Project Summary

The Luquillo Experimental Forest Long-Term Ecological Research program (LUQ) focuses on the long-term dynamics of tropical forest ecosystems characterized by large-scale, infrequent disturbance, rapid processing of organic material, and high habitat and species diversity. Research by LUQ has stimulated a new appreciation of the significance of large-scale disturbances in tropical forested ecosystems and the key role of the biota in shaping the response to these events. Hurricanes occurring one and 10 years after the LTER program began permitted us to capitalize upon landscape-scale natural experiments which we continue to follow closely. Among our most important findings from these natural experiments is that detrital dynamics plays a central role in forest recovery by influencing carbon and nutrient storage and flow.

The central theme we propose is **that disturbance, through its effects on detrital dynamics, is a dominant ecosystem driver in the Luquillo Experimental Forest**. A common feature of all disturbances is the generation of dead organic matter that must be processed by the biota as part of the ecosystem's response to disturbance. Pulses of detritus shift the flow of energy within the food web, modify the availability and distribution of nutrients, and feed back on the composition and productivity of plant and animal communities. Rapid processing of detritus distinguishes the Luquillo Experimental Forest (LEF) from other forested LTER sites, where decomposition takes two to 20 times as long. In this proposal, we combine long-term measurements, field experiments, simulation modeling, and cross-site comparisons to address five questions: (1) *How do climatic factors, litter quality, and detritivore diversity regulate decomposition of detrital pulses*? (2) *How do terrestrial and aquatic food webs differ in response to detrital pulses*? (3) *What is the effect of disturbance frequency on nutrient cycling, plant community composition, and the accumulation of soil organic matter*? (4) *To what degree is the export of carbon and nutrients from watersheds a result of soil characteristics that are affected by detrital dynamics*? (5) *How do elevationally related changes in climate impact plant and detritivore communities, and how do these feed back on the quantity and quality of litter inputs and decomposition*? Through our focus on disturbance and detrital dynamics, we build on existing strengths in integrating community and ecosystem ecology and the research opportunities provided by infrequent, large-scale disturbance, high diversity, and pronounced elevational gradients in the LEF.

Our research will be conducted in two spatial contexts. In mid-elevation tabonuco forest, we will continue long-term measurements of ecosystem response to hurricanes, landslides, and anthropogenic disturbance. We will initiate an experiment mimicking increased frequency of hurricanes to investigate the effect of increased detrital inputs on nutrient cycling, community composition, and organic matter accumulation. We also will manipulate key functional groups of invertebrates to gain a better understanding of similarities in detrital processing between aquatic and terrestrial food webs. In a landscape context, we will establish new plots to examine the effect of elevationally related changes in climate, plant communities, and decomposers on detrital processing. Manipulative experiments will compare the relative importance of abiotic and biotic controls on decomposition in terrestrial and aquatic habitats. Long-term measurements of hydrological and nutrient fluxes in watersheds will relate soil characteristics to stream nutrient and organic matter losses and provide information to gauge the effects of future disturbances. Simulation models of key population, community, biogeochemical, and landscape processes provide null-model predictions to inform these new observations and experiments.

Section 1 Results From Prior NSF Support

Long-Term Research in the Luquillo Experimental Forest 2 & 3; NSF Grants DEB-9411973 and DEB-9705814, Oct. 1994 - Nov. 2000 [$3,600,000], and DEB-00805238, Nov. 2000 - Oct. 2002 [$1,400,000])

The Luquillo Experimental Forest LTER program (LUQ) has shown how a diverse biota interacts with a varied disturbance regime and environmental gradients to determine habitat structure, nutrient cycling, community organization, and food web relations in terrestrial and aquatic ecosystems (Walker et al. 1991, 1996a, 1996b, Lugo & Scatena 1995, Covich et al. 1996, Reagan & Waide 1996). Building on a history of research in forestry (Wadsworth 1995) and ecosystem ecology (Odum & Pigeon 1970), the Luquillo LTER program focused initially on the importance of hurricanes and landslides within four forest types in the Luquillo Experimental Forest (LEF). We emphasized the significance of the biota in restoring ecosystem productivity after disturbance events at two study sites (El Verde and Bisley; see **Fig. 2.1.1**) in one of these forest types, tabonuco. In preparation for experimental studies of disturbance planned for LTER 1, we established long-term measurements of ecosystem characteristics to understand the spatial and temporal dynamics of tabonuco forest. These measurements provided background to assess the impacts of Hurricane Hugo and associated landslides in 1989 and to evaluate biotic responses to these disturbances. In LTER 2, we continued our intensive studies of the effects of and response to hurricanes and landslides, while expanding our focus to encompass other forms of disturbance including historical and present-day agriculture. Hurricane Georges in 1998 provided an opportunity to assess the interaction between disturbance events. To test our understanding of forest processes against a broader range of biotic and abiotic conditions, LUQ expanded its research from mid-elevation tabonuco forest (200 to 600 m) to the summits of the LEF (1000 m) during the first two years of LTER 3. We are now poised to 1) investigate how the effects of repeated disturbance (canopy opening and pulses of detritus) propagate through the system to modify other forest characteristics, and 2) examine how a key ecosystem process, detrital dynamics, changes along elevationally related gradients of climate and biodiversity.

LUQ was initiated in 1988 and renewed in 1994 and 2000. During the last 13 years, we have provided a platform for research within Puerto Rico and for comparisons across the LTER Network by establishing a point of reference in which climatic conditions are continuously warm and wet and the biota diverse. LUQ involves researchers from the University of Puerto Rico, the International Institute of Tropical Forestry and Forest Products Lab (USDA Forest Service), and 11 mainland institutions. Since its inception, LUQ has produced 348 peer-reviewed journal articles, 89 book chapters, 7 books, and 32 scholarly reports as well as 56 theses and dissertations. Please see our web page (**http://luq.lternet.edu**) for a complete list.

1.1 Major Findings
Research conducted by the Luquillo LTER program has changed how ecologists view the importance of large-scale disturbances in maintaining rain forest biodiversity and ecosystem functions (Sugden 1992, Lodge et al. 1994, Whittaker 1995, Miller & Lodge 1997, Willig & Walker 1999). Pioneering work on the effects of hurricanes on tropical forests and the interaction between natural and anthropogenic disturbances has stimulated reconsideration of the resilience of rain forest ecosystems and contributed to the development of a new vision of rain forests as

dynamic systems (Walker et al. 1996a, Walker 1999, Foster 2000). This new vision is widely applicable to forested ecosystems with other characteristic large-scale disturbances such as fires or droughts. Comparison of our results with those from other forests (Boose et al. 1994, Turner et al. 1997, Dale et al. 1998, Walker 1999, Foster 2000) is leading us towards a conceptual model of how disturbance structures LEF ecosystems. Although disturbance takes many forms, the conversion of live biomass into detritus is a factor common to all disturbances (Sousa 1984, Dale et al. 2001). The mechanisms by which ecosystems process pulses of detritus thus determine their response to disturbance by regulating critical ecosystem fluxes and storages. Hence, our results strongly support the emerging concept that **disturbance, through its effects on detrital dynamics, is a dominant ecosystem driver in the Luquillo Experimental Forest.**

1.1.1 Disturbance regime: Although we anticipated in LTER 1 that disturbance was a major force structuring LEF ecosystems, the degree to which this prediction has been substantiated is nevertheless surprising. In 13 years, two major and four lesser hurricanes have affected our study sites (**Fig. 2.1.1**), widespread landslides have occurred associated with specific landscape features (Walker et al. 1996b), and floods and droughts have modified stream environments and populations (Covich et al. 1996, 2000). In addition to documenting the effects of these natural disturbances, we have found that legacies from various human disturbances (mainly agriculture and logging) in some areas of tabonuco forest have long-lasting effects (Thompson et al., in press b). This cumulative evidence reaffirms our initial view of disturbance as a dominant driver of structure and function in LEF ecosystems (Waide & Lugo 1992).

The effects of hurricanes are widespread and severe and have thus provided the major focus for our research on disturbance impacts. Hurricanes strike the LEF on average every 55-60 years and pass within 60 km every 20-25 years (Scatena & Larsen 1991). Simulation of historical hurricanes has demonstrated a strong, cumulative spatial pattern in impact (Boose et al. 1994; see **Fig. 2.1.1**). Tabonuco forest models have predicted strong effects of repeated hurricanes on long-term forest composition (Doyle 1981) and ecosystem characteristics (Sanford et al. 1991), but these predictions have yet to be verified experimentally.

1.1.2 Hurricane disturbance and recovery: During Hurricane Hugo defoliation and branch loss were widespread and, depending on site exposure, 18 to 76% of trees were snapped off or uprooted (Walker 1991, Basnet et al. 1992). Mortality of large trees varied spatially from 0 to 37% (Lugo & Scatena 1996). However, tree mortality was low enough in many areas that species composition changed little (Zimmerman et al. 1994, Walker 1995). Massive mortality of fine roots occurred after Hurricane Hugo (Silver & Vogt 1993). Animals were greatly affected by changes in habitat structure and food resources (Waide 1991a,b). Frogs and snails that rely on litter for shelter or food increased in abundance following Hugo (Woolbright 1996, Willig et al. 1998). Nectar- and fruit-feeding birds and bats declined following both hurricanes (Gannon & Willig 1994). In streams, high flows moved storm-generated detritus into debris dams. Increased detritus and microbial biomass led to increased detritivore abundance, particularly Atyid shrimps (Covich et al. 1991, 1996, Johnson et al. 1998, Johnson & Covich

2000).
Hurricanes Hugo and Georges opened the forest canopy and produced large pulses of litterfall and woody debris (Lodge et al. 1991, Scatena et al. 1996). Hugo deposited approximately 1 kg/m2 of litter on the forest floor and the subcanopy vegetation intercepted and suspended a like amount. Total litterfall from Hugo was 1.2 times the annual litterfall, but delivered in just one day. Nutrient delivery to the forest floor was proportionally greater, because hurricane litterfall and fine root inputs had high concentrations of N and P (Lodge et al. 1991, Lodge & McDowell 1991). Nutrient losses to streams were smaller than expected, given the amount of damage, because soil retention and nutrient uptake by pioneer plants quickly restored aboveground nutrient pools and ecosystem function (Scatena et al. 1996, Silver et al. 1996, McDowell et al. 1996). While highly dynamic in their chemistry compared to streams in other ecosystems (e.g., HBR, Bormann & Likens 1981), streams draining the LEF went from elevated levels of nitrate and potassium to normal within 1 to 2 years of the hurricane (Schaefer et al. 2000).
Sprouting of damaged trees and recruitment of pioneer trees quickly restored forest structure (Walker 1991, Brokaw et al., in press), producing a temporary increase in net primary productivity (NPP; Scatena et al. 1996). Within five years, many ecosystem state variables and functions (e.g., leaf litterfall, aboveground forest biomass, NPP, some soil nutrient pools) and the abundances of many plants and animals had returned to or were approaching pre-Hugo levels (Zimmerman et al. 1996). Exceptions include pioneer trees and shrubs, particularly Cecropia schreberiana, whose abundances remained high long after the hurricane (Brokaw 1998).
In the short term (1 to 2 yr), the combination of a detrital pulse and canopy opening increased light levels (Fernández & Fetcher 1991) and soil moisture (Steudler et al. 1991), increased nutrient inputs to forest floor and streams, and altered N and P cycling (McDowell et al. 1996, Silver et al. 1996), increased nitrate concentrations in streams and soil (Silver & Vogt 1993), elevated rates of denitrification (Steudler et al. 1991), increased the functional diversity of soil microbial communities (Willig et al. 1996), differentially affected survival of litter fungi (Lodge & Cantrell 1995), differentially affected germination and seedling survival in pioneer and late successional species (Guzmán-Grajales & Walker 1991), and accelerated growth (Scatena et al. 1996). **In particular, the post-hurricane pulse of detritus and the decrease in canopy biomass redirected energy away from herbivores to detritivores, with significant effects on abundance and population structure. The relative importance of canopy opening and the pulse of detritus in regulating these effects has yet to be determined.**
We are beginning to understand the longer-term dynamics of post-hurricane detrital pulses. Decomposition of both leaf litter and wood is extremely rapid in the LEF compared to other sites within the LTER Network (Gholz et al. 2000). The combination of warm, moist conditions in the litter layer after Hugo led to complete decomposition of tabonuco leaves in less than a year and of 3 to 6 cm wood in 7 to 16 years (Vogt et al. 1996). Ongoing studies of bole decomposition

suggest a residence time of a few decades (versus centuries in temperate forests). The decomposition of coarse woody debris (> 5 cm diameter) can regulate productivity for long periods of time (up to 13 years) by immobilizing nutrients as it decomposes (Zimmerman et al. 1995b). **Simulations of long-term dynamics of tabonuco forest using the CENTURY model predicted that repeated disturbance by hurricanes would result in higher soil organic matter (SOM), P availability, N-mineralization, and productivity and lower forest biomass (Sanford et al. 1991). Simulation results suggested that higher productivity from repeated disturbance was driven by increased SOM through its effect on P availability. Recent data show significantly more SOM and N under decomposing logs from Hurricane Hugo (Lodge et al. 2001). Silver et al. (1996) however, found no change in SOM after Hurricane Hugo and suggested that increased decomposition and soil respiration rates may have balanced the SOM added. A thorough examination of this suggestion and predictions from Sanford et al. (1991) requires long-term experiments.**

1.1.3 Human disturbance and recovery: Human disturbance was widespread in tabonuco forest during the last century (Foster et al. 1998), and these disturbances exhibit strong legacies. For example, the Luquillo Forest Dynamics Plot (LFDP), a 16-ha grid at El Verde, has been free of human disturbance since the 1930s, but its tree species composition reflects past land use more strongly than damage from hurricanes in 1932, 1989 and 1998 (Thompson et al., in press b). In general, second growth forests in the LEF demonstrate the legacy of human disturbance in their altered species composition rather than in their biomass, tree density, or species richness (Zimmerman et al. 1995a, Thompson et al., in press b). In streams, we have shown strong impacts of water diversion on organisms and ecosystem processes, and we developed instream flow models to help manage water resources (Pringle 1997, March et al. 1998, Benstead et al. 1999, Pringle et al. 1999, Scatena & Johnson 2001).

1.1.4 Interactions between disturbances: We have shown how disturbance effects are conditioned by previous disturbances (Willig & Walker 1999). High rainfall associated with hurricanes initiates many landslides (Scatena & Larsen 1991), but these occur mainly where roads have changed local topography (Guariguata 1990). Hurricanes Hugo and Georges were comparable in strength, but Hugo felled and delimbed so many susceptible trees that Georges, coming nine years later, had much less effect (Brokaw et al., in press). The tabonuco forest is less resistant to hurricanes in areas that have been disturbed by humans. In the LFDP, Hurricane Hugo caused most damage to trees in areas cleared 70 years ago, because secondary tree species were more susceptible to damage than were old-growth species (Zimmerman et al. 1994, Everham 1996, Thompson et al., in press b). These anthropogenically altered areas are likely to remain in secondary forest indefinitely because the high return frequency of hurricanes perpetuates destruction of and recolonization by secondary tree species.

1.1.5 Beyond tabonuco forest: Ascending the Luquillo Mountains, climate becomes cloudier, wetter, and cooler, and forests become shorter, denser, less species-rich, and less productive (Waide et al. 1998). Oxygen depletion in saturated soils limits productivity and decomposition at high elevations (Silver et al. 1999, McGroddy & Silver 2000). Thus, elfin forests at 1000 m were slow to return to pre-hurricane levels of productivity compared to tabonuco forest (Walker et al. 1996b). We extended our understanding of tabonuco forest processes to the full elevational range of the LEF by integrating CENTURY with a climate model developed by LUQ (TOPOCLIM; Wooster 1989) and a primary production model (Marley 1998) coupled with a geographic information system. The resultant landscape model (L-CENTURY) provided reasonably accurate estimates of spatial and temporal variability in gross and net primary production as well as storages and fluxes of soil organic carbon and nitrogen (Wang 2001, Wang et al. in press). However, the scarcity of appropriate data from higher elevations prevented a full validation of the model predictions.

1.1.6 Cross-site studies: As the only tropical LTER site, LUQ plays a valuable role in cross-site comparisons within the LTER network and between the LTER network and other tropical sites (Heneghan et al. 1998a,b, Thompson et al., in press a; see **Section 2.6**). For example, in the Long-term Intersite Decomposition Experiment (LIDET) our diverse, warm site had higher decomposition rates than less diverse, cooler sites (e.g., KNZ, CWT) but had rates similar to those in other wet tropical sites (Costa Rica; Gholz et al. 2000). Comparative studies between LUQ and NWT show how the biota and climate affect decomposition and soil processes (González & Seastedt 2001). The Lotic Intersite Nitrogen Experiment (LINX) showed that in our N-rich site, ammonium turnover in streams is very rapid, due largely to nitrification rates that were higher than those at any other site in the study (Peterson et al. 2001, Merriam et al. 2002). Results from LUQ and the USGS-sponsored cross-site Water, Energy, and Biogeochemical Budgets (WEBB) project have been instrumental in establishing the importance of temperature in controlling global variation in weathering rates (McDowell & Asbury 1994, White & Blum 1995, White et al. 1998).

1.1.7 Major publications: We summarized results of LUQ research in three books (Lugo & Lowe 1995, Reagan & Waide 1996, Walker 1999) and two special issues of Biotropica (Walker et al. 1991, 1996a). LUQ scientists led or participated in publications of cross-site results on the relationship between primary productivity and species richness (Waide et al. 1999, Gross et al. 2000, Scheiner et al. 2000, Mittelbach et al. 2001), on the effects of large infrequent disturbances (Turner et al. 1997, Dale et al. 1998), on the biology of key forest species (Lugo et al. in press), and on measuring primary productivity (Clark et al. 2001a,b). A synthesis of LUQ results to date is being prepared for the LTER-Oxford book series. The Supplementary Documentation provides a list of LUQ publications during the past six years (total = 271).

1.1.8 Human resources: Ten post-doctoral associates have worked with LUQ during the past six years. Fifty-six students have completed doctoral or masters' degrees working with LUQ (see list of publications), 26 during the past six years. Fifty students (62% female, 66% minority) have been involved in Research Experience for Undergraduates (REU) projects, supported by supplemental funds to the LTER project or by a site grant to the University of Puerto Rico. For the current census of the LFDP, we supported (A. W. Mellon Foundation grant) over 50 student volunteers and technicians, a first experience for many in the tropics. Six high schools throughout Puerto Rico have experimental plots near their schools and participate in a research network with LUQ as part of the Schoolyard LTER program (Lugo 1999).

1.2 Response to Previous Reviewers' Comments

We submitted a renewal proposal in 2000 and were asked to prepare a new proposal for the period 2002-6. Thus, the present proposal will support the final four years of LTER 3. We were asked to address the following major points in this new proposal:

1.2.1 Conceptual framework: Based on an evaluation of results to date, LUQ principal investigators jointly identified the need for a better understanding of the interaction between disturbance and detrital dynamics as our next major research priority. While recognizing the need for future work on a variety of topics, we agreed upon an integrative conceptual framework for research in LTER 3: **disturbance, through its effects on detrital dynamics, is a dominant ecosystem driver in the LEF**. The scientific justification for this conceptual framework arises from results presented above and is considered in detail below. In brief, we propose to continue our focus on disturbance through a closely integrated approach to linked ecosystem processes, the production of detritus by disturbances and the role of the biota in recycling of carbon and nutrients via decomposition. Emphasis on disturbance and detrital dynamics also provides a framework for our recent initiative to extend our research to the entire elevational gradient represented in the LEF. We have revised and reduced the number of proposed hypotheses and field projects, such that these all contribute directly to the investigation of disturbance and detrital dynamics. We also have revised modeling and long-term measurement programs to eliminate redundancy and to insure that these guide and support the new research.

