J. Biosci., Vol 18, Number 4, December 1993, pp. 475-481. © Printed in India.

Catastrophic and background disturbance of tropical ecosystems at the Luquillo Experimental Forest

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MS received 14 August 1992; revised 20 August 1993

Abstract. The forests of the Luquillo Experimental Forest Long-Term Ecological Research site are subject to low-intensity, widespread disturbance that establishes levels of background mortality that contrast with periodic catastrophic mortality resulting from hurricanes and landslides. Although catastrophic mortality is more dramatic, background mortality is still more important in determining population turnover.· However, catastrophic mortality may still be an important agent in determining ecosystem structure. Catastrophic disturbances affect forest function in many ways besides mortality, some of which are only apparent in the context of long-term studies. Since most ecosystems are subject to some form of catastrophic disturbance, general principles can be derived from comparative studies of disturbance in different systems.

Keywords. Disturbance; mortality; tropical forest; landslides; hurricanes.

1. Introduction

The Luquillo Mountains of Puerto Rico rise abruptly from sea level to an elevation of 1000m less than 10 km from the Atlantic Ocean. They intercept several global airsheds including NE trade winds, cyclonic activity that originates in east Africa, northern fronts produced at high latitudes over continental North America, and cloud systems from the Amazon basin. The ecosystems of the Luquillo Experimental Forest (LEF) are zoned altitudinally and include five of the six subtropical life zones that occur in Puerto Rico, *e.g.* moist, wet, lower montane wet, lower montane rain, and rain forest life zones *sensu* Holdridge (Brown *et al* 1983). These life zones encompass a rainfall gradient from 2500 to > 5000 mm/yr and mean maximum temperatures from 23-27°C Forest associations under study through the Long-Term Ecological Research (LTER) Program of the National Science Foundation include tall and species-rich tabonuco (*Dacryodes excelsa*) forests, dwarfed cloud forests, monospecific palm forests, Colorado (*Cyrilla racemiflora*) forests, and plantations. Also under study are the stream systems that traverse these ecosystems (Covich 1988; Pringle *et al* 1993). These range from black to white waters and from small streams to large rivers.

The forests of Luquillo are subject to persistent but low-intensity disturbance (*e.g.* canopy gap formation) over large land areas. We term the mortality resulting from the natural death of individual trees and from these low-intensity disturbances "background mortality". Periodically, these forest lands are exposed to disturbances of high intensity such as hurricanes and landslides. Intense disturbances are termed catastrophic because they disrupt and modify ecosystem structure and function. The type of disturbance found in the LEF is representative of tropical forests in lower montane regions whose forest products are increasingly harvested to support the intense human activity that has already developed and/or damaged most of the tropical lowlands. The long-term dynamics of lower montane tropical ecosystems must be understood if people are to implement sustainable uses of tropical landscapes that are compatible with the conservation of their high biological diversity.

2. Current status of programme

The ecological study and conservation of tropical forests has been based on the paradigm that the remaining mature forests are pristine and fragile areas that have escaped damage from human activity (Farnsworth and Golley 1974). However, recent findings of charcoal and human artifacts in the soil profiles of tropical forests long-believed to be pristine (Sanford *et al* 1985) and the realization that the species composition of large areas of these forests is the result of human activity (Gomez-ompa *et al* 1987) have largely discredited the paradigm of the pristine tropical forest. Simultaneously, it is becoming evident that forest disturbance is necessary for forest regeneration (Denslow 1987). If the biota of tropical forests are sufficiently resilient to overcome frequent disruption, including catastrophic changes caused by hurricanes, landslides, volcanoes, and fires, the paradigm that casts all tropical forests as fragile must be revisited.

With the preceding in mind, our research effort has been organized around two principal questions (Waide and Lugo 1992): (i) what is the distribution of different disturbance types within the landscape of the LEF, and how does the disturbance regime at a given site affect the structure and function of the ecosystem, and (ii) what is the response of the biota to disturbances differing in scale, severity, and frequency, and how does this response affect a site's recovery toward mature forest?

These questions stem from the observation that the results of succession after different types of disturbance are difficult to distinguish in the LEF. The structure of regenerated mature forest displays convergence across a range of initial conditions.

