Checked	Date of Rate Sheet	Initials - DGC
Juan A. Bonnet, Jr. Juan A. Bonnet, Jr.	1/29/88			Prog

NSF Form 1030 (1-87) *Supersedes All Previous Editions*

*SIGNATURES REQUIRED ONLY FOR REVISED BUDGET (GPM 233)

Budget Justification

Additional Senior Personnel

Ned Fetcher	Biology Department, University of Puerto Rico	0.2 FTE
D. Jean Lodge	CEER	0.8 FTE
William J. Pfeiffer	CEER	1.0 FTE
Fred Scatena	ITF	0.4 FTE
Lawrence Walker	Biology Department, University of Puerto Rico	0.2 FTE

In addition to the 25% of his time that Dr. Ariel Lugo will devote specifically to the LTER project, a further 30% of his time will be devoted to research in the ITF Watershed Project and to other investigations that directly address the goals of the LEF LTER.

Salaries and wages

This proposal is a joint effort between the Center for Energy and Environment Research of the University of Puerto Rico and the Institute of Tropical Forestry, U. S. Forest Service. As a means of sharing the cost of the proposed research, we have established the policy of contributing salary support for all CEER and ITF senior staff. In addition, collaborators from Harvard, SUNY-Albany, and the Andrews Experimental Forest have not requested salary support for their participation. This results in an annual contributed cost in salaries ranging approximately $270,000 including overhead. Moreover, CEER and ITF will contribute partial salaries of clerical staff and field personnel on a routine basis. This latter contribution will often take the form of combining sampling for the LTER program with sampling trips for other purposes.

In addition, the University of Puerto Rico will assign $150,000 annually to the LTER program. These funds will be used for to pay the salaries of five additional technicians (bringing the total dedicated to the LTER program to 10), to support 2-4 graduate and 4 undergraduate students, and to pay for equipment and materials and supplies not covered by NSF funds.

Ten technicians (five paid for by NSF) will be employed to collect and collate data from the LTER program. One of these technicians will assume the added responsibility of field manager, whose duties will be to coordinate sampling schedules and personnel. Funds for three graduate students are requested in the main budget and eight in subcontracts. Other graduate students will be funded from University of Puerto Rico matching funds. Funds for undergraduate students will be requested from NSF under the Research Experience for Undergraduates Program. We feel that this work force is sufficient as many of the chemical samples to be run can be included in normal analytical loads in laboratories run by CEER and ITF.

Salaries and other costs for collaborators are detailed in budgets found at the end of this proposal. Collaborators who requested salary support have prepared itemized budgets, while those who requested only travel, per diem, and supplies totalling less than $3000 annually are included in the main budget.

A data management professional will be hired in March, 1988, to implement the data management system developed with the assistance of Dr. William Michener. Salary for this person and a data entry technician will initially be paid from NSF funds assigned on the basis of our previous proposal. The data entry technician will enter existing data and data collected during 1988 so that we will have an operating data base by the time the LTER award begins.

All salaries have been calculated at the prevailing wage scale with annual increments based on the normal practice of the home institution.

Equipment

Our equipment requests are modest, principally because we have already received funds from NSF to purchase the major parts of the data management system and the meteorological stations that were requested in our previous proposal. In addition, the sophisticated image analysis system needed for the rhizotron work was purchased from another grant. We request funds for an IBM PC Model 80 computer to satisfy our data manager's need for a machine to handle large data manipulations quickly. We also request an upgrade for an existing LI-COR system for use in the revegetation experiments.

Materials and Supplies

The major expenditures in this category will come for supplies for laboratory analyses, expendable supplies for computer analysis and data management, and field supplies. Funds requested from NSF in this category will be augmented from matching funds supplied by UPR.

Travel

Travel to and from Puerto Rico will be by the most inexpensive carriers possible. Local transportation will be by vehicles rented from GSA. Rental costs will be contributed by CEER and ITF, but mileage charges at $0.31/mile are included in the travel budget. This will cover all local travel needs of all program participants, including transportation to and from San Juan (about 20 miles from the LEF) and local travel within the LEF. The total budgeted for local travel is $7440/yr.

National travel includes funds for local scientists to attend national meetings and LTER workshops ($7000) and for one on-site meeting of the National Advisory Committee per year ($4000).

Other Direct Costs

We have included funds for annual aerial photography to be used in the analysis of disturbance regime. Some of this money will be used for satellite data if we find that such data would be useful in the disturbance or meteorology projects. In general, however, satellite data will be obtained through three other projects being conducted in the LEF in collaboration with NASA laboratories.

We request funds for electronic maintenance for the upkeep of the data management network, laboratory analysis systems, and meteorological stations.

SUMMARY OF ALL CURRENT AND PENDING RESEARCH SUPPORT

	Source of Support[3]	Project Title[2]	Award Amount	Period Covered by Award	% of Effort Committed To The Project	Location of Work
I. Robert B. Waide						
A. Current Support	DOE	Rain Forest Cycling and Transport	$150K	Oct 1, 1987-Sept 30, 1988	20%	El Verde
	NSF	Addendum to Long-term Ecological Research on the Luquillo Experimental Forest	$150K	Oct 1, 1987-Dec 31, 1988	14%	El Verde
	NASA	The Use of Landsat TM Data to Study Above-Ground Biomass Accumulation in Secondary Tropical Forests in the Early Successional Stages	$217K	March 1985-March 1988	5%	El Verde
	NASA	UPR/NASA Cooperative Research	$260K	Jan 1, 1987-Dec 31, 1988	17%	El Verde
	World Wildlife Fund	Critical Habitats for Migrant Birds in the West Indies	$48K	Jan 1986-Dec 1988	20%	Greater Antilles
B. Proposals Pending	NSF	Control of Primary Productivity Along a Complex Environmental Gradient in a Tropical Rain Forest	$750K	Sept 1, 1988-Aug 31, 1992	10%	El Verde
	NSF	Long-Term Ecological Research in the Luquillo Experimental Forest	$2000K	Jan 1, 1989-Dec 31, 1994	70%	El Verde
	DOE	Rain Forest Cycling and Transport	$150K	Oct 1, 1988-Sept 30, 1989	10%	El Verde
	NASA	UPR/NASA Cooperative Research	$250K	Jan 1, 1988-Dec 31, 1988	10%	El Verde
II. Ariel E Lugo - Federal Employee						
A. Current Support	DOE	Global Carbon Dioxide Project			5%	
B. Proposals Pending	NSF	Long-Term Ecological Research in the Luquillo Experimental Forest	$2000K	Jan 1, 1989-Dec 31, 1994	25%	El Verde