1.2.2 Data management: LUQ data sets are accessible through a new searchable web interface on our revamped web page (http://luq.lternet.edu). All data sets and metadata have been updated and are freely available (see Supplementary Documentation).

1.2.3 Cross-site comparisons: Cross-site research has always been a strength of LUQ, but our 2000 proposal did a poor job of making that point. We describe cross-site research projects in detail in the body of the proposal (**Section 2.6**).

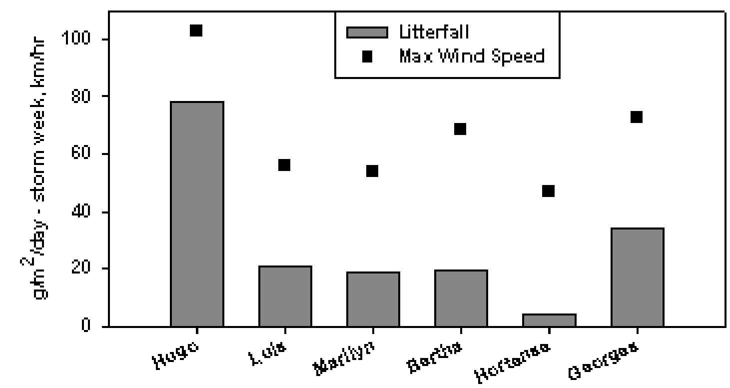
Section 2 Proposed Research

2.1 Introduction

Incorporating disturbance regime as a fundamental attribute of an ecosystem or landscape has revolutionized the way scientists view ecological systems (Sousa 1984, Pickett & White 1985, Walker 1999). Numerous studies show that disturbance imparts a distinctive signature to the structural and functional attributes of most ecosystems, including tropical forests (Garwood et al. 1979, Sanford et al. 1985, Gómez-Pompa & Kaus 1990, Walker et al. 1991, 1996a, Ashton 1993, Clark et al. 1995, Walker 1999, Willig & Walker 1999). In the Luquillo Mountains, hurricanes are the dominant disturbance type, and, with landslides and land use, constitute a disturbance regime whose impacts range from decadal to generational (Walker et al. 1991, Waide & Lugo 1992, Lugo & Scatena 1995, Walker et al. 1996a). Previous research by the Luquillo Experimental Forest LTER program focused on understanding the effects that hurricanes in 1989 and 1998 had on the structure and function of mid-elevation tabonuco forest and how the biota responded to these disturbances (**Fig. 2.1.1**). This focus, together with studies of landslides and human land use, provided insights into the key characteristics of disturbance that alter forest function in tropical montane ecosystems over long time scales. One primary effect of disturbance is to redistribute organic matter from live biomass compartments to the detrital pool. The dominant biotic and abiotic processes that contribute to the production and decomposition of detritus and to the subsequent fate of associated C and nutrients are shown in bold in **Fig. 2.1.2**. These processes, which define detrital dynamics, play a central role in the recovery of forest structure and function by regulating carbon and nutrient storage and flow. Thus, **disturbance, through its effects on detrital dynamics, is a dominant ecosystem driver at the Luquillo LTER site.**

The disturbance regime determines the temporal, spatial, and chemical characteristics of litter inputs to the detrital system and thereby controls critical parameters and dynamics of terrestrial and aquatic compartments of the LEF ecosystem. Disturbance produces a pulse of detrital material (fine litter and coarse woody debris), modifies the microclimate, and changes decomposer species composition. The key factor, however, is the pulsed nature of inputs of detrital material (Sousa 1984), and thus the long-term response of the biota to disturbance is constrained by the quality, quantity, and distribution of detritus. Changes in microclimate and species composition (particularly detritivores) modify the rate at which the detrital pulse propagates through the system. Our previous research in tabonuco forest has shown that post-disturbance conditions determine the response rate and trajectory of the modified ecosystem (Willig & Walker 1999) by influencing germination, growth, survival, nutrient export, soil conditions, plant community composition, and consumer trophic structure. In this proposal, we build upon our earlier studies to focus on the critical linkages between disturbance and the production and processing of detritus, and the influence of these linkages on the long-term dynamics of ecosystems. We address five questions fundamental to understanding the interaction between disturbance and ecosystem function in the Luquillo Mountains:

(1) How do climatic factors, litter quality, and detritivore diversity regulate decomposition of detrital pulses?
(2) How do terrestrial and aquatic food webs differ in their response to detrital pulses?
(3) What is the effect of disturbance frequency on nutrient cycling, plant community composition, and the accumulation of soil organic matter?



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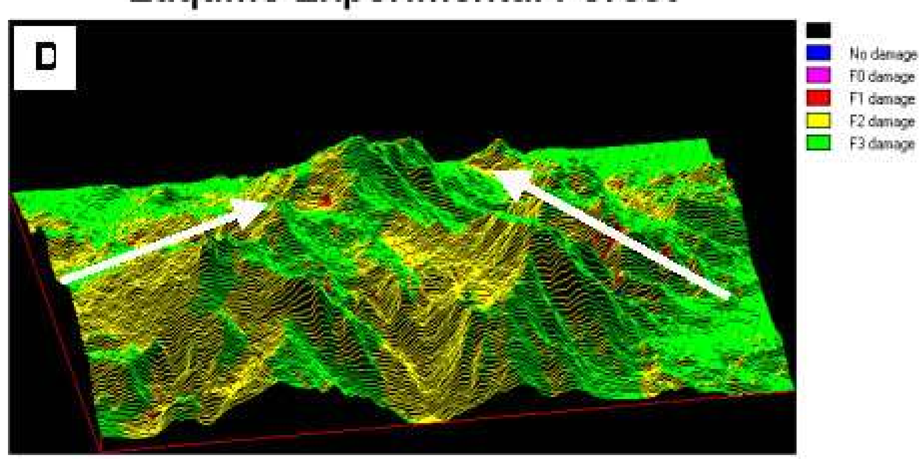


1886-1996 Maximum Predicted Damage (view toward north)

Figure 2.1.1. Hurricane damage to (A) forest near El Verde Field Station showing (B) detritus deposited on forest floor. Winds and litterfall deposited at Bisley Experimental Watersheds (C) by storms experienced at the LEF during 1988 - 2001. A century of maximum exposure to hurricane winds (D; as estimated by the HURRECON and EXPOSE models, Boose et al. 1994, unpublished) shows that all areas of the LEF sustained severe damage sometime during 1886 to 1996 and that topographic position modifies patchiness of wind damage. Legend shows none to high damage categories, yet most of the surface was highly or very highly damaged over 100 years.

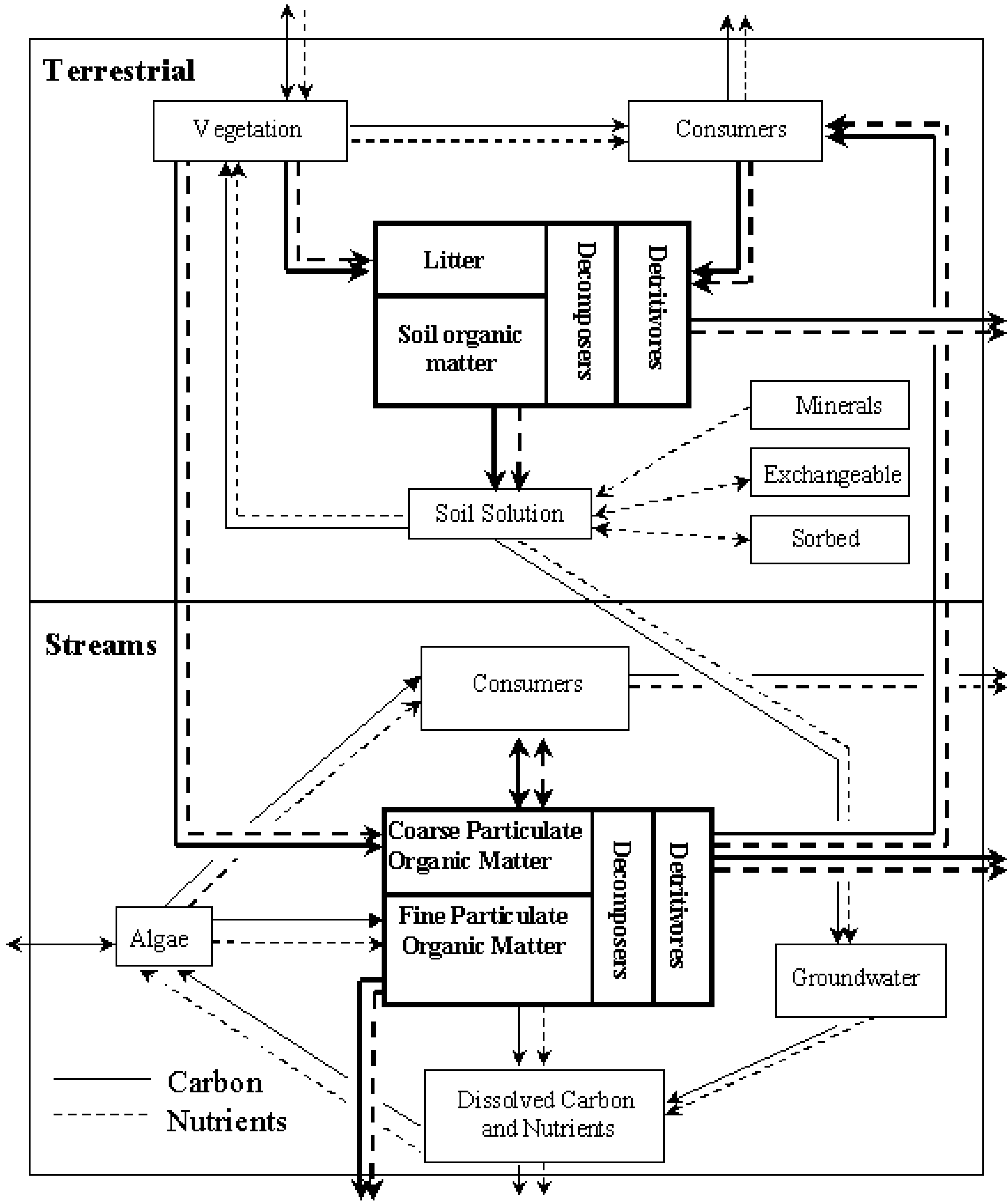


Fig. 2.1.2. A generalized box model of material flow in terrestrial and aquatic ecosystems in the Luquillo Experimental Forest. Compartments and arrows in bold indicate major pools and fluxes of carbon and nutrients associated with detrital dynamics.

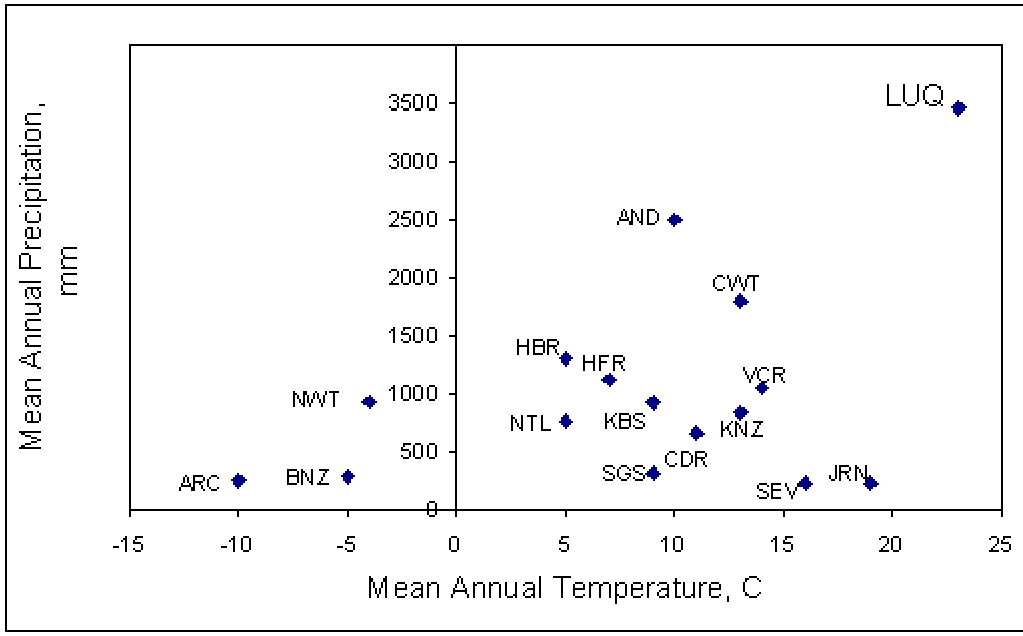


Fig. 2.1.3. Mean annual temperature and precipitation of the Luquillo Experimental Forest relative to other US-LTER sites in the Long-term Intersite Decomposition Experiment. As a result of higher rainfall and temperatures, decomposition in the LEF takes less time than in any of the other US-LTER sites (Gholz et al. 2000).

(4) To what degree is the export of carbon and nutrients from watersheds a result of soil characteristics that are affected by detrital dynamics?

(5) How do elevationally related changes in climate impact plant and detritivore communities, and how do these feed back on the quantity and quality of litter inputs and decomposition?

We have assembled a diverse scientific team to address these questions (**Table 2.1.1**).

Detrital dynamics and its linkages with disturbance have broad relevance to the fields of ecology and biogeochemistry and contribute to our understanding of global change. Controls on the fluxes of organic matter through ecosystems have important feedbacks to soil C sequestration, atmospheric CO2, and the export of terrestrial C to rivers and oceans (Schlesinger 1999). Although detrital food webs are the major pathway for carbon mineralization in many ecosystems and release most of the essential nutrients for primary producers, relatively few studies have explored the functional aspects of detrital food webs compared to other food webs (Moore et al. 1993, Jefferies et al. 1994, Polis & Hurd 1996, Hooper et al. 2000).

2.2 Conceptual Approach

Disturbance alters ecosystems in many ways, and response to repeated disturbance may occur at both ecological and evolutionary time scales. A comprehensive approach to understanding the effect of disturbance on ecosystems recognizes this complexity and addresses it by focusing on critical regulating processes. In the LEF (Fig. 2.1.3), high, seasonally constant temperatures and rainfall, high biotic diversity, and repeated large-scale disturbance regulate the rapid rates of growth and decomposition that characterize Luquillo and many other tropical rain forest ecosystems. By affecting the timing, magnitude, and quality of inputs of detritus into the system, disturbance drives the temporal and spatial dynamics of decomposition. The rate at

Table 2.1.1. Participants in LTER 3. An Executive Committee comprised of the four PIs and three rotating senior personnel (current members in bold) directs the research program. The LTER Program is also supported by additional key scientific personnel: a Data Manager, the Project Director of the Luquillo Forest Dynamics Plot (LFDP), and the Director of El Verde Field Station.

	Participant	**Present Affiliation**	**Specialty**	**Years of Tropical Experience**
Principal Investigators	**J.K. Zimmerman**	University of Puerto Rico	Plant ecology	17
	A.E. Lugo	Int. Inst. Tropical Forestry, USDA FS	Ecosystem analysis, nutrient cycling	42
	D.J. Lodge	Forest Products Lab, USDA FS	Nutrient cycling, fungal systematics	20
	N. Brokaw	University of Puerto Rico	Forest ecology	28
Senior Personnel	G. Belovsky	Notre Dame University	Population and ecosystem modeling	2
	A. Covich	Colorado State University	Stream ecology	26
	T. Crowl	Utah State University	Quantitative analysis, stream ecology	14
	E. Cuevas	University of Puerto Rico	Decomposition, belowground processes	25
	G. González	Int. Inst. Tropical Forestry, USDA FS	Decomposition, nutrient cycling	8
	C. Hall	SUNY-ESF	Modeling, stream ecology	16
	P. Klawinski	William Jewell College	Insect ecology	4
	W. McDowell	University of New Hampshire	Biogeochemistry	20
	C. Pringle	University of Georgia	Stream ecology	15
	W. Silver	University of California – Berkeley	Biogeochemistry	21
	F. Scatena	Int. Inst. Tropical Forestry, USDA FS	Geomorphology, hydrology	25
	J. Thomlinson	University of Puerto Rico	Landscape ecology, GIS	9
	R. Waide	University of New Mexico	Avian ecology	31
	L. Walker	University of Nevada – Las Vegas	Succession, primary production	18

	M. Willig	Texas Tech University	Invertebrate ecology, quantitative analysis	25
	X. Zou	University of Puerto Rico	Nutrient dynamics, earthworm ecology	13
Data Manager	E. Meléndez-Colom	University of Puerto Rico	Information management	13
Project Director LFDP	J. Thompson	University of Puerto Rico	Forest ecology	15
Director **El Verde Field Station**	A. Ramírez	University of Puerto Rico	Stream ecology, insect systematics	8

which detrital pulses are processed has implications for other ecosystem fluxes and storages (e.g., nutrient cycling and export, soil organic matter, biomass, productivity), as well as for community and population structure and dynamics. Climate and the biota also influence ecosystem processes, but these factors themselves are mediated by disturbance. The Luquillo LTER program focuses on a comprehensive understanding of these complex interactions by integrating population, community, and ecosystem ecologists under a common conceptual approach.

Our present approach incorporates long-term measurements of forest and stream response to natural and anthropogenic disturbance, associated short- and long-term manipulative experiments to develop a process-level understanding of results from our long-term measurements, validation of this understanding through parallel experiments and measurements along gradients of climate and species richness, and comparison of results from LUQ with other LTER and non-LTER sites. By integrating investigations of disturbance, organic matter processing and accumulation, nutrient cycling and export, consumer populations, and productivity, our research addresses the five core LTER research areas.

1) Measurements of long-term changes in climatic, biotic, and biogeochemical characteristics resulting from disturbance in tabonuco forest (Section 2.3)

We use standard measurements of key organisms, processes, and ecosystem characteristics to identify and quantify changes in tabonuco forest in the LEF. This approach takes advantage of natural (e.g., hurricanes, landslides, droughts, floods) and anthropogenic (e.g., previous land use) disturbances to examine the effect of and response to disturbance. While natural disturbances are not controlled experiments, the existence of pre-disturbance data and topographic variation in the intensity of disturbance permits us to quantify the severity of effects among and within disturbance types. Simulation models (HURRECON, CENTURY) provide information about the effects of hurricanes of different intensities and paths. This approach includes the collection and management of core long-term datasets. We will add two new long-term datasets in LTER 3: one on coarse woody debris, an important structural and functional feature of the forest floor, the other on herbivory, a process which under certain circumstances may be an important regulator of detrital processing. In addition, we will expand collection of selected core data sets to other forest types within the LEF, as described in (3) below.