The LEF is ideal for testing the emerging paradigm that suggests tropical forest ecosystems are resilient and are constantly undergoing modification due to natural and human-induced disturbances. The LEF has been studied holistically for many years, has a well-documented history of human use, contains outstanding examples of mature and secondary forest stands typical of a wide geographic region, and is periodically exposed to natural disturbance events with a wide range of intensities and periodicities (Brown *et al* 1983).

We organized our research according to an hierarchical model of ecosystem function in order to take full advantage of disturbance types (gaps, landslides, hurricanes, modification by humans) found in the forest. For each of the four types of disturbance, we ask questions at the individual, population, community, and ecosystem level with a focus on both the organisms (plants, animals, microbes) and the processes (e.g., nutrient cycles, life histories, productivity; Lugo and Scatena 1993). All studies contribute to a synthesis whose aim is to understand how a complex tropical forest disorganizes under the effects of disturbance and then reorganizes when the level of stress is reduced. Our goal is to extrapolate stand-level information from specific sites in the LEF to the landscape and to large-scale processes through the application of modelling, geographic information systems, and other synthesis tools (Hall *et al* 1992).

Results

The site was struck by a hurricane during the second year of LTER funding, providingus with an opportunity to fully document ecosystem response to a catastrophic disturbance along a gradient of disturbance intensity (Walker *et al* 1991). Forest stands of the LEF experience a background rate of tree mortality similar to forests anywhere in the world (2–5%/yr). The initial and most dramatic effect of any disturbance on forests is the increase in the rate of mortality. Hurricanes can cause sudden catastrophic mortality that elevates the rate to about 40% of total stems in highly impacted areas. Intermediate rates of mortality can occur depending on the force and direction of hurricane winds and topography. The dramatic mortality associated with a hurricane, however, may still take second place to steady background mortality as the principal factor determining population turnover (table 1).

Table 1. The range of tree (> 10 cm dbh) mortality and turnover time as a result of background and catastrophic mortality in the Luquillo Experimental Forest. Hurricanes of the intensity shown have a return time of 60 yrs. Treefall gaps are defined as the death (and generally the fall) of individual trees unrelated to major weather events. In the absence of hurricanes, background mortality results in a turnover time for trees that is less than the hurricane return time. Hurricane and gap data are from the LTER site at Bisley.

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

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

Data on background mortality collected from long-term study plots provides a mechanism to evaluate the importance of catastrophic events like hurricanes in determining forest structure and function. The relative impacts of background and catastrophic mortality are quite different ecologically, so that the comparison of average rates over time may not reveal the whole picture. Catastrophic mortality may be less important quantitatively and yet may be a distinctive and even critical structuring agent in the LEF.

The main ecological effect of hurricanes is to modify stand conditions that influence forest succession and allow the establishment of new combinations of species in the forest. Our observations of landslides suggest a similar role, but landslides have a more severe effect at a more localized scale. Guariguata (1989) reported that landslides affect 0·08–0·20% of the forest over a period of 100 yrs. Mortality in some sectors of landslides reaches 100%.

Landslides create new environmental conditions, set back succession to primary conditions (exposed soil B horizons), and favour different combinations of species. Along with hurricanes, landslides tend to diversify the landscape, both geomorphologically and ecologically. In contrast, the small treefall gaps characteristic of the LEF modify existing species combinations very little.

In addition to sudden mortality, catastrophic disturbances have many other implications for forest function, some of which are visible and others that are invisible (table 2). The visible effects of a catastrophe are obvious even to an observer with no prior knowledge of the site (figures 1-6). The invisible effects are

Table 2. Visible and associated invisible effects of hurricane disturbance in the Luquillo Experimental Forest.

Visible	Associated invisible
Drought	Cloud line higher in elevation Massive sporulation of VA- mycorrhizal fungi Fungi fruiting under litter layer Decrease in frog and snail populations, principally in smaller size classes
Decrease in bird, rat and bat populations	Transient movement of frugivores, nectarivores, and granivores Increase in disperser range and diet Most rat mortality among juveniles
Massive litter fall	*P* input several times greater than annual mean; *N* input double annual mean Increased nutrients in soil solution Increased nutrient leaching to ground water Increased CO_2 evolution Decrease in *N* in stream water immediately post-hurricane Large increase in NO_3 in stream water
Widespread defoliation	Widespread fine root mortality Decreased evapotranspiration
Increased stream flow and peak flow	Increased throughfall Decreased nutrient transport
Reduction in dicot tree flower and seed production	Hiatus in recruitment of seedlings
Massive wood fall	Shift in wood-decomposing fungi to species tolerant of high temperatures and drought; drop in diversity
Increased landscape heterogeneity	Increase in habitat diversity
Windthrow mounds and pits	Increase in variety of seedling microsites Mixing and drying of soil layers
High mortality of large trees	Reduced mortality of suppressed trees Decreased productivity in large size classes Increased productivity in small size classes
Increase in herbaceous layer	More rapid increase in herbaceous layer in preexisting gaps
Increase in herbivore damage	Decrease in populations of some herbivores (walking sticks)
Outbreaks of caterpillars and leaf hoppers	
Stream siltation increased	Stream pools filled in
Increased formation of debris dams	Slow release of detritus from dams Increased shrimp populations