2) Experiments to determine how disturbance alters detrital dynamics (Section 2.4)
To examine key processes identified through long-term measurements we use focused, short- and long-term experiments. In LTER 3 we will focus experiments on the processes that contribute to and control detrital dynamics in tabonuco forest. We will conduct experiments that address the importance of different elements of disturbance (e.g., detrital pulse, changes in microclimate) on decomposition (Question 1), the functional characteristics of invertebrate detritivores on the forest floor and in streams (Question 2), the potential for interactions between autotrophic and detrital food webs, and the effect of disturbance frequency on organic matter accumulation, species composition, and the export of carbon and nutrients (Question 3).

3) Experiments and measurements along gradients of climate and species richness (Section 2.5)
In the first part of LTER 3, we have initiated a gradient analysis of forest communities and ecosystem attributes with elevation. Results from this analysis will increase our understanding of the relative roles of climate, litter quality, and decomposer communities in determining decomposition rates in terrestrial and aquatic habitats (Question 5), evaluate landscape-scale patterns of SOM and nutrient stores predicted from simulation models, and determine the role of soil characteristics influenced by detrital dynamics in controlling carbon export in streams (Question 4). This gradient analysis will allow us to scale results from forest stand to landscape perspectives and will establish a research infrastructure throughout the LEF on which to base the future development of our research program.

4) Comparison of results from LUQ with other LTER and non-LTER sites (Section 2.6)
Continued participation in ongoing network comparisons (e.g., LIDET, LINX) will be augmented by involvement in new cross-site studies. These new comparative studies will focus on developing an improved understanding of processes involved in detrital dynamics across diverse ecological systems.
In the following four sections, we provide detail about each of these approaches and how they address the five scientific questions raised above. A final section indicates how research conducted under these approaches will lead to a synthetic understanding of disturbance and response in tropical forest ecosystems. Additional methodological details are provided on our website (http://luq.lternet.edu).

2.3 Measurements of Long-Term Changes in Climatic, Biotic, and Biogeochemical Characteristics Resulting from Disturbance in Tabonuco Forest

2.3.1 Background and approach: Measurements of long-term changes in climatic, biotic, and biogeochemical characteristics in the LEF were initiated to determine background levels of spatial and temporal variability, detect rare or gradual events, measure deviations from background as a result of disturbance, and quantify the responses to disturbance. Some of these measurements (e.g., climate, primary production, species abundances) were continuations from earlier research, and others were initiated to address specific goals of the LTER program. Long-term measurements originally were intended to provide a backdrop for watershed-scale manipulation experiments, but the occurrence of Hurricane Hugo and associated landslides refocused our research on these critically important types of disturbance.

Naturally occurring disturbances provide opportunities to observe responses to forces that have shaped ecosystems over evolutionary time. Measurement of the effects of disturbance against background levels constitutes a kind of natural experiment, which, although without a control, can provide important insights into the dynamic behavior of ecosystems. In Caribbean forests, hurricanes are the dominant disturbance type affecting ecosystem structure and function, but other kinds of disturbance also have important effects. Infrequent events such as hurricanes have strong, multi-year to decadal effects on forest and stream functioning (Scatena et al. 1996, Schaefer et al. 2000), while drought has more subtle but equally important long-term impacts on some organisms (Covich et al. 1996, 2000). Likewise, the effects of human disturbance, such as clear-cutting, agriculture, and gradual shifts in the landscape mosaic (Silver et al. 1996, Thomlinson et al. 1996, Silver et al. 2000) can persist for decades and longer (Zimmerman et al. 1995a, Willig et al. 1996). Understanding these effects requires long-term measurements.

Studies of these natural experiments of disturbance and response involve a series of long-term measurements of meteorology, hydrology, ecosystem parameters, and plant and animal populations. These core measurements also reveal long-term changes not associated with episodic events and provide context for short-term, manipulative experiments, such as those on detrital processing (see **Section 2.4**). Long-term measurements (**Table 2.3.1**) were defined in LTER 1 and refined as our understanding of tabonuco forest dynamics increased. Long-term measurements are conducted principally at two study sites, El Verde Research Area and the Bisley Experimental Watersheds, in the Espíritu Santo and Mameyes drainages (**Fig. 2.3.1**). Additional measurements are made in the Río Blanco Watershed, in landslides throughout the LEF, and in sites extending to elfin forest at the summits of the Luquillo Mountains (**Fig. 2.3.1**).

2.3.2 Disturbance experiments: Hurricanes in 1989 and 1998 and landslides associated with these hurricanes and other storms provide the setting for long-term measurements of forest response. These measurements include:

> (1) Environmental properties (e.g., light, nutrients, moisture, temperature) that vary with disturbance size, age, and origin;
> (2) Biological properties that are expected to vary with environmental properties (e.g., population density, species composition, growth, nutrient uptake, reproductive success, and

carbon fixation);
(3) System-level properties that emerge from the effects of the disturbance regime on the mutual interaction of abiotic environment and biota (e.g., decomposition, nutrient cycling, SOM, resilience, and food web structure).

Measurements of these properties address the following hypothesis, as articulated in LTER 2:

Hypothesis 1: *The response to disturbance and the subsequent trajectories of recovery are determined by 1) location along abiotic gradients, 2) the abiotic and biotic conditions resulting from disturbance, and 3) biotic processes sub*sequent to disturbance. The relative importance of these three factors will vary with the severity of the disturbance. **(Brokaw, Covich, Klawinski, Lugo, McDowell, Ramírez, Scatena, Silver, Thompson, Waide, Walker, Willig, Zimmerman, Zou)**

Rationale - Results from LTER 1 and 2 demonstrate that understanding of ecosystem recovery after disturbance requires knowledge of 1) the spatial distribution of resources needed for growth (e.g., water, light, and nutrients distributed along gradients of slope, aspect, elevation, and geology), 2) legacies of natural and anthropogenic disturbances, and 3) the properties of nutrient storage and cycling, decomposition, reproduction, dispersal, establishment, growth, and survival inherent in the biota. In LTER 3, we continue measurements of these factors in tabonuco forest to compare responses to specific disturbances and to understand the complex interactions that result from serial disturbances.
Workplan: meteorology - Meteorological measurements answer questions of how average, unusual, and changing climatic patterns affect LEF ecosystems. In LTER 1 we initiated meteorological measurements (Table 2.3.1) at multiple sites conforming to LTER Level 3 weather stations. Those data and historical records were extrapolated to the whole LEF using mechanistic models (Wooster 1989, Hall et al. 1992, García-Martinó et al. 1996a,b). We augmented these permanent stations with short-term measurements of environmental variables associated with particular experiments. Long-term measurements revealed the surprising incidence of droughts, a natural phenomenon that has important impacts on some organisms (Covich et al. 1996, 2000). In the first part of LTER 3, we initiated intensive micrometeorological measurements in tabonuco forest. In addition, we expanded our long-term meteorological measurements along the elevational gradient to help understand how climate

Table 2.3.1. Long-term measurements associated with the Luquillo LTER research program. Legend: B = Bisley, E = El Verde, L = Landslides, P = Pico del Este, LEF = other areas in the LEF.

Measure	Initiation	Funding	Location	Frequency
METEOROLOGY				

Rainfall	1975, 1987 1994	NSF, DOE USFS, Mellon	E, B, P, LEF	Hourly and daily totals Daily NOAA records to turn of century
Temperature (air and soil)	1975, 1987 1994, 1997	NOAA, NSF, USFS, USGS, Mellon	E, B, P, LEF 12 stations	Hourly and daily totals with Level 3 Stations
Humidity, wind speed and direction	1988, 1994	NSF, USFS, USGS, Mellon	B, E, P, LEF 6 stations	Continuous measurement with Level 3 Stations and vertical profiles at El Verde
Light (PAR, total radiation, albedo)	1988, 1994,	NSF, USFS, USGS	E, B, P, LEF	Continuous measurements at 4 stations
HYDROLOGY				
Stream discharge	1945	USGS, USFS	LEF	Daily discharge, 18 historical streams, 12 currently active
Throughfall	1987	USFS, NSF	B, LEF	Daily and weekly in Bisley
CHEMISTRY (major cations and anions)				
Rain	1983, 1988	NSF, NADP NSF	E, B, P	Bulk and wet-only; wkly samples major ions
Throughfall	1988, 1994	UPR, NSF	B	Weekly
Streamwater	1983, 1988 1997 (DON)	UPR,NSF, NASA	B, E, LEF	Weekly samples from 8 long-term streams; Periodic sampling of 13
Litterfall	1989, 1994	NSF, USFS	B, E, P	2 week sampling
Groundwater, soil water, soil oxygen	1988, 1994	NSF, USFS, Mellon, USGS	LEF	Weekly to periodic
VEGETATION				
Forest structure and composition (i.e., density, composition, biomass)	'>1988	'>NSF, USFS, Mellon	B, E, LEF	1-5 year intervals
Belowground biomass	1988	NSF, Mellon	B, E	Yearly
Canopy structure and leaf area index	1989	NSF	E, B	Every 3 years
CWD distribution	2002	NSF, USFS	E, B	Every 3 years
Seedling dynamics	1989	NSF, USFS	B, E	Monthly to yearly
Flowering phenology	1989	NSF, USFS	B, E,	Weekly to monthly
Herbivory	2002	NSF	E	Yearly
Litterfall, litter decomposition	1987, 1994, 1996	NSF, USFS	B, E, L, P, LEF	Weekly to periodic
Arial;'>Landslide revegetation	'>1988	'>NSF	LEF	Every 6 months to yearly
Abandoned pasture revegetation	1996	NSF	LEF	Yearly
FAUNA				
Key species inventory	1988	NSF	E, B	Yearly
DISTURBANCE				
Inventory of gaps, landslides, and stream channel change	1988	NSF,USFS, USGS	B, E, LEF	Yearly to periodic

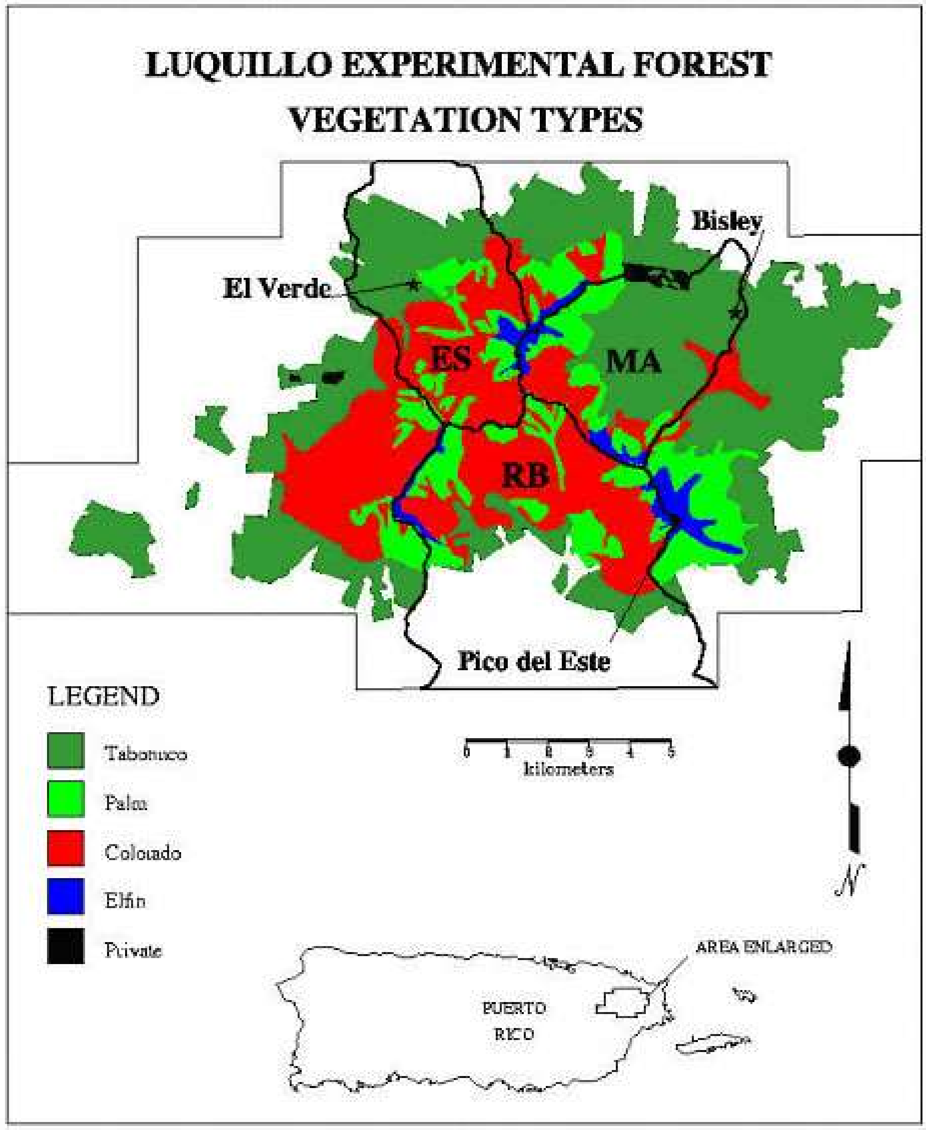
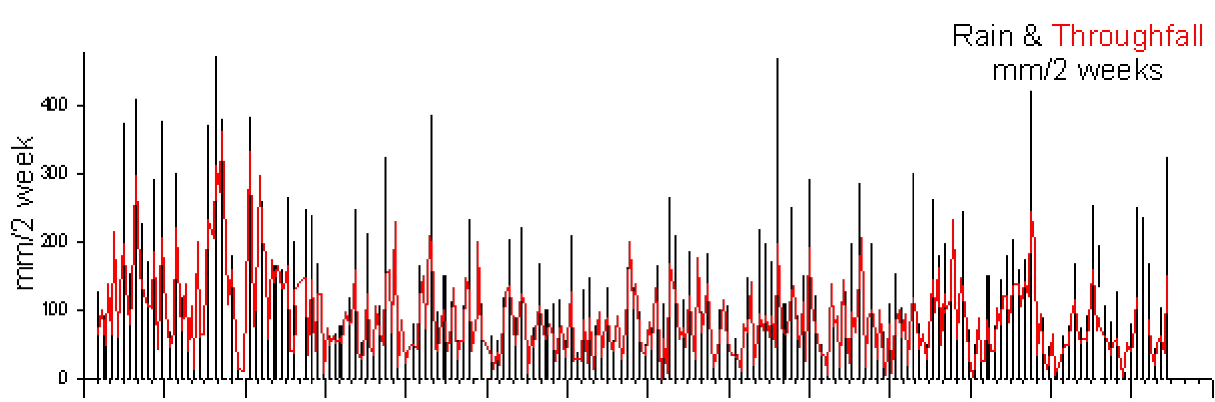


Figure 2.3.1. Vegetation of the Luquillo Experimental Forest. Currently, the vegetation is classified into four forest types, described by dominant species or physiognomy. Lower elevations of the LEF (200-600 m) include tabonuco (Dacryodes excelsa) forest, the subject of LTER 1 and 2, which is studied intensively at El Verde Field Station and the Bisley Experimental Watersheds. Elfin forest occurs at the summits of the Luquillo Mountains over 900 m where conditions are extremely wet, cloudy, and windy; Pico del Este is a commonly used study site. At intermediate elevations, colorado (Cyrilla racemiflora) and palm (Prestoea

montana) forest occur, with the latter occupying the steepest slopes and riparian areas. Our current and proposed research is aimed at extending our detailed understanding of disturbance and ecological response in tabonuco forest to all vegetation types. Efforts to document community variation in biotic communities are utilizing elevational transects in the Espíritu Santo (ES), Mameyes (MA) and Río Blanco (RB) watersheds.

affects detrital processing (**Section 2.5**). Both of these measurement programs use state-of-the-art wireless technology being implemented under a separate grant from NSF.

Workplan: hydrology and nutrient cycling - Our measurements of hydrology and nutrient cycling (**Table 2.3.1**) are used to show how fundamental ecosystem processes are affected by disturbance, and how they change over the long term and along the elevational gradient. Our primary measurements include whole-watershed mass balances for nutrients and other elements (measuring precipitation inputs, biomass accumulation of trees, and stream exports; e.g., McDowell & Asbury 1994); measurement of internal nutrient fluxes (throughfall, litterfall, and litter decomposition; **Fig. 2.3.2**); and changes in nutrient stocks in soils and vegetation in forested plots as well as during primary succession on landslides. During LTER 1 and 2, these measurements demonstrated the impacts of hurricanes, landslides, and clearcutting on nutrient cycling (Zimmerman et al. 1995b, Zarin & Johnson 1995a,b, Scatena et al. 1996, Silver et al.1996, McDowell et al. 1996, Walker et al. 1996a,b, Schaefer et al. 2000, Lodge et al. 2001). Several of our projects have shown that coarse woody debris (CWD) is particularly important in regulating productivity in tabonuco forest (Zimmerman et al. 1995b, Miller & Lodge 1997, Waide et al. 1999, **Fig. 2.3.3**), and thus we have begun long-term studies of the distribution of CWD at several sites (Harmon & Sexton 1986). During LTER 3, we will continue all of these basic measurements of hydrology and nutrient cycling at our current sites and expand to



include more measurements at higher elevations (**Section 2.5**).

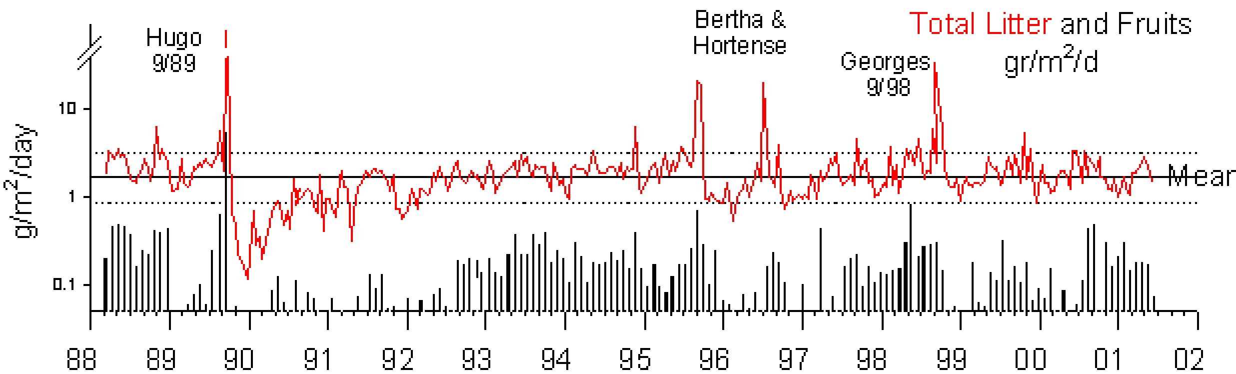


Fig. 2.3.2. Rainfall, throughfall, and litterfall collected in the Bisley Experimental Watersheds from 1988 - 2002. Note that litterfall is plotted on a log scale to illustrate large inputs of litter during hurricanes and to show the response of fruitfall.

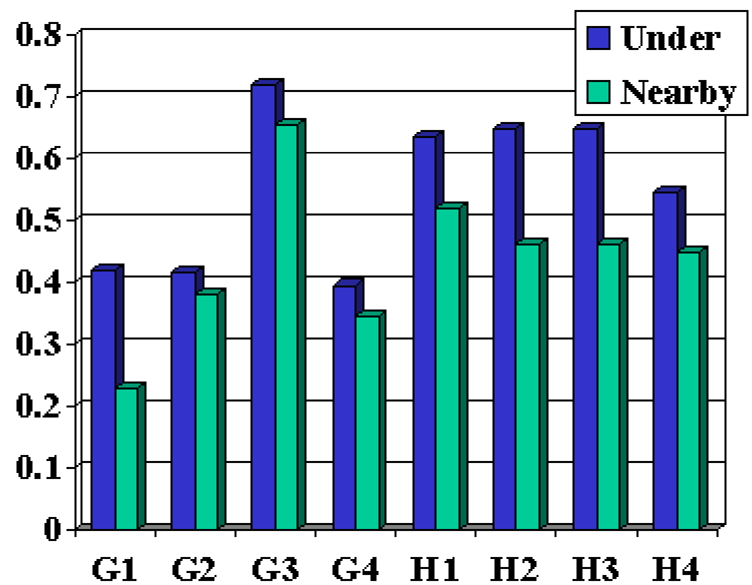


Fig. 2.3.3. Decomposing logs have a significant effect on soil carbon (Lodge et al., in prep.). Data compare logs felled in Hurricane Georges (G1 - G4; 0.6 yr prior to sampling) and Hurricane Hugo (H1 - H4; 9.6 yr) and show significant increases in soil carbon under logs vs. soils sampled nearby. There were parallel differences in total nitrogen and soil microbial biomass.

Workplan: vegetation - The principal goals of long-term vegetation measurements (**Table 2.3.1**) are to quantify the effects of and the responses to disturbance, and to provide information to interpret changes in faunal populations and ecosystem properties. Information from annual measurements of forest plots at Bisley is used to assess change at fine temporal scales. These data have been instrumental in demonstrating the rapid recovery of biomass and nutrient capital after Hurricane

Hugo (Scatena et al. 1996). Shortly after Hurricane Hugo, we established the 16-ha Luquillo Forest Dynamics Plot (LFDP) at El Verde to track vegetation changes at fine spatial scales. In the LFDP, all trees and shrubs ³ 1.0 cm dbh (c. 130,000 stems) have been marked, measured, and mapped (Thompson et al., in press a). The size of the LFDP is necessary to understand the dynamics of a species-rich community in a heterogeneous landscape. Three censuses of the LFDP (the third with Mellon Foundation support) have given us an unprecedented, detailed record of stability and change in a tropical forest subjected to two severe hurricanes (**Fig. 2.3.4**; Brokaw 1998, Brokaw et al., in press) and various human land uses (Zimmerman et al. 1994, Willig et al. 1996, Thompson et al., in press b). Results from the LFDP underscored the long-term persistence of secondary species after land use, which has important implications for detrital processing, because primary and secondary species differ in decomposition rate. Plant responses also are measured over the long term in 20 landslides throughout the LEF (Walker et al. 1996b; **Fig. 2.3.5**) and in two clearcuts at Bisley (Scatena et al. 1993, Silver & Vogt 1993, Silver 1994, Silver et al. 1994).

In addition to continuing long-term vegetation measurements, we will initiate measurements to determine long-term patterns of herbivory in two ways. As in most tropical forests, herbivores mainly eat young leaves (Coley & Barone 1996), which flush during May and

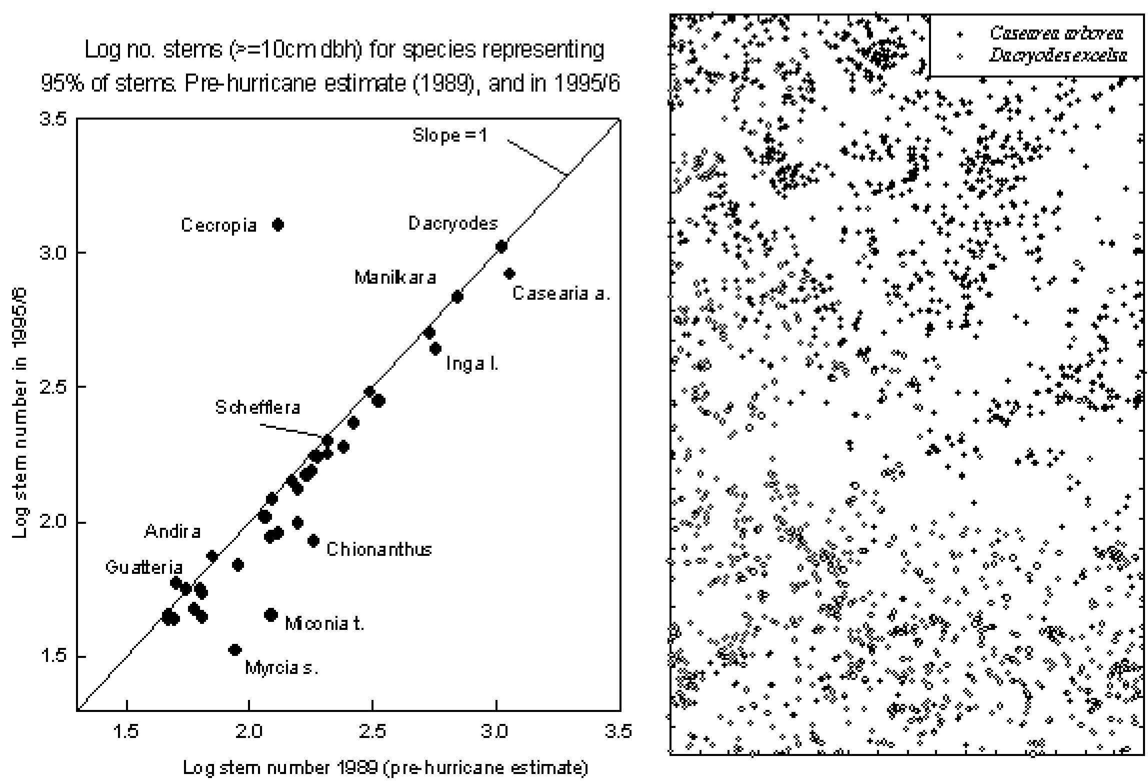


Fig. 2.3.4. Results from the 16-ha Luquillo Forest Dynamics Plot showing (lefthand graph) the stability of species composition in response to Hurricane Hugo (1989). Note the exceptional increase

in the abundance of the pioneer Cecropia schreberiana (Brokaw 1998). The temporal response to hurricane damage is in contrast to the legacy of human disturbance evident in species distributions (right-hand graph). The northern (upper) portion of the plot was clear-cut in the 1920s and the present-day forest is dominated by Casearia arborea, a successional species. The lowermost portion of the plot was subject to selective logging and maintains a near native composition of species, including tabonuco (Dacryodes excelsa; Thompson et al., in press b).

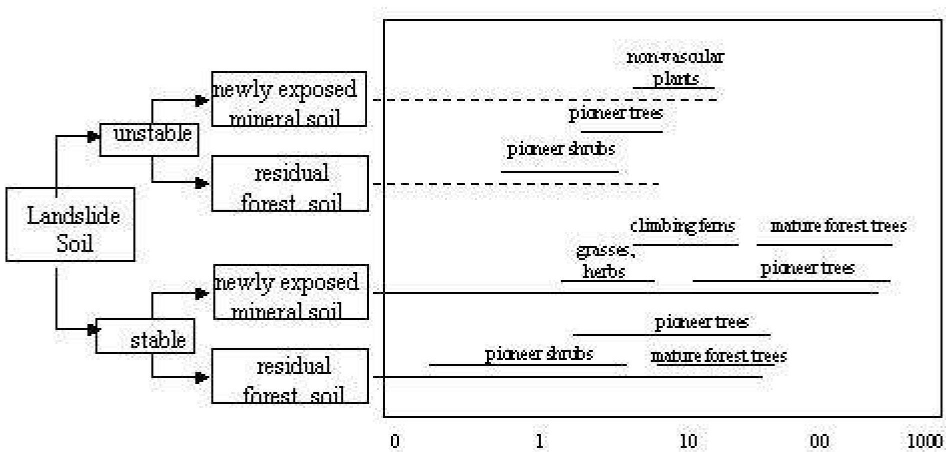


Fig. 2.3.5. A model of landslide succession for the Caribbean developed by Walker et al. (1996) from long-term and retrospective studies showing the importance of slide stability (dashed vs. solid lines) and soil organic matter for the rapidity with which landslides become revegetated.

June in the tabonuco forest or following disturbance (Angulo-Sandoval & Aide 2000). We will measure percent herbivory on new leaves of focal species marked each year in May and June. The second measurement will be of inputs of green leaf litter and insect frass to the forest floor. These measures will be used to gauge the changes in rates of herbivory during recovery from disturbance, with the ultimate goal of evaluating the role of herbivory in succession.

Workplan: fauna - Long-term measurements continue to address questions of how animal and microbial communities respond to disturbance (Covich et al. 1996, Secrest et al. 1996, Woolbright 1996, Gannon & Willig 1997, Huhndorf & Lodge 1997, Reed 1998, Willig et al. 1998, Pyron et al. 1999, Lodge et al. 2001). Surveys of stream decapods, mollusks, birds, frogs, lizards, and arthropods are coordinated with plant surveys in the LFDP and Bisley to determine the importance of habitat structure and resource availability in faunal response to disturbance (**Table 2.3.1**). Key terrestrial detritivores are monitored in both the LFDP and Bisley watersheds (Willig & Camilo 1991, Secrest et al. 1996, Willig et al. 1998) and, since 1998, in a series of plots surrounding the LFDP (Klawinski, unpub.). Detritivores in aquatic habitats (shrimp) have been monitored since 1988 (Covich et al. 1991, 1996). These measurements will be continued under this proposal.

2.4 Experiments to Test how Disturbance Alters Detrital Dynamics in Tabonuco Forest

2.4.1 Background and approach: Results from observations of disturbance and response in LTER 1 and 2 define the gaps in our knowledge of tabonuco forest and establish a priority for experiments to be conducted during the next four years. Strong hurricanes reposition living plant materials (e.g., leaves, flowers, fruits, and branches) from the forest canopy to the forest floor (Zimmerman et al. 1994, 1995b) increasing the levels of detritus on the ground. Light level, soil moisture, and temperature simultaneously increase after disturbance (see Prior Results for more details) and may interact with the pulse of detritus to affect subsequent community and ecosystem changes. For example, increased light promotes the establishment of pioneer and shrub species, but the litter deposited by the hurricane inhibits the germination of these same species (Guzmán-Grajales & Walker 1991). Populations of herbivores, detritivores, and decomposers also respond to both altered microclimate and shifts in resource availability (Waide 1991b, Covich et al. 1994, 1996, Lodge 1996, Zimmerman et al. 1996, Willig et al. 1998). Nutrient pools change dramatically over a period of 6 to 18 months as a function of the rapid decomposition of high-quality leaf litter, decreased uptake because of fine root mortality, and microbial immobilization (McDowell et al. 1996, Silver et al. 1996, Schaefer et al. 2000). Over the long-term, decomposition of low quality CWD and regenerating vegetation regulate nutrient losses from the forest system (Zimmerman et al. 1995b, Scatena et al. 1996). Hence, the two primary effects of hurricane disturbance, changes in microclimate and redistribution of biomass, propagate through the system in complex ways.

A fundamental priority for future research becomes clear from examining results from LTER 1 and 2: the need to assess the independent effects of detrital inputs, microclimate, and different functional groups of invertebrates in detrital processing after hurricanes. This assessment will depend on experimental manipulations and modeling that focus on predicting how changes resulting from disturbance interact to determine the subsequent behavior of the system. Our present understanding of hurricane impacts comes from measurements of the effects of naturally occurring hurricanes on tabonuco forest and comparisons with similar disturbances in other forests (Walker et al. 1991, 1996a). These measurements are informative but cannot tease apart the effects of various aspects of hurricane disturbance and suffer from the lack of a control or reference condition. Experimental and modeling approaches described below complement the long-term measures described in **Section 2.3**.

We will establish an experimental arena where the primary hurricane effects - changes in microclimate and redistribution of the forest canopy to the forest floor - can be studied independently. Long-term manipulations will increase the frequency of hurricane effects against the background levels of natural disturbance to test predictions about the impacts of an increased disturbance frequency on species composition, productivity and storage and export of C and nutrients (Sanford et al. 1991). We also will establish short-term experiments to determine the role of different groups of invertebrate detritivores in processing detritus on the forest floor and in streams, and we will measure interactions between detrital and autotrophic food webs.

Results from biotic manipulations will be used to develop a Trophic Interaction Model (TIM) for tabonuco forest that will incorporate the role of biota in the processing of detritus on the forest floor and in streams. TIM emphasizes the roles of functional groups in decomposition and other ecosystem processes. There is growing awareness that the autotrophic food web (primary producers, herbivores and their associated carnivores) and detrital food web (detritus produced by the autotrophic food web, decomposers and their associated carnivores) mutually influence each other and affect ecosystem processes (DeAngelis 1992, Adams & Wall 2000, Hooper et al. 2000, Palmer et al. 2000). Thus, combining autotrophic and detrital food webs into integrated models (such as TIM) incorporates the ecological interactions created by biodiversity into ecosystem functioning (nutrient release, primary production, C storage). This type of model has provided exciting new insights into how biota accelerate or decelerate ecosystem processes (DeAngelis 1992, Pastor & Naiman 1992, Jefferies et al. 1994, Polis & Strong 1996, Polis et al. 1996, Pastor & Cohen 1997, Belovsky & Slade 2000, Ponsard et al. 2000, Crowl et al. 2001).

2.4.2 Experiment 1 - Canopy Trimming Experiment: This long-term experiment will increase the frequency of simulated hurricane effects above background levels to once every six years. The experiment will determine effects of repeated disturbance of the forest canopy and increased detrital inputs to the forest floor on germination, growth, survival, nutrient cycling, soil conditions, and trophic structure. Climate change models predict increased frequency and intensity of Caribbean hurricanes (Emmanuel 1987, Goldenberg et al. 2001), and our goal is to evaluate predictions regarding the effects of an increased rate of hurricane disturbance on tabonuco forest (Sanford et al. 1991). The experiment also is designed to decouple the effects of canopy disturbance (e.g., light levels, temperature, moisture, etc.) from those of increased detrital inputs on rates of detrital processing and resultant community and ecosystem processes. Manipulations and measurements of detrital processing, SOM, and soil properties associated with SOM will continue for at least three more funding periods (until 2024). In the short-term, we will use faunal manipulations nested within the canopy trimming experiment to measure the strength of interactions between autotrophic and detrital food webs in the context of hurricane-like disturbance. These results will be directed specifically at parameterizing the Trophic Interaction Model (see below). This experiment also will provide a physical and intellectual focal point for the project participants.

The Canopy Trimming Experiment has two parts: 1) a forest canopy manipulation with measurements of coupled changes in microclimate, structure, and biota and their associated impacts on ecosystem processes, and 2) specific manipulations of the biota that assess the importance of components of the food web. Measurements of ecosystem parameters within the experimental treatments will address the following hypotheses:

Hypothesis 2: *Short-term dynamics of key response variables after disturbance will be a function of the interaction between microclimate and detrital inputs, whereas long-term dynamics (particularly of SOM and NPP) will be a function of detrital inputs.* (**All**)

Rationale - Zimmerman et al. (1996) summarized short-term (5 yr) patterns in response to hurricanes (**Fig. 2.4.1**) but were unable to establish causality for many of these patterns because of the lack of controlled experiments. For example, net primary productivity following Hurricane Hugo was augmented by regeneration of pioneer species responding to high light levels (Scatena et al. 1996), but the effect was reduced to some degree by nutrients immobilized in decomposing woody debris (Zimmerman et al. 1995b) and low capacity for uptake because of root mortality (Silver & Vogt 1993). Decomposition of high quality, hurricane-generated leaf litter, which should decompose rapidly, was slowed by drier post-hurricane conditions (Ostertag et al., in revision). Populations of snails initially declined in response to changed microclimate then rebounded quickly, apparently in response to increased ground cover and regeneration of the understory (Willig & Camilo 1991, Secrest et al. 1996, Willig et al. 1998). These examples (and others; Zimmerman et al. 1996) suggest that interactions between microclimate and detrital pulses are important for short-term forest dynamics and emphasize the necessity of controlled experiments to decouple their effects.

Long-term predictions are derived from the CENTURY model, which was parameterized for the tabonuco forest (Sanford et al. 1991) using detailed information on carbon and nutrient stocks in above- and belowground biomass (Odum & Pigeon 1970). Simulations with hurricanes rates, and organic soil P. A hurricane-disturbed forest was predicted to have higher overall productivity than a forest without disturbance (Sanford et al. 1991). The Canopy Trimming Experiment will allow us to test the contention (Sanford et al. 1991) that increased forest productivity in hurricane disturbed forests is the result of increased available levels of nutrients mineralized from high SOM rather than via effects on the canopy, i.e., via the maintenance of a young, open-canopy, fast-growing forest.

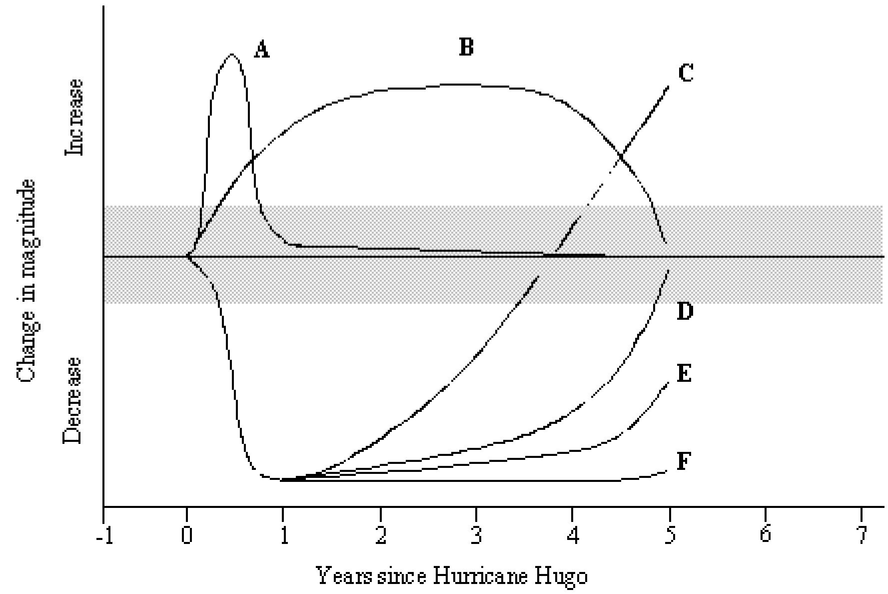


Fig. 2.4.1. Idealized 5 yr trajectories of responses of different components of wet subtropical forest in the Luquillo Experimental Forest, Puerto Rico, to disturbance caused by Hurricane Hugo (from Zimmerman et al. 1996). The shaded portion of the graph represents +/- 15 percent variation indistinguishable from pre-hurricane values. Curve A: transient (<1 yr) increase. Examples include forest floor biomass, some soil nutrient pools, and nitrate concentrations in streams. Curve B: slow increase and return to pre-hurricane levels. Examples are net primary productivity, abundance of Atya shrimp in streams, of adult coqui frogs, and of the terrestrial snail, Cepolis squamosa. Curve C: catastrophic decrease and subsequent rise above pre-hurricane levels. Examples are aboveground pools of potassium and magnesium and of several species of terrestrial snails. Curve D: catastrophic decrease and return to near pre-hurricane levels. Examples are tree biomass and tree density. Curve E: a catastrophic decline and steady increase, but not to within 15 percent of pre-hurricane levels. An example is fine total litterfall. Curve F: catastrophic decline and little recovery until 5 yr post-hurricane. Examples are fine root biomass and abundance of the walking stick, Lamponius portoricensis. Both of the latter returned to near normal values subsequently.

<u>Workplan: forest canopy and structure manipulations</u> - Four blocks of four plots (30 x 30 m) will be identified on the basis of similar slope, soil characteristics, and forest canopy species composition; aspect will be the blocking variable. This plot size was chosen to provide sufficient space for long-term monitoring of plot responses as well as the biotic manipulations discussed below. This level of replication has proven sufficient to measure ecosystem responses to manipulations of detritus in previous experiments in tabonuco forest (Zimmerman et al. 1995b, Walker et al. 1996b). Two plots within each block will have the branches of the canopy trees trimmed by a professional arborist to open the canopy, which is roughly equivalent to the action of a hurricane with sustained winds of more than 150 kph. The recurrence interval for hurricanes of this strength is 55-60 yrs for the LEF (Scatena & Larsen 1991). The other two plots will not experience canopy manipulation and will be subject to normal hurricane frequency. This

experiment will be initiated in year 2 of funding because of the need to coordinate the logistics of an experiment of this scale and conduct one year of pre-manipulation measurements.
The experimental manipulations will create four treatments in a 2 x 2 factorial design in each block:

(1) Canopy trimmed and removed biomass distributed on forest floor. This simulates the changes in microclimate (openness) and structure (redistribution of biomass) created by a hurricane;
(2) Canopy trimmed and removed biomass eliminated. This simulates the changes in microclimate (openness) created by the hurricane without the associated change in forest structure (redistribution of biomass);
(3) Canopy untrimmed with canopy biomass from a trimmed plot distributed on the forest floor. This simulates the changes in forest structure (redistribution of biomass) created by the hurricane without the associated change in microclimate;
(4) Canopy untrimmed and no canopy biomass added to forest floor. This maintains the forest unmodified by hurricane disturbance.

Within each plot measurements will be made within a core (20 x 20 m) area to minimize edge effects. The measurements and their frequency are listed in **Table 2.4.1**. Sampling for some variables will be quarterly for one year prior to and after the canopy manipulations and annually thereafter until the next scheduled manipulations. The inner plots will be divided into 1 x 1 m quadrats and randomly allocated to be measured for either plant or invertebrate densities, or for soil characteristics (10 quadrats each; Guzmán-Grajales & Walker 1991, Walker et al. 1996b). Vertebrates will be recorded using the entire inner plot. Litterfall will be measured using baskets placed 1 m above the ground. Litter samples will be collected biweekly. Root production and turnover will be measured using sequential ingrowth cores. Soil nutrient pools and fluxes will be measured using standard methods (Robertson et al. 1999). Export of nutrients will be measured using soil solution collected from tension lysimeters. Statistical analyses will be made using repeated measure MANOVA by block. Measured ecosystem variables (Table 2.4.1) will be compared to CENTURY predictions (see below).
In addition to distinguishing the relative importance of microclimatic changes versus detrital inputs in determining responses of tabonuco forest to severe hurricane damage (Zimmerman et al. 1996), this experiment will also determine the contribution of decreased nutrient uptake to the flush of nutrients into groundwater and streams (McDowell et al. 1996, Schaefer et al. 2000) by isolating two potential causes of fine root mortality, lack of carbohydrate from leaves versus soil drying (a third being the physical disruption of root systems; Silver & Vogt 1993).
Canopy manipulations will be repeated every six years. This interval was chosen because it is approximately ten times the average frequency of storms of this magnitude (Scatena & Larsen 1991) and many relevant ecosystem parameters return to near pre-hurricane values after five years (Zimmerman et al. 1996).

Table 2.4.1. A list of measurements to be made in the Canopy Trimming Experiment and associated food web manipulations.

Abiotic/structural characteristics				
Temperature	✓			Continuously
Humidity	✓			Continuously
Light	✓			Continuously
Biotic characteristic				
Leaf area index	✓			Quart./Annually
Canopy height profiles	✓			Quart./Annually
Density of understory plants	✓	✓	✓	Quart./Annually
Microbial biomass	✓	✓	✓	Quart./Annually
Density of snails	✓	✓	✓	Quart./Annually
Density of herbivorous insects	✓	✓	✓	Quart./Annually
Density of predaceous invertebrates	✓			Quart./Annually
Density of frogs	✓			Quart./Annually
Density of anoles	✓			Quart./Annually
Ecosystem processes				
Litterfall	✓		✓	Biweekly
Tree diameter increment	✓			Quart./Annually
Root production/turnover	✓			Quart./Annually
Litter decomposition rates	✓	✓	✓	Annually
Herbivory rates	✓	✓	✓	Quart./Annually
Soil C, N, P pools	✓	✓	✓	Quart./Annually
Soil N, P mineralization rates	✓	✓	✓	Monthly
Soil respiration and trace gas fluxes	✓	✓	✓	Monthly
Soil solution N, P	✓			Mo./Quarterly

Two sets of biotic manipulations will be conducted within the main treatments of the Canopy Trimming Experiment: one will manipulate detritivory (detrital-based food web) and the other will manipulate herbivory (autotroph-based food web). These experiments will employ small-scale mesocosms and removal of organisms to isolate the potential effects of food web components thought to influence ecosystem processes. Because of the intense maintenance requirements of these manipulations, they will be conducted for only two years.

Hypothesis 3: *The absence of invertebrate detritivores will have strong effects on detrital dynamics, retarding decomposition rates and related processes. Microclimatic changes associated with canopy opening will reinforce these effects, but the addition of detritus will buffer the effects of canopy opening.* **(Belovsky, Crowl, González, Klawinski, Lodge, Willig, Zou)**

<u>Rationale</u> - Cross-site studies involving LUQ show that removal of microarthropods from the litter layer (Heneghan et al. 1998a) and litter microarthropods and macrofauna from the soil

(González & Seastedt 2001, Liu & Zou, in press) significantly slows litter decay rates in terrestrial ecosystems. González and Seastedt (2001) reported that faunal effects on litter breakdown can reach 66% in tabonuco forest. We believe that these effects are important under typical conditions, but that they will be modified by changes due to disturbance. Specifically, we predict a three-way interaction between the main effects of the Canopy Trimming Experiment and the presence/absence of invertebrate detritivores, as stated in the hypothesis.
Workplan - Detritivores will be manipulated with selected measurements from **Table 2.4.1** made in each subplot: **[Note: protocol was changed in December 2003; naphthalene and eletroshocking are not being used in this experiment.]**

> (1) Invertebrate detritivores excluded - microbial decomposition only. Subplots (2 x 2 m) will be trenched and barriers placed to prevent earthworm immigration. Earthworms will be eliminated from subplots by electroshocking (Liu & Zou, in press). Naphthalene will be placed at ground level in each subplot to exclude arthropod detritivores (González & Seastedt 2001). These subplots will be isolated in corners of the inner plots at a distance of 5 m from monitoring areas and other experiments. The experiment will eliminate essentially all invertebrate detritivores (and understory herbivores) to examine microbial decomposition of litter in the context of the Canopy Trimming Experiment.
> (2) Invertebrate and microbial decomposition. Subplots will be trenched and barriers placed but earthworms will not be removed nor will naphthalene be applied. These subplots will be placed in the remaining inner plot corners.
> Data from the experiments on the detrital-based food web will be analyzed using repeated measures MANOVA by block. Estimates for particular effects will be used to develop modeling parameters (see **2.4.4**).

Hypothesis 4*: Presence of herbivores will significantly alter patterns of detrital processing by differentially reducing the abundances of early successional plant species. This effect will be most pronounced under open canopy conditions.* (**Belovsky, Crowl, Waide, Willig**)

Rationale - Considerable recent evidence suggests that interactions between autotrophic and detrital food webs can strongly influence fluxes of C and nutrients (DeAngelis 1992, Pastor & Naiman 1992, Adams & Wall 2000, Hooper et al. 2000, Palmer et al. 2000). This experiment specifically addresses the impact of species with low- vs. high-quality litter on detrital dynamics, and how this impact varies with the presence of herbivores. Following disturbance, and in the absence of herbivores, fast-growing plant species will dominate and their high quality litter should prime decomposition and rates of nutrient cycling, producing a positive feedback to plant growth. Where present, herbivores should preferentially consume high-quality leaves and hence reduce the average quality of litter inputs. Under open canopy conditions, where the difference in growth rates between fast- and slow-growing species is greatest, the effect of herbivores on detrital processing should be disproportionately greater.
Workplan - Herbivores and the plant community will be manipulated in screened cages (2 x 2 x 3 m). Each plot will contain four cages, randomly located but at least 5 m from the detrital-based food web experiments to prevent interference. The litter and soil down to 2 cm will first be cleared and homogenized between plots within the block and then redistributed in each cage to minimize variability. The caged area also will have understory vegetation removed and will not

contain tree trunks. Crossed wooden walkways will be placed within each cage, for access with minimal disturbance to the soil. Cage roofs will be constructed to deflect litter input from the canopy. Thus, subsequent litter inputs will come only from the artificial community and any consumers that might be present.
Within each cage a simplified understory community of two species will be transplanted from nearby forest. Piper glabrescens is a common, fast-growing shrub in closed canopy forest and openings. Manilkara bidentata is a common, slow-growing canopy tree. Individuals of each species approximately 1 m tall will be planted within each subplot and measured for size (total branch length and leaf number) as an estimate of aboveground biomass. We will manipulate numbers of an herbivore, the walking stick Lamponius portoricensis. These are common herbivores in the understory of tabonuco forest and are generalists feeders that nonetheless exhibit a preference for P. glabrescens and are present throughout the year (Willig et al. 1993). Cages (two in each plot) will be stocked with adult individuals of an average size to achieve the average forest density and sex ratio (Willig et al. 1993). Initial stocking densities are at the forest average, because this would be the number at the time that a hurricane strikes. Walking sticks will be surveyed in the cages every month and the numbers will be reduced or augmented to maintain experimental densities. Two cages will contain no herbivores, to measure ecosystem processes in the absence of any consumers. The autotroph-based food web experiment will include the measurements listed in **Table 2.4.1**.
The experiments with the autotroph-based food web will be run for two years and will be analyzed using repeated measures MANOVA by block. Estimates from post-hoc comparisons for particular effects will be used to develop modeling parameters for TIM (see below).

2.4.3 Experiment 2 - Detritivore Functional Group Experiment: The contributions of different groups of invertebrates to decomposition and nutrient mineralization after hurricanes are not fully understood. In stream ecosystems, these two groups of decapod invertebrates are necessary for the complete processing of hurricane-generated detritus (Covich et al. 1999, Crowl et al. 2001, March et al., in press). Terrestrial ecosystems have groups of detritivores that are analogous in function to stream invertebrates (Schowalter 2000). Experimental manipulations in which we tease apart the independent effect of particular groups of the biota in aquatic and terrestrial ecosystems are proposed to address two hypotheses:

Hypothesis 5*: Within ecosystems: decomposition rates will be most rapid in the presence of all detritivore functional types. The effect of excluding functional groups will vary depending on the group excluded*. (**Crowl, González, Klawinski, Pringle, Ramírez**)

Hypothesis 6*: Between ecosystems: exclusion of analogous functional groups will have parallel effects on decomposition rates in the two ecosystems.* (**Crowl, González, Klawinski, Pringle, Ramírez**)

Rationale - Diverse assemblages of invertebrates consume disturbance-generated detritus on the forest floor and in streams in tabonuco forest. In tropical headwater streams, shrimps are often the main group of detritivores, followed by crabs and insects (Covich & McDowell 1996, Covich et al. 1999). Variation in shrimp densities among streams results in large differences in particle export to downstream reaches at landscape levels (Pringle et al. 1999). Two shrimp species, Xiphocarus elongata and Atya lanipes, are important processors of detritus in headwater streams

(Crowl et al. 2001, March et al., in press). In terrestrial ecosystems, millipedes and isopods are mainly responsible for the fragmentation of litter, while mites and collembolans are important microbial grazers (Schowalter 2000). As in the stream, invertebrates play a significant role in litter decomposition in terrestrial ecosystems (Heneghan et al.1998a, González & Seastedt 2001, González et al. 2001), but we lack information on the importance of particular functional groups of detritivores (e.g., fragmenters, grazers) in terrestrial ecosystems. Furthermore, our past studies of aquatic ecosystems have only considered species of decapods and not other detritivore groups (e.g., insects). This set of experiments will investigate the relative importance of different functional groups of invertebrates in detrital processing in terrestrial and aquatic environments of the tabonuco forest. The experiments are based on a single pulse of detritus as occurs after a hurricane and provide a base for comparing detrital food webs between terrestrial and stream habitats. The results from this experiment will allow us to investigate the utility of TIM at finer scales of biotic resolution (i.e., among detritivores).

Workplan - In terrestrial habitats we will create a series of enclosures (2 x 2 m; Lawrence & Wise 2000) that will limit the passage of litter invertebrates. We will extract litter invertebrates from each of these plots and then recolonize them with normal densities of combinations of fragmenters and microbial grazers (see **Table 2.4.2** for details). Mites and collembolans are grazers, and millipedes and isopods are fragmenters. These are the four most numerically dominant groups of detritivores in tabonuco forest litter (Pfeiffer 1996). All enclosures will be covered with window screening to prevent passage of invertebrate detritivores. Five replicates of each treatment will be constructed, and 12 litterbags will be placed in each enclosure. The bottom layer of these bags will be made from fiberglass window screening (1 mm mesh), and the top layer of these bags will be 0.5 cm plastic mesh. This will allow the entry of larger detritivores. These bags will contain either 5 g of air-dried, fresh leaves of Cecropia schreberiana or Dacryodes excelsa (tabonuco), common fast- and slow-growing species, respectively, that have been used previously (Crowl et al. 2000).

One bag per month will be removed at random from each enclosure. We will extract invertebrates from the bags and then oven-dry the litter and weigh, grind, and determine its ash-free dry weight. Subsamples will be analyzed for nutrient content and secondary chemistry. The results will allow us to determine the degree to which proposed functional groups affect rates of decomposition individually and in combination. Because of the large number of potentially important decomposer groups and their interactions, logistic considerations do not allow us to consider more than a single disturbance and two litter types in this initial experiment.

To determine the relative roles of the different functional groups of stream detritivores (shrimp, insects, crabs), we will use multiple exclusion methods at multiple spatial scales. This study builds on our collective experiments in which we have used a combination of whole-pool manipulations (Crowl & Covich 1994, Crowl et al. 2001), electrical exclusion patches (March et al. 2001, in press, Pringle 1996, Pringle et al. 1999, Ramírez 2001), and litter bags (Ramírez 2001) to exclude insects, shrimps, and crabs in a nested design (**Table 2.4.3**). To exclude all invertebrate taxa, we will use fine mesh litter bags that prevent insect colonization. The insects-only treatment will consist of coarse mesh litter bags placed within an electrified fence.

Table 2.4.2. Summary of the Decomposer Functional Group Experiment. The design for the experiment parallels the aquatic study of Crowl et al. (2001) by excluding grazers, fragmenters and both in a 2 x 2 factorial design.

Treatment	Mites	Collem.	Millipedes	Isopods
Control	+	+	+	+
Grazer exclusion	-	-	+	+
Fragmenter exclusion	+	+	-	-
Total exclusion	-	-	-	-

Variable	Time Schedule	Sampling Unit
Invertebrate density	Monthly	Litter bags
Decomposition rate	Monthly	Litter bags
Soil C, N, P	2x per year	Soil cores

Decapods will be excluded by a combination of electricity and manual removal from fenced pools. We will employ a split-plot design to minimize the total number of pools necessary. Bags will contain 5 grams of fresh C. schreberiana or D. excelsa litter (Crowl et al. 2001). Leaves will be prepared by the methods described in Heneghan et al. (1998a) and removed from each replicate on weeks 2, 4, 8, 16, and 32 or until litter has been completely decomposed within any treatment plot. Upon removal, invertebrates will be extracted from the litter, oven-dried, weighed, and ground, and ash-free dry weight will be determined. Subsamples also will be analyzed for nutrient content.

2.4.4 Synthesis and integration: We are working with two models to interpret the results of the experiments described above, CENTURY and TIM. These models take complementary approaches to understanding ecosystem function. CENTURY is a linked production-decomposition model operating at relatively large scales that aggregates much biotic detail. TIM is a food chain model operating at relatively small scales that explicitly considers effects of functional groups thought important to ecosystem function. The first tropical version of

CENTURY was developed for tabonuco forest (Sanford et al. 1991) because it was the only tropical site where detailed data on C and nutrient stocks in above- and belowground biomass had been gathered (Odum & Pigeon 1970). This model greatly aided previous experimental studies of detrital effects on ecosystem productivity in the LEF (Zimmerman et al. 1995b) and has been extended to the entire LEF landscape using GIS and other models we developed (Wang 2001, Wang et al. in press). LUQ researchers are currently working with the developers of CENTURY to improve the P submodel (Silver et al. 2000) and to incorporate variable soil moisture. The refinements of P-cycling in the model are important to this proposal because Sanford et al. (1991) emphasized mineralization of elevated organic P to explain increased NPP after repeated hurricane disturbance. Comparisons of predictions of measured variables in the Canopy Trimming Experiment using the revised version of CENTURY should greatly enhance our understanding of the treatment effects and the utility of the model for understanding disturbance effects on production and decomposition in wet tropical forests.

Table 2.4.3. Summary of the Aquatic Decomposition Experiment. The design builds on previously reported experiments (Crowl et al. 2001, March et al. 2001) and will use a nested design with insect exclusions (fine/coarse litter bags) and macro-fauna exclusions (electric exclosures) nested within whole pool manipulations. At the whole-pool level, shredders and filter feeders will be excluded in 2 x 2 factorial design.

Treatment	Insects	Shrimp	Crabs	Shrimp & Crabs
Control	+	+	+	+
Whole pools (decapod treatments)	+	+/-	+/-	+/-
Electricity (excludes decapods only)	+	+/-	+/-	+/-
Fine/Coarse bags (insect exclusions)	-	-	-	-

Variable	Time Schedule	Sampling Unit
Algae	Weekly	Pools and electric exclosure
BOM	Weekly	Pools and electric exclosure
POC export	Weekly	Pools
Decomposition rates	Weekly	Pools, exclosures, litter bags

We are developing the mathematical model, TIM, to examine how trophic interactions influence ecosystem functioning. Because there are limited data from the LEF to parameterize models, we initially constructed a simple model in which all transfers (consumption) of matter and energy in the autotrophic and detrital food webs are assumed to follow, at the outset, Lotka-Volterra kinetics, and all other mortality is assumed to be density independent. The terrestrial and aquatic ecosystems are linked because the majority of matter and energetic inputs into streams are terrestrial in origin (allocthonous), and large amounts of matter and energy are lost by downstream transport. We categorized the various parts of the autotrophic food web's primary producers by their resistance to decomposition (leaves and fine roots < small wood such as twigs and medium roots < large wood such as branches, trunks and large roots). From past experience and knowledge of leaf secondary compounds and wood chemistry and density, we categorized different primary producer species as producing parts that are generally more or less resistant to decomposition (slow versus fast decomposing species). Primary consumers, detritivores, microbial decomposers and their respective predators are initially treated as discrete functional groups. Hurricane disturbance is treated as an instantaneous short term increase in the density-independent death rate (death rate increases with hurricane intensity) that impacts fast- and slow-decomposing primary producers equally, and thereby increases detrital inputs (leaves, fine roots, small wood, large wood). The model has been initialized using observations from our previous studies and other information for tabonuco forest. Given the variety of detrital sources that vary in ease of decomposition, and the watershed perspective of TIM, even the simple model becomes very complex. Therefore, as a starting point, TIM has been constructed using STELLA to aid us in accounting for the variety of possible linkages that need to be parameterized. As we identify which linkages are more important and develop a better understanding of their specific dynamics from the proposed experiments, more sophisticated models will be developed.

The Canopy Trimming Experiment and its biotic manipulations will provide information on interactions between detrital inputs, microclimate, and major components of the detrital and autotrophic food webs. As a refinement to this type of model, we will investigate whether consideration of functional groups of detritivores (depending on the results of the Decomposer Functional Group Experiment) significantly improves the interpretation of the model results. TIM allows us to examine ecosystem functioning at greater detail (e.g., finer spatial and temporal scale) than does CENTURY. It also specifically allows us to begin to address how biotic diversity, which is so striking in tropical rainforest ecosystems, may influence ecosystem functioning. This influence is often glossed over in other ecosystem models.

2.5 Experiments and Measurements Along Gradients of Climate and Species Richness

2.5.1 Background and approach: Our previous work has focused on tabonuco forest, in the lowest forested elevations of the Luquillo Mountains. As one ascends in elevation, the climate becomes cloudier, colder, and wetter (**Fig. 2.5.1**), and distinct changes occur in the structure and composition of the vegetation (Beard 1949, Wadsworth 1951, Brown et al. 1983). These changes, typical of tropical montane systems (Grubb 1977, Tanner 1981, Bruijnzeel & Veneklas 1998, Tanner et al. 1998), include decreasing tree heights (Weaver 1992, 2000), lower species richness (Weaver 1994), increasing sclerophylly (Weaver et al. 1973), and lower productivity in the uppermost elevations (Weaver et al. 1986, Walker et al. 1996c). Soil organic matter content (SOM) and C:N ratios of the litter (Weaver et al. 1973, Zou et al. 1995) and SOM (Silver et al. 1999) also increase with elevation and are expected to influence stream chemistry (Aitkenhead & McDowell 2000). Changes in plant communities, growth, and soil conditions are undoubtedly important in determining how high elevation ecosystems respond to disturbance.

However, we lack the detailed understanding of high-elevation forests in the LEF that we have for tabonuco forest. Many of the edaphic and climatic factors that determine ecosystem response to disturbance are intercorrelated along elevational gradients, making it difficult to decipher ultimate causation (Waide et al. 1998). Silver (1998) concluded that experiments where climate and other ecosystem characteristics can be systematically varied are needed to understand landscape variation in production and decomposition in tropical montane forest ecosystems. Our long-term goal is to address how disturbance interacts with detrital dynamics to determine key ecosystem characteristics throughout the LEF. Achieving this goal first requires a critical assessment of patterns of productivity and decomposition and the factors controlling these patterns in tropical montane habitats. To accomplish this we will determine: (1) how climate structures plant communities; (2) how plant community composition determines litter quality; and (3) how litter quality interacts with climate to determine the composition of decomposer communities and decomposition rates.

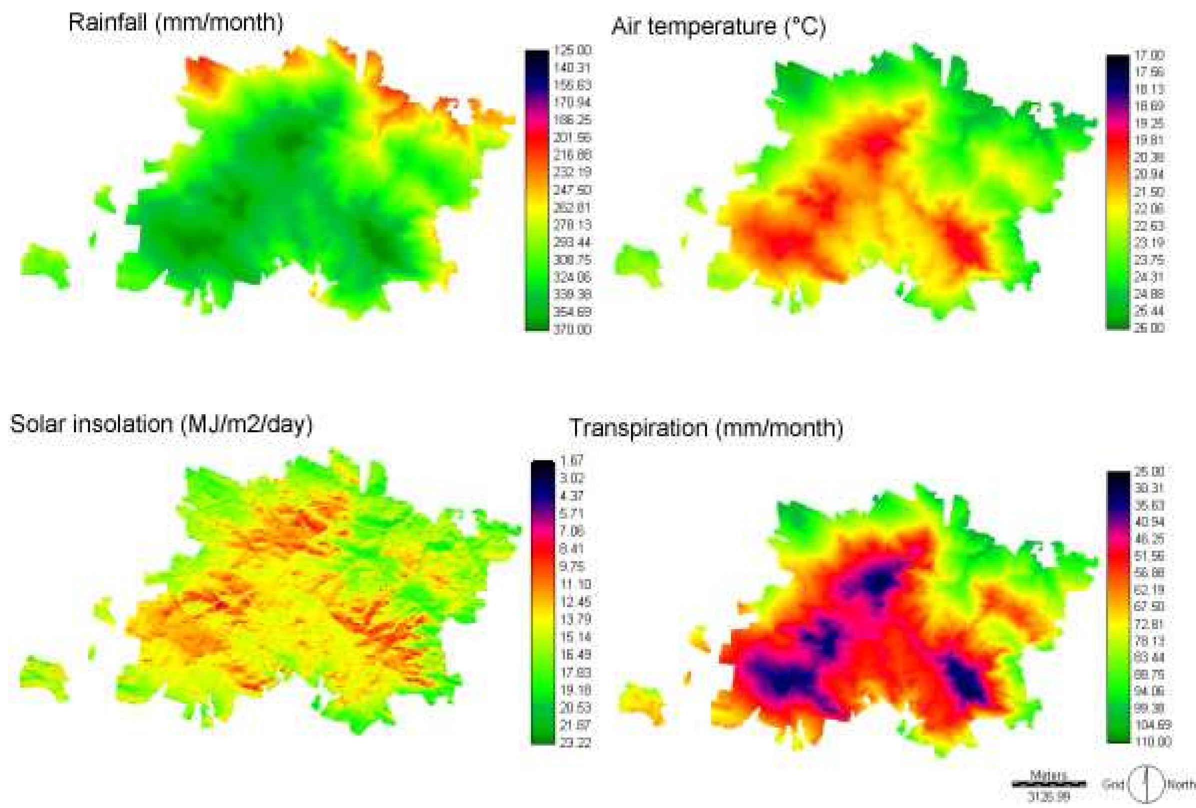


Fig. 2.5.1. Climate variation in the Luquillo Experimental Forest as depicted in the L-CENTURY model (from Wang 2001). Note that less intense colors represent higher values.

In this section, we describe ongoing and proposed efforts to examine the interactions of climate and biotic communities in determining detrital dynamics in the LEF as a backdrop to understanding the effects of disturbance. To expand observations throughout the LEF, we are establishing a network of Extensive and Intensive Plots. Extensive Plots are used to determine variation in the plant community and in soil C and nutrient pools. Information on plant community variation will be used to locate Intensive Plots for detailed, long-term measurements (climate, rate processes), determination of detritivore community variation, and experiments designed to test how climate and litter quality affect detrital dynamics. Spatially explicit versions of community dynamics (Doyle 1981, Acevedo et al. 1995, 1996, Urban et al. 1999) and production/decomposition (Wang 2001, Wang et al., in press) models will be used to integrate these observations. In the future, we will study the effects of disturbance on these plots to test our hypotheses developed for the tabonuco forest on other forest types in the LEF.

2.5.2 Variation in biotic communities and soils with elevation: The distribution of existing Forest Service and LTER plots does not allow a straightforward assessment of community variation in the LEF. With current LTER funding, we are establishing a series of plots that span the elevational gradient in the LEF in three focal watersheds: the Sonadora, the Mameyes, and the Icacos/Río Blanco. We will address the following three hypotheses:

Hypothesis 7: *As plant diversity declines with elevation, important functional groups will be lost from communities at higher elevations.* (**Brokaw, Hall, Silver, Thomlinson, Zimmerman**)

Hypothesis 8: *Community structure of the vegetation will conform to the hierarchical continuum model and not the community unit or community continuum models.* (**Brokaw, Hall, Silver, Thomlinson, Waide, Willig, Zimmerman**)

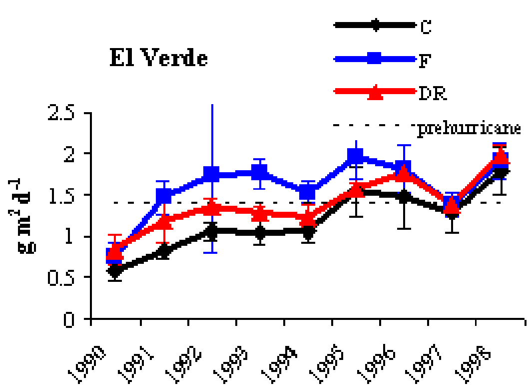
Hypothesis 9*: Diversity of the detrital community will decline with elevation and biotic communities will be less functionally redundant at higher elevations or will lack important functional groups.* (**González, Lodge, Pringle**)

Rationale - It is well known that high elevation tropical forests have lower species diversity than low elevation forests. High rainfall and winds in the upper elevations of the LEF impose constant stress on the vegetation in the form of branch damage and defoliation (Cordero 1998), low light, low soil oxygen, and high nutrient leaching (Silver et al. 1999), and increased toxicity resulting from Fe and Mn mobility (Grubb 1977). These conditions may limit functional plant types to slow-growing species able to persist under harsh conditions (Chapin 1980, Bloom et al. 1985). Weaver (1991) suggested, based on patterns of succession, that elfin forests lack secondary species. Walker et al. (1996c) indicated that differences in the rate of recovery of litterfall in tabonuco and elfin forests following hurricane disturbance (**Fig 2.5.2**) was attributed to divergence of life history strategies of species composing the two different communities, with elfin forest dominated by slow-growing species that have little capacity to respond to disturbance or large changes in resource availability. Evaluation of these suggestions requires better information on the distribution of species with elevation.
Previous studies of specific forest types of the LEF (Beard 1942, Wadsworth 1951, (Crow & Grigal 1979, Weaver 1991; **Fig. 2.3.1**) suggest that plant communities are structured following the "community unit" model, with distinct zonation of the vegetation with elevation. Studies in other tropical forests suggest that forest composition varies continually with elevation without the appearance of distinct zones (Lieberman et al. 1996, Lovett 1998). These studies have not directly tested the hypothesis that distributions of less common species are nested within those of more common species (the "hierarchical continuum"; Hoagland & Collins 1997). If communities are structured, they are likely to exhibit some version of a hierarchical continuum

rather than the extremes represented by the community unit and community continuum models. To the degree that communities are structured and species turnover leads to changes in growth rate and litter quality, community structuring will be important to understanding landscape patterns of disturbance response and detrital dynamics.

Detritivore communities are not well documented along elevation gradients in the tropics (but see Richardson et al. 2000), but similar to plants, they are likely to vary in response to increasingly stressful conditions with elevation. We predict that low C:N ratios, low soil O2 availability, cooler temperatures, and potential increases in secondary compounds in plants and soils could limit detritivore communities.

Workplan: plant communities and soils - Forest plots (0.1 ha) are being placed at 50 m intervals from the lower boundary of the LEF at 250 m to 1000 m in three focal watersheds. Initially, results from the surveys will test competing models of community structure: community-unit, continuum, or hierarchical continuum (Hoagland & Collins 1997). In addition, results will be compared to a model of forest dynamics (FACET/MOSAIC; Doyle 1981, Acevedo et al. 1995, 1996, Urban et al. 1999) being developed under current funding that will, among other things, assess variations in life histories of common



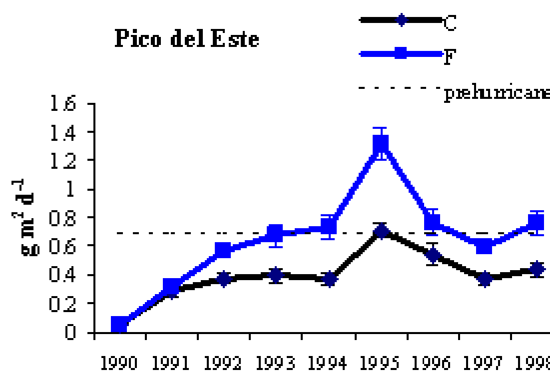
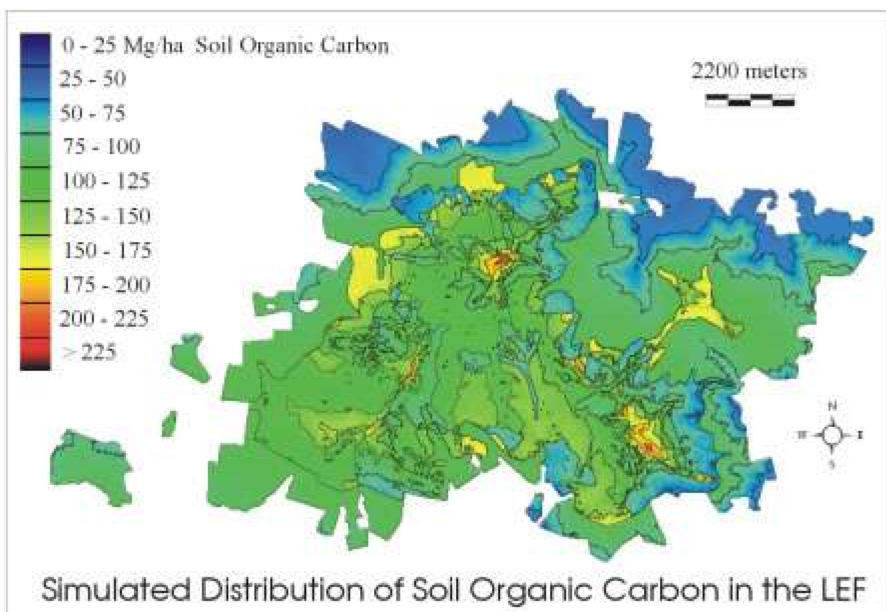


Fig. 2.5.2. Comparison of leaf litter production in (a) mid-elevation (400 m; El Verde) and (b) high elevation (1000 m; Pico del Este) forest plots (Walker et al. 1996, Warren et al. unpublished). The studies began within one year of Hurricane Hugo and show the effect of quarterly fertilization (F: NPK + micronutrients) compared to unmanipulated plots (C). At El Verde, a one-time removal of hurricane generated debris (DR) was also studied (Zimmerman et al. 1995). At El Verde, litter production returned to pre-hurricane levels within seven years of the storm while at Pico del Este this has yet to occur (except during one unusual year). Plots at El Verde also responded more quickly to the addition of supplemental nutrients.

tree species throughout the LEF. Soil samples will be taken from these same plots and used to test predictions about SOM and other soil characteristics from L-CENTURY (landscape version of CENTURY; Wang et al., in press; Fig 2.5.3). In the future, forest composition will be surveyed at 5-year intervals and after hurricane disturbances in order to determine changes in community composition resulting from disturbance and long-term climate change.

Workplan: detrital communities - The Intensive Plots will be selected in four study areas from 400 m to 1000 m elevation, located to sample the relevant variation in plant communities as identified in the Extensive Plot study as well as with respect to logistic considerations. Lowest and highest elevation plots will include existing plots in tabonuco and elfin forest; the significant increase in research effort will occur at intermediate elevations. Plots will be replicated four times within each study area.

We will use the Intensive Plots to characterize the composition of invertebrate, fungal, and bacterial groups in litter and soil. For invertebrates, we will characterize the micro-, meso-, and macrofauna using a combination of extraction techniques and pitfall traps. A parallel effort will be made to describe the changes in invertebrate communities in streams in high elevation streams. For fungi in terrestrial litter, we will examine functional groups, and focus primarily on the occurrence, diversity, and abundance of white- and brown-rot fungi. White-rot fungi have special significance for decomposition processes because of their relative ability to degrade recalcitrant compounds such as lignin. We will capitalize on existing studies funded through the A.W. Mellon Foundation to characterize bacterial functional groups, including some groups that can influence C processing in soils (Silver et al. 2001). We currently have funding to examine the distribution and activity of methane oxidizers, nitrifiers, denitrifiers, Fe reducers, and organisms capable of dissimilatory reduction of NO3 to NH4. Furthermore, we hope to develop an assay to examine characteristics of methanogens, organisms that participate in several key



biogeochemical processes that are likely to vary with elevation.

Fig. 2.5.3. Estimated distribution of soil organic carbon in the Luquillo Experimental Forest. The estimates were generated using

a spatially explicit model of the forest version of CENTURY (Sanford et al. 1991, Wang et al., in press) that incorporated the abiotic data on the various forest types represented in the LEF. The estimates show that soil carbon is expected to increase with elevation, exhibiting a maximum in elfin forest at the summits of the mountains.

The data collected on detritivore communities will add an important component to the biotic inventory and will be used to plan future experiments on the interactions of detritivore communities, climate, and litter quality in decomposition. The sampling and description of detritivore communities depend on the results of the ongoing survey, so the exact nature of the manipulations will await the completion of these studies. These manipulations will parallel those performed in tabonuco forest and will likely be initiated at the beginning of the next funding cycle in 2006.

2.5.3 Litter and detrital dynamics along the elevation gradient of the LEF: The Intensive Plots provide an arena to perform long-term measurements and controlled experiments. During the next four years we will establish the infrastructure for long-term measurements along the elevational gradient and perform an experiment addressing the following hypothesis:

Hypothesis 10: *Litter production will vary as a function of light and temperature, while litter decomposition rates will be best predicted by litter quality along the elevation gradient with climate having a smaller but significant influence. This will result in a decoupling of litter production and decomposition along the elevation gradient* (**Lodge, González, Silver**)

Rationale - Few studies have adequately examined the mechanisms responsible for changes in community composition, productivity, and decomposition rates along elevation gradients in the tropics (Heaney & Proctor 1989, Vitousek et al. 1992, 1994, Schuur 2001). Current studies in the LEF show a strong linear decline in productivity above 700 m, approximately at the cloud line (**Fig. 2.5.4**). L-CENTURY predicts that light is the dominant regulator of NPP along the gradient (Wang 2001). We hypothesize that the observed change in litter production results from decreased light availability at the cloud line coupled with lower temperatures with elevation. We know comparatively little about the corresponding changes in rates and regulation of decomposition with elevation. Global studies of decomposition rates indicate that litter quality is a more important determinant of decomposition at this spatial scale (Meetenmeyer 1978, Aerts 1997, Silver & Miya 2001). Constant warm temperatures relative to temperate zone forests and the lack of moisture limitation along our gradient strengthen this argument. Sensitivity analyses conducted using L-CENTURY (Wang et al., in press) suggest that the most important factor controlling decomposition rate is temperature, but the current version of L-CENTURY does not address the effects of changes in litter quality (Wang 2001). If litter production and decomposition are controlled by different factors, then these rate processes can become decoupled in space and time and lead to non-linear trends in C and nutrient storage. A next step in our studies is to address the interactive effects of climate on litter production, and climate and litter quality on rates of decomposition. We will use the L-CENTURY output as our null model in which only climate influences production and decomposition.

Workplan: long-term measurements - Initially, we will survey the Intensive Plots for plant community composition, structure, and plant chemical properties of common species within each plot. Litter production will be sampled every two weeks from litter baskets (Vogt et al. 1996). These will be established along the catena (geomorphic profile from ridge to ridge) in each plot so that terrestrial studies can be integrated with aquatic studies in the future. Replicate samples of forest floor standing stocks will be collected monthly in a buffer zone outside the plots to minimize side effects. Data from permanent weather stations located at each site will provide background information that will guide us in understanding interactions between climate

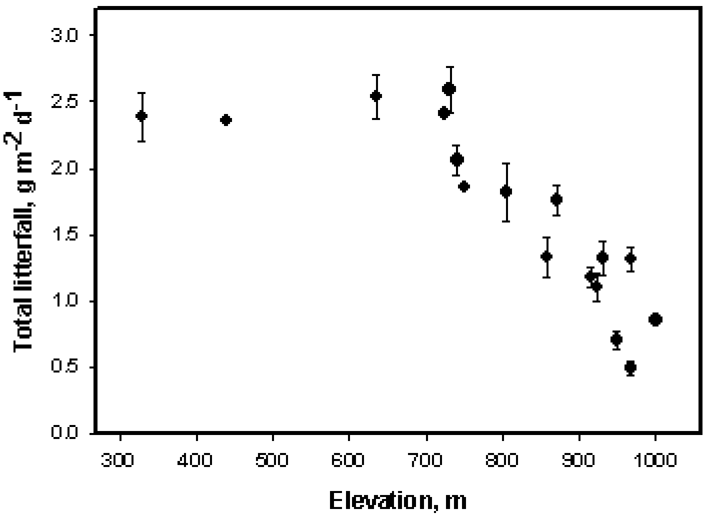


Fig. 2.5.4. Aboveground litter production as a function of elevation in the LEF. Data are from Weaver and Murphy (1986), Scatena et al. (1996), and Silver et al. (in prep.).

and biotic components of the LEF ecosystem. In addition, these data will allow us to more precisely parameterize new versions of L-CENTURY at each elevation in the LEF. Finally, these data will be used to provide the context for a series of future experiments designed to examine the role of climate, litter quantity and quality, and plant and detritivore communities in SOM processing and storage.

Workplan: reciprocal litter transplant experiment - We will address the effects of climate and litter quality on terrestrial decomposition rates by factorial experiments with litter types from each of the 16 intensive plots. Leaf litter from each plot will be decayed in situ, and litterbags will be transplanted to each of the other sites along the gradient. The transplant experiment will provide us with information about the potential sensitivity of litter decay to climate and edaphic conditions. We will include a common substrate (birch craft sticks, previously tested) as a control on litter quality effects.

To describe the potential effects of disturbance on litter decay along the gradient, and as a way of potentially altering litter chemistry within sites and species, we will include a treatment that looks at the potential priming effects of fresh leaves on decomposition rates in each forest type. We will construct litterbags that: 1) include only green leaves (picked from a random selection of trees in the plot); 2) include only naturally senesced litter; and 3) include 40% green leaves and

60% naturally senesced litter. This approximates the ratio of green leaves to brown litter recorded immediately after Hurricane Georges (Ostertag et al., submitted).
Subsamples of green leaves and senesced litter from each plot will be analyzed separately for nutrient and C content, exchangeable Al, and the concentration of secondary compounds. Decomposition rates will be determined as k yr-1 using the best fit among exponential, double exponential or linear models (Wieder & Lang 1982). Soil organic matter fractions, soil nutrient availability, and microbial biomass also will be measured four times per year. The response of decay rates to climate, litter quality, and soil characteristics will be tested using analysis of variance. Values for these variables also will be compared to estimates from L-CENTURY.
We will determine the degree of coupling of production and decomposition along the gradient by comparing the flux of litter and nutrients to the forest floor, the changes in standing stocks of forest floor over time, and the flux of carbon and nutrients via decomposition. These data will be compared to data on soil C and nutrient pools to arrive at a preliminary C and nutrient budget for the forest floor and surface soil layers.

2.5.4 Linking litter, soils and watersheds: The interaction of climate and plant characteristics also can affect watershed exports through effects on soil carbon and nutrient dynamics. Recently, Aitkenhead and McDowell (2000) showed that the C:N ratio of a watershed's soils is a good predictor of differences in DOC flux among biomes. Soil C:N ratio is a product of long-term interactions between climate, the chemistry and quantity of plant litter inputs, and decomposition processes. Here, we will focus on examining relationships between soil properties and watershed export at the landscape scale:

Hypothesis 11: *Export of inorganic nutrients and dissolved organic matter (DOC and DON) will vary across the Luquillo Mountain landscape as a function of soil C:N. High soil C:N will be associated with high DOC and DON losses and low inorganic N losses.* (**McDowell, Scatena**)

Rationale - The carbon quality of litter is generally derived from plant traits and/or the interaction of plant traits and environmental conditions. Because litter quality, climate, and decomposer communities interact to determine SOM quality, they can each affect C export in streams. Variation in DOC flux among biomes is related to soil quality (C:N ratio; Aitkenhead & McDowell 2000). Thus we suspect that at the landscape scale, variation in soil C:N might similarly drive variability in DOC export in the LEF. Nitrogen immobilization by decomposing litter also varies as a function of litter quality, with high C:N litters tending to retain more N over the course of decomposition (e.g., Aber & Melillo 2001, Zou et al. 1995, Sullivan et al. 1999). Consequently, watersheds dominated by vegetation with low-quality litter should have lower rates of inorganic N loss. Recent work in the Catskill Mountains of New York supports this hypothesis; nitrogen export differs with vegetation type, with low-litter quality forests (predominantly oak) showing lower N export (Lovett et al. 2000).

Workplan - We will augment an existing network of gauged watersheds to characterize the relationship between soil characteristics and stream nutrient and organic matter losses. Linking stream chemistry to characteristics of watershed soils and vegetation (litter quality, soil C:N, soil C and N standing stocks) can be done within the timeframe of the current funding request. The network of gauged watersheds will become a long-term commitment of the LTER. With this expanded network we can address variation in the response of watersheds to disturbance along the elevation gradient. Previous work on disturbance response focused on lower elevation watersheds in the tabonuco forest type, as well as a few larger watersheds that span the range in elevation (Schaefer et al. 2000). Funds to characterize soil C:N and analysis of DOC and DON export from multiple watersheds during a single year are available from a recent NSF award to McDowell. The LTER contribution will be to establish three new, gauged, long-term sites, continue sampling of existing sites, and provide data on litter quality and soil characteristics from the Extensive Elevation Plots along the elevation gradient. Two gauged watersheds in elfin forest at 900 to 950 m elevation will be added to the set of LTER study watersheds. The third, the Quebrada Guaba, drains a watershed ranging from 750 to 900 m elevation and is currently gauged by the USGS WEBB project. Samples will be collected weekly, as at other LTER streams. With the addition of these watersheds, we will have data from small gauged watersheds spanning a range of 200 to 900 m in elevation, including representative watersheds from the three major forest types: elfin forest (two new unnamed watersheds); colorado forest (Río Icacos and Quebrada Guaba); and tabonuco forest (Quebrada Prieta and Bisley 1, 2 and 3). We also will have two gauged basins (Mameyes and Sonadora) that span the whole elevation range of the mountain and include all three vegetation types.

2.6 Comparison of results from LUQ with other LTER and non-LTER sites

Results from our studies of disturbance and detrital dynamics may identify key differences between the LEF and other LTER sites. The rapid processing of post-disturbance pulses of detritus distinguishes the LEF from temperate sites and may help explain other differences between temperate and tropical sites. Continued participation in the LIDET experiment and several post-All Scientists Meeting comparisons will address this possibility. In addition, we are involved in new efforts to extend studies of decomposition processes (e.g., DIRT) to the LEF. Because of the LEF's unique physical and biological parameters, LUQ plays a key role in these cross-site comparisons. Selected cross-site activities that currently involve LUQ researchers are shown in **Table 2.6.1**.

The Luquillo LTER site represents the tropical terminus of the LTER Network, and, as such, provides extreme conditions of climate and biodiversity for cross-site comparisons. LUQ has encouraged such comparisons in a number of ways. Many LUQ scientists also are involved in research at other U.S. LTER sites (McDowell, Zou, AND; Silver, BNZ; Pringle, Zou, CWT; McDowell, HFR; McDowell, HBR; González, NWT; McDowell, PIE; Waide, SEV) and with international sites and networks

Table 2.6.1. Selected ongoing cross-site projects (from a list of over 30 ongoing and recent projects) conducted at LUQ, including collaborating sites and colleagues (italics indicate current LUQ researchers).

1. LIDET (Long-Term Intersite Decomposition Experiment Team); 28 LTER/ International Sites (Silver, Lodge, Harmon).
2. DIRT (Detrital Input and Removal Treatment - Proposed); 6 LTER and other sites (Zou, Lodge, McDowell, Lajtha, Nadelhoffer).

3. LINX (Lotic Intersite Nitrogen Experiment); 10 LTER and other sites (McDowell, Mulholland).
4. DONIC (Dissolved Organic Nitrogen Intersite Comparison); LUQ, NWT, SBC, others (McDowell).
5. Chronic nitrogen addition to forest soils; LUQ, HFR (McDowell, Aber).
6. WW-DECOEX (World Wide Aquatic Leaf Decomposition Experiment); LUQ + 10 tropical sites (Crowl, Covich, Wantzen).
7. Dissimilatory nitrate reduction in humid ecosystems; LUQ, BNZ, La Selva; (Silver, Firestone, Chapin).
8. Carbon, nitrogen, and phosphorus dynamics in tropical forest ecosystems; LUQ, Tapajós, Brazil (Silver, Keller).
9. Comparative study of terrestrial and aquatic decomposition rates; LUQ, CWT (Zou, Pringle, Coleman, Hunter).
10. Earthworms and soil processes in tropical ecosystems; LUQ, Xishuangbanna, China (Zou).
11. Comparisons of hydrology, nutrient cycling, and canopy dynamics following severe storm damage; LUQ, HBR, Taiwan (Zou, Scatena, Hamburg, King).
12. Relationship between nutrient inputs and faunal diversity; LUQ, 2 international sites (Richardson, Srivastava).
13. Comparison of bromeliad phytotelmata in tabonuco and elfin forests; LUQ, Dominica (Richardson).
14. Canopy herbivory and soil processes in a temperate and tropical forest; LUQ, CWT (Schowalter, Lowman, Hunter).
15. Cross-site comparison of aquatic insect emergence; LUQ, La Selva (Ramírez, Pringle).
16. Network analysis of food webs; LUQ and six LTER sites (Waide, Covich, Christian).
17. Global forest dynamics network - CTFS (Center for Tropical Forest Science); LUQ + 17 tropical sites (Brokaw, Thompson, Zimmerman, Losos, Condit).
18. SORTIE forest dynamics model; LUQ, HFR (Brokaw, Thompson, Canham).
19. Primary succession; LUQ and four international sites (Walker).
20. Landscape fragmentation and forest fuel accumulation: Effects of fragment size, age, and climate; LUQ, BNZ, Idaho (Gould, González, Hudak, Scatena).

(Covich, Zou in Taiwan; Pringle, Silver, Zou in Costa Rica; Thompson, Brokaw in Panama; Silver, Willig in Brazil). These participations assure cross-fostering of ideas among scientists and sites. In particular, we have developed close working relationships with sites that share common research goals (hurricane effects, HFR; litter and soil invertebrates, CWT, KNZ, NWT; canopy arthropods, AND). LUQ has participated or participates in several activities involving multiple sites (LINX, DIRT, network analysis, DONIC) and the network as a whole (e.g., LIDET). In addition, LUQ participates in the Center for Tropical Forest Science, a network of 18 large forest dynamics plots in the tropics.
In LTER 3, we propose to strengthen the regional focus of our work by increasing interactions with colleagues in countries fringing the Caribbean Basin. We propose to engage scientists in Panama, Costa Rica, and Mexico in collaborative efforts by proposing a Research Collaboration Network to address issues of common interest to tropical ecologists. In addition, discussions regarding the submission of joint proposals to NSF's Biocomplexity competition have been initiated, and we have met with representatives of the Barro Colorado and La Selva sites to discuss a possible collaboration in the proposed National Ecological Observatory Network.

2.7 Synthesis
The proposed research makes three unique and major contributions to understanding the interactions between disturbance and detrital dynamics in tropical forests. Our long-term

approach provides the capacity to examine and compare independent disturbance events and to analyze the cumulative effects of repeated disturbance. Few other tropical research sites combine comprehensive studies of dynamic ecosystems with the research infrastructure and long-term support available to LUQ. Our common conceptual framework integrates mechanistic studies across terrestrial and aquatic habitats, and provides the means to link population, community, ecosystem, and landscape investigations, resulting in a deeper understanding of disturbance and detrital dynamics (**Fig 2.7.1**). From its inception, LUQ has had the intellectual integration of scientists with different ecological approaches as a fundamental goal. Finally, our close collaboration with scientists at other LTER and non-LTER sites provides a powerful framework for identifying the general principles that underlie ecosystem dynamics.

Our work addresses critical issues about global climate change, tropical forest carbon dynamics, and changes in biodiversity by: 1) chronicling the effects of repeated hurricane disturbance and climatic gradients on the long-term dynamics of a tropical forest ecosystem, 2) providing long-term assessments of carbon storage in tropical biomass and soils, and 3) examining the degree to which species and functional groups contribute to detrital dynamics and the ability of an ecosystem to recover following disturbance. By extending our understanding of the LEF to other disturbance-driven systems, LUQ is poised to make a significant contribution to our knowledge of the mechanisms by which disturbance structures ecosystems.

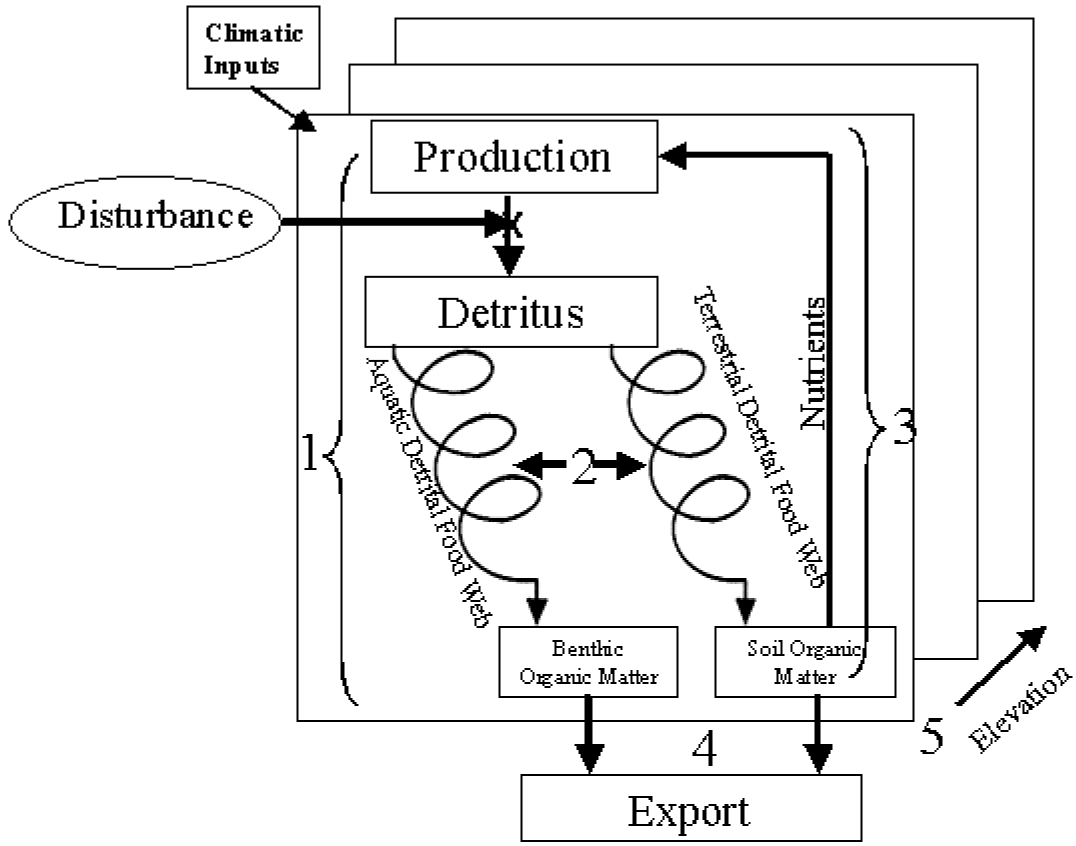


Fig. 2.7.1. Schematic representation of the scientific questions addressed by LUQ during LTER 3:

1) *How do climatic factors, litter quality, and detritivore diversity regulate decomposition of detrital pulses?*
2) *How do terrestrial and aquatic food webs differ in their response to detrital pulses?*
3) *What is the effect of disturbance frequency on nutrient cycling, plant community composition, and the accumulation of soil organic matter?*
4) *To what degree is the export of carbon and nutrients from watersheds a result of soil characteristics that are affected by detrital dynamics?*
5) *How do elevationally related changes in climate impact plant and detritivore communities, and how do these feed back on the quantity and quality of litter inputs and decomposition?*

Section 3 Site Management

Site management of LUQ will continue in a manner similar to LTER 1 and 2. Jess Zimmerman (with LUQ since 1991 and co-PI since 1994) continues as Lead-PI and guides the program on a day-to-day basis. Nick Brokaw, with the program since its inception, has recently taken a position with UPR and will also serve as Co-PI, assisting Zimmerman with day-to-day management of the project. Robert Waide, who was Lead-PI for the program in LTER 1 and 2, has left UPR but will continue as Senior Personnel. Also, Fred Scatena has stepped down as Co-PI and has been replaced by D. Jean Lodge. Lodge has been with the LUQ-LTER since its inception. Ariel Lugo remains as Co-PI.

During LTER 3, Zimmerman, Lugo, Lodge and Brokaw will guide the program as an Executive Committee (EC) with the participation of three other rotating members chosen from among the Senior Personnel at mainland institutions. The decision to include off-island collaborators on the Luquillo EC was made so that they would have more influence on decision making in the program. Currently, the off-island members of the EC include Robert Waide, Whendee Silver, and William McDowell. Each rotating member will have a term of two years and will be chosen by the extant EC. Rotating members will meet with the rest of the EC at bi-annual investigator meetings (see below) and at two other times during the year.

The Lead PI and two members of the EC (Nick Brokaw and Jean Lodge) also serve on the Data Management Committee with the Data Manager.

The Executive Committee is aided by a National Advisory Committee (NAC). Currently, this committee is composed of Julie Denslow (USDA Forest Service), David Coleman (CWT), Ernesto Medina (Venezuelan Institute for Scientific Investigation), John Porter (VCR), and Deborah Clark (La Selva Biological Station). The NAC attends annual meetings in January and reviews program goals and accomplishments for the EC in a report that is distributed to all Senior Personnel.

Investigators in the LUQ-LTER will meet twice during the year to review research progress, consider new research opportunities, and to discuss management issues related to the site. January meetings will include a public symposium on long-term ecological research where LUQ and other interested researchers and students present the results of their work. A second day is devoted to research planning, while the third is reserved for a meeting between the Advisory Committee and PIs/Senior Investigators. A second meeting will be held each summer and will be devoted entirely to research planning. Only signatory PIs and Senior Personnel attend summer meetings. Meetings of subgroups of investigators are held whenever the need arises.

Continued participation by Senior Personnel in LUQ is based on contributions to the program and is evaluated by the Lead-PI in consultation with the EC. Investigators are evaluated on number and impact of publications, disciplinary expertise and experience at the site or in the tropics, participation in program planning, cooperation with data and information management goals, graduate student participation, cross-site activities, and ability to attract complementary funding. LUQ actively seeks to expand the diversity of the program when adding new investigators. At the end of LUQ 2, there were 31 Principal Investigators and Senior Personnel associated with LUQ. As a result of an analysis of research productivity conducted by the Executive Committee and of attrition, this number was reduced to 25 at the beginning of LUQ 3. The current proposal lists 20 PIs and Senior Personnel plus three individuals who have key scientific roles in the program. Thus, researchers associated with the project have been reduced by over one-quarter in the past three years.

Associate researchers (**Table 3.1**) provide critical added expertise and data to LUQ. Beginning in LTER 3, unfunded Associates are provided seed funds (materials or travel) to continue their participation. Funds will be awarded on an annual basis by the EC based on the needs of the program.

Research is coordinated through the El Verde Field Station (UPR) and Sabana Field Station (USDA-FS) near the Bisley Experimental Watersheds. Alonso Ramirez is currently the Director of El Verde and coordinates administration of this facility. Fred Scatena continues to manage the Bisley site.

Table 3.1. Scientists associated with the Luquillo LTER program. These scientists contribute to the program with complementary research studies, usually funded through outside grants. These individuals are not funded from the core grant.

L.A. Bruijnzeel, Vrije Universiteite of Amsterdam (hydrology, elfin forest ecology)
Charles Canham, Institute for Ecosystem Studies (forest ecology, modeling)
Stephen B. Cox, National Center for Ecological Analysis and Synthesis (community ecology)
Ned Fetcher, Scranton University (light dynamics, carbon gain)
Robert Edwards, Retired (spider systematics and ecology)
Heather Erickson, Metropolitan University, San Juan (nutrient cycling)
Mary Firestone, University of California-Berkeley (microbial ecology)
Michael Gannon, Pennsylvania State University - Altoona (ecology of bats)
William Gould, International Institute of Tropical Forestry, USDA-FS (landscape ecology)
Bruce Haines, University of Georgia (nutrient cycling in plants)
Arthur H. Johnson, University of Pennsylvania (biogeochemistry)
Matthew C. Larsen, USGS, San Juan (biogeochemistry)
Margaret Lowman, Marie Selby Botanical Gardens (canopy studies)
Howard Odum, University of Florida (ecosystem studies, emergy analysis)
Rebecca Ostertag, Univ. of Hawaii-Hilo (biogeochemistry)
Barbara Richardson, Retired (insect systematics and ecology)
José Rincón, Universidad de Zulia, Maracaibo, Venezuela (litter decomposition)
Joanne Sharpe, No present affiliation (fern ecology)
Tim Schowalter, Oregon State University (plant-insect interactions)
Daniel Vogt, University of Washington (nutrient cycling)
Kristiina Vogt, University of Washington (ecosystem dynamics, decomposition)
Hans F. Vugts, Vrije Universiteite of Amsterdam (meteorology)
Lawrence Woolbright, Siena College (herpetology)
Joe Wunderle, International Institute of Tropical Forestry, USDA-FS (avian ecology)

Section 4 Data and Information Management

4.1 Goals and Objectives

The primary goal of data and information management (IM) by LUQ is to insure the long-term availability and security of all data sets collected at our site. Standards for metadata and quality control assure that both researchers at the site and the larger ecological community will be able to use the data. Our information management system (IMS) has been developed with the following components:

(1) Metadata: the provision of standardized metadata informs both current and future scientists and the general public about how our data were collected.
(2) Quality control: quality control procedures insure the validity and integrity of data and metadata.
(3) Access: Web access to archived data sets allows scientists and the general public to readily locate and retrieve data in a usable form.
(4) Security: establishment and enforcement of security procedures protect against loss or damage of data due to natural disaster, theft, etc.
(5) Development: development and implementation of new methods and technologies enhance the value of the IMS for conducting research.
The IMS is dedicated to helping local researchers in the process of gathering data and placing them in the IMS, training users in the use of the IMS and the network, providing network and systems administration and technical support, participating in the LTER Network Information System (NIS) project, and improving intra-site and inter-site communication.

4.2 Historical Perspective

During LTER I, a centralized, computer-based IMS was developed and implemented. It has since served as the central depository and metadata center, as well as the data entry, management, and sharing facility for all the data sets generated at our site. It also has served as a computer technology resource for the local and remote LUQ scientific community. Since then, the site has had a LAN on which the Intranet is defined, with at least 20 computers and a central file server. By 1992, a Novell file server housed the major project's data sets, two data set catalogs, a word processor program, a spreadsheet program, a Data Base Management System (DBMS), a group calendar utility, and statistical and graphics programs. As networking technology evolved, the Intranet data were decentralized and distributed into MS Networking-based computer systems.
In 1989, prompted by the need to organize and recover pre-LTER data, the development of metadata standards for site data sets became the most important task for IM. By 1991 metadata standards (**http://luq.lternet.edu/datamng/imdocs/metadata-standard.htm**) were developed and made available along with guidelines (**http://luq.lternet.edu/datamng/imdocs/MetadataGuidelines.htm**). Since 1990, two computer database catalogs (inherited and LTER data) have been maintained at the site as the framework for the maintenance and use of the metadata and data.
Since 1995, our Web page has provided an updated list of all released data sets, linked to their metadata, data, and a Data Management Policy (**http://luq.lternet.edu/datamng/imdocs/dmpolicy.htm**). The number of data sets that have been made available on our Web site has increased since then to a total of 74. This site provides information beyond scientific data, including:

(1) Field station usage (**http://luq.lternet.edu/calendar**);
(2) Indexed list of publications (**http://luq.lternet.edu/publications**);
(3) Personnel listing (**http://luq.lternet.edu/people**);
(4) Documents that support the project and serve the IM community in general (Data request: **http://luq.lternet.edu/datamng/98-99req.htm**; Past proposals: **http://luq.lternet.edu/publications/**; Photographic images: **http://luq.lternet.edu/images/luq/Georges-1998/indexfin.htm**; IM development

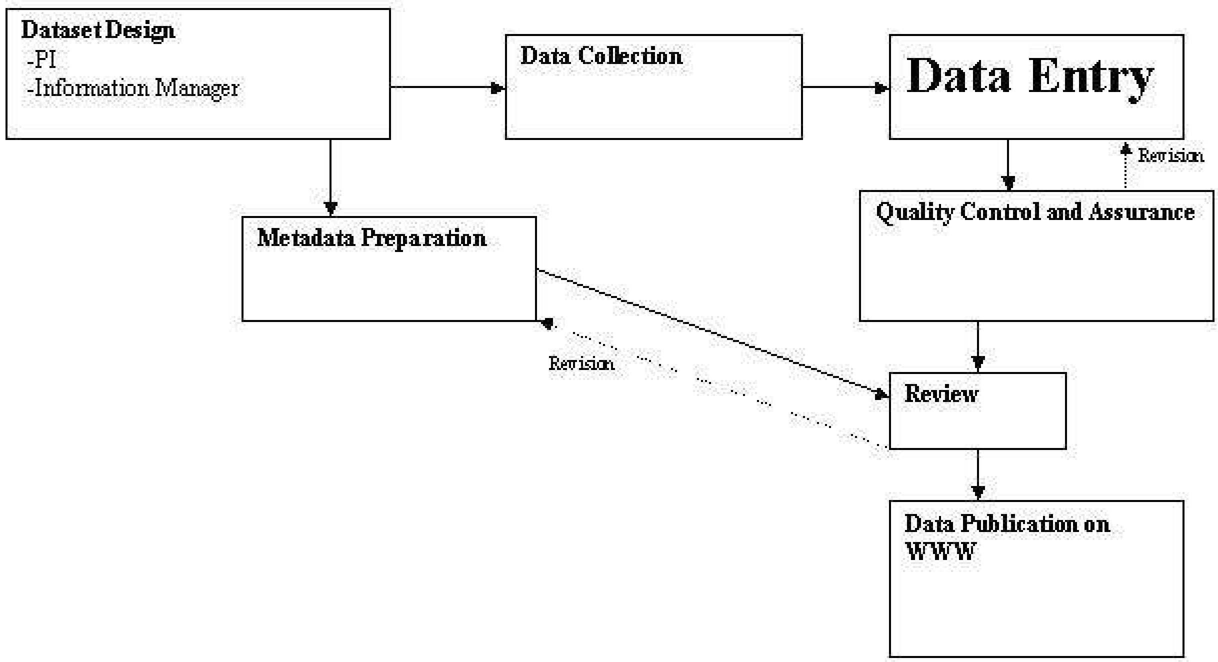
documents: **http://luq.lternet.edu/datamng/reports/DMatLUQdocuments.htm**).

4.3 Current System
The LUQ LTER IMS provides the basic elements of a Common Information Management Framework (**http://luq.lternet.edu/publications/reports/informationmanagement/LTERSurveys/ANDLUQcommonframe-version2.htm)** necessary for accessing and sharing of data among the scientific community.

4.3.1 A common information management framework (CIMF): The basic information elements of a CIMF (publication and personnel databases, metadata catalog, and data with its metadata) are accessible or in the process of being made accessible by the LUQ IMS.
An online form to submit publication references is at: **http://www.ites.upr.edu/cgi-bin/publication_submit/mewebkey.html**. A searchable personnel database is available on the Web (**http://luq.lternet.edu/people**) and is updatable using a password-Web form (**http://luq.lternet.edu/admin**). The data set catalog exists as a searchable Web database (e.g., **http://luq.lternet.edu/cgi-bin/metadata_submit/test/testform1pi.pl**) and will provide a central framework for the access, entry, and update processes of the IM data in the near future. At present, new or updated data and metadata files are filed mostly by electronic mail or handed in on magnetic media or CD personally by the investigators to the information manager. IM is developing mechanisms to allow the investigators to remotely deposit their information to the IMS: Web forms (**http://luq.lternet.edu/datamng/imdocs/division.html**) and scripts to enter and update the metadata and data files into the Web server.
Investigators that have access to the Local Area Network at ITES deposit their data and metadata files using Microsoft (MS) Networking folder sharing capabilities on the IM computer that holds the LUQ and LEF catalogs. A Windows 2000 server obtained recently by IM will serve as the local mirror to our Web site's IMS, and will hold a software interface between desktop applications and the LUQ publication database.

4.3.2 The role of the information manager in research: An investigator is encouraged to meet with the site information manager at the beginning of a project to discuss the best data set design and computer software for entering and manipulating the data. In cases where IM will be responsible for the entry of the data (**http://luq.lternet.edu/datamng/Reports/PROPOSAL2002-ONdm/Table5-1.htm**), investigator and information manager will jointly complete the metadata forms the project will generate.
The information manager regularly attends research symposia and planning meetings held by PIs and Senior Personnel. She is directly supervised by the Lead-PI who, together with an IM Committee (composed of two Executive Committee members, Nick Brokaw and Jean Lodge), assists her in developing the IMS by providing guidance and scientific input.

4.3.3 Filing data in the IMS: Data sets are only included in the catalog when metadata have been completed. The following depicts the process of filing data with the LUQ LTER IM:



4.3.4 Making data available on the LUQ Web site: Data sets normally are made available to other researchers within the two year period suggested by the National Science Foundation. Delays have occurred in the past because researchers were not sufficiently encouraged to provide their data to the IMS. The Executive Committee, working with the Information Manager via the IM Committee, are committed to routinely examining ongoing data sets and recent publications to make sure the data sets are up-to-date. Cooperation with the IMS is one criterion the EC uses to judge the value of the participation of researchers. The data sets managed directly by the IM staff are routinely updated and published on the Web. Few data sets have limited access. Only in the case where a student is still developing their thesis or dissertation will we waive the two-year rule to publish data on the Web.

Published data (Type I) are made available on the Web (**http://luq.lternet.edu/data/)** when corresponding to a LUQ core database. Collective data (Type II) are posted on the Web after the data have been collected, entered, and gone through QA/QC processes at both the project level and the IM level. This takes about one month. Original measurements by individual scientists (Type III) are deposited annually or bi-annually into the system's Intranet, depending on the periodicity of the project's sampling. These data are made available on the Web two years after the collection of the data. The IM Committee decides about the availability of special long-term data collected by individual scientists (Type IV), based on the difficulty or complexity of the data collection and QA/QC processes.

Our Web site is referenced by a range of other Web sites on the Internet. When the Internet is searched for "Luquillo Experimental Forest", eight sites indicate that the LUQ site has been used as a model for their own site development and 13 sites list LUQ as a resource or as part of their "best sites" list. Additional sites indicate that university classes are using LUQ data for projects, presentations, and online publications.

4.3.5 Participation of LUQ in Network activities: LUQ IM participates actively in NIS projects. Distributed and centralized databases are maintained locally as part of our participation in the NIS: a Data Table of Contents (DTOC) (**http://luq.lternet.edu/datamng/nis/luqdtoc.htm**) links to the NIS DTOC (**http://www.lternet.edu/DTOC/dtoc_form.html**), the LUQ bibliography (**http://luq.lternet.edu/publications/lterpub/peerbib.html**) links to the all-site bibliography (**http://www.lternet.edu/biblio/**), and likewise with personnel databases. The site is also participating in the Hydrology database project, currently under development at the Andrews site.

4.4 Future Developments

Future plans for the development of the LUQ IMS include:

(1) Link descriptions of principal research activities to their online metadata and data;
(2) Participate in the LTER Network all-site project on Ecological Metadata Language that will eventually give us the capability to access data from any participating site;
(3) Prepare data and metadata files to participate in the NIS Climate database;
(4) Link servers at ITES and EVFS to automate transfer of data from data loggers;
(5) Complete a database containing a list of all our research sites with the global positioning system and elevation that will become part of the metadata for each database.

Section 5 Outreach Activities

5.1 Educational Activities

LUQ is participating in education at the K-12 levels in two ways. We have established a Schoolyard LTER program in Puerto Rico involving teachers at six high schools. Expanding on a program established by the USDA Forest Service at two rural high schools, we have added four schools to form a network of four rural and two urban schools. The focus of the activities will be on factors that affect water quality and quantity, and the role of forests in maintaining both of these ecosystem services. An additional focus of the urban schools will on the effect of urban forests on local climate. As part of this program, schools are provided with materials to establish their own weather stations. Each school also will have research programs associated with their own nearby forests or streams. Teachers are given guidance in curriculum development and research goals at weekend retreats at El Verde Field Station. LUQ researchers provide workshops on research projects in the classroom and at field localities and teachers are instructed

in data management techniques. Yearly symposia are planned where teachers and students from the network of schools will come together to share the results of their individual programs (Lugo 1999).
A second outreach program directed at K-12 students is being conducted in collaboration with the Center for Educational Technologies (CET), Wheeling Jesuit University in West Virginia. LUQ researchers are assisting CET in the development of interactive software for middle school students that will teach students rain forest ecology using examples from the LEF. This collaboration builds on CET's experience developing the NASA Classroom of the Future. Seed funding for the project was obtained through a NSF-SGER grant to CET, and CET recently received a $500,000 grant from NSF to complete development of the program (Zimmerman is Co-PI on the proposal). The new program will consider the impacts of hurricanes, and will teach students the basic ecology of the main groups of fungi, plants, and animals in the forest. Focusing on life history variation and trophic interactions among species, students will investigate the impacts of hurricanes on individual study organisms by collecting their own data and then comparing it to long-term data maintained by LUQ Information Management. Then, combining their data sets, the students will assess the impact and recovery of the entire rainforest system as a group. Progress to date has included the identification of critical components to be developed in this program and the use of frog population dynamics as a first subject.
LUQ has been very successful at incorporating undergraduate students in research at our site and at collaborating institutions on the mainland. UPR received a site REU grant for El Verde Field Station in 1999. Combined with supplemental funds to the LTER grant, we have hosted 50 REU students in the last six years. Sixty-six percent of these students were underrepresented minorities (primarily Puerto Rican students from both the island and the mainland) and 62% were women. In addition, one our associate researchers, Heather Erickson, from a local undergraduate institution Metropolitan University, routinely incorporates undergraduate students in her field studies in the LEF.

5.2 Local activities

LUQ has been instrumental in the management and monitoring of the lower Mameyes River, the largest unregulated river draining the LEF. The Puerto Rico Water Company (PRWC) had intended to dam the lower Mameyes and install a water intake that would frequently reduce water flow to levels below the normal minimum levels. Research by LUQ investigators indicated this would impede the migration of shrimp and fish along the river corridor, and that low water levels would allow water with abnormally high salinity to enter the lower river basin. In response to these results, the PRWC redesigned the water intake such that waters are withdrawn from the hyporheic zone without the use of a dam, and agreed not to reduce water flow to below the natural minimum levels. Modeling studies (Scatena & Johnson 2000) indicated that this design would have minimum impact on shrimp and fish populations and would maintain normal salinity levels in the lower basin. LUQ-LTER researchers continue to participate in a monitoring program aimed at assessing the impacts of water withdrawals on the stream ecosystem. Recently, State and Private Forestry of the USDA Forest Service provided funds to the LUQ to develop two Spanish-language posters portraying the importance of watershed protection and stream biodiversity in Puerto Rico. This follows on a similar successful program developed through La Selva Biological Station in Costa Rica. The posters will be distributed to local schools and government agencies.
Ariel Lugo and John Thomlinson continue to serve on the Science Technical Advisory

Committee for the Federal San Juan Bay Estuary Program. This committee is currently reviewing a Comprehensive Conservation and Management Plan, various long-term monitoring activities, and the results of all the studies conducted as part of the program. Jess Zimmerman, Fred Scatena and John Thomlinson have participated in activities of the Eastern Ecology Coalition, a grass-roots environmental group in eastern Puerto Rico. Fred Scatena continues to consult with local government groups on issues related to public water supply in Puerto Rico.

5.3 International activities

Our Data Manager has participated in two symposia of the Latin American International LTER Network. Her presentations were directed at the development of data management systems in a tropical setting. A copy of her presentation can be found at **http://luq.lternet.edu/ltexmoni/datamng/ilter/sld001.htm**.

As part of an NSF grant to Jean Lodge, "Basidiomycetes of the Greater Antilles, with special emphasis on the Luquillo LTER Site", workshops were held in conjunction with the 1998 Annual Meeting of the Mycological Society America. Workshops were held in Puerto Rico and Venezuela and involved 72 participants, mostly college teachers, from 22 countries. Nine identification manuals were produced, four in English and five in Spanish.

As part of an outreach program between UPR and Haiti, six government agency workers and college teachers were hosted at El Verde Field Station for a period of ten days. Participants were exposed to aspects of both basic research and management pertinent to our site.

LUQ has made an effort to integrate its studies with similar ongoing studies of cyclone disturbance in Taiwan. LUQ researchers visited the Fushan site in 1999 and established a project to compare long-term data sets on hydrology, decomposition, and forest canopy dynamics. During the 2002-03 academic year, Dr. Xiaoming Zou will be a visiting faculty member at National Cheng Kung University in Tainan where he will be conducting studies on controls of decomposition in the Ta-ta-chi Mountains of southern Taiwan.

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