Figures 1-6. The effect of hurricane Hugo in the Luquillo Experimental Forest in Puerto Rico. Despite the apparent widespread damage from this type of catastrophic event, tree mortality from hurricanes is less important than background mortality in population turnover (table 1). **(1)** High winds stripped leaves from canopy trees, but new leaves were produced rapidly. **(2)** Dwarf forest sites on the windward slope were hard hit by the hurricane, and recovery was slow. **(3)** In many places *Cecropia schrebcriana* formed dense clumps after the hurricane. **(4)** Dense concentrations of brush were formed in the understory, providing new habitat for some organisms such as spiders. **(5)** Three months after the hurricane, most of the live leaves were within a few meters of the ground. **(6)** The Bisley LTER site, which was in the direct path of hurricane winds, showed few signs of recovery one month after the hurricane. Photographs by Fred Scatena and Robert Waide.

too subtle to be appreciated by the casual observer and can only be appreciated in the context of an intensive, long-term study (Magnuson 1990).

Since all ecosystems are subject to one kind of catastrophic disturbance or another, the ideas developed in connection with the effects of hurricanes have general applicability to other sites. The views of mortality presented above were initially generated at an intersite LTER workshop and were influenced by experience elsewhere, particularly at the Andrews Experimental Forest in Oregon and Mount St. Helens in Washington, USA. The latter site is currently the focus of research on the impact of volcanoes in temperate forests. Ongoing experiments with streams, roots, soil, and wood decomposition are all heavily influenced by inter-site comparisons.

4. Discussion

Following the initial effects of a disturbance (ecosystem unravelling), populations and ecosystems enter a long period of repair and change. System resiliency can be measured by the speed and direction of change. Higher resiliency systems are those that change rapidly toward a state similar to the initial conditions. Systems with low resiliency will change at a slower rate and may change direction to a new terminal state.

Our observations suggest that assessments of tree mortality immediately after the hurricane are complicated by the fact that apparently dead trees were really alive and others that survived the hurricane subsequently died (Walker 1991; Walker *et al* 1992). Moreover, stumps and stems that had been recorded as dead for many years re-sprouted after the hurricane. Among animals, the decrease in bird populations observed immediately following the hurricane was a result of emigration (rather than mortality) because of a temporary loss of resources for some species (Waide 1991). These decreases have proven to be transient as forest resources return to their pre-hurricane levels. Therefore, the evaluation of population and ecosystem resiliency requires both an established data base to provide a context for the disturbance event and subsequent long-term observation. Our objective for the future is to understand fully the long-term aspects of tropical forest recovery from disturbance, *i.e.* ecosystem reorganization and readjustment to new conditions (Waide and Lugo 1992).

We envision our future studies in a comparative mode because the events that are taking place in the LEF are not unique to the tropics. They occur in other ecosystems within the temperate United States as well (e.g., Yellowstone, Mount St. Helens, North Inlet). The difference is the tropical context. This includes the greater complexity of the ecosystem, the nature of the environment in which recovery takes place, and the different attitudes toward forest conservation by peoples with different cultures and needs. How do these differences modify ecosystem responses? How do they affect management strategy and human use of the resource? These questions must be answered in concert with a network of sites subjected to similar intensities and patterns of disturbance but under different human and natural scenarios.

Acknowledgements

This statement is based on the results obtained by our colleagues in the Luquillo

LTER program including F N Scatena, D J Lodge, J F McCormick, D R Foster, W T Lawrence, A P Covich, M R Willig and B L Haines. This research was performed under grant BSR-8811764 from the National Science Foundation to the Center for Energy and Environment Research (University of Puerto Rico) and the Institute of Tropical Forestry (Southern Forest Experiment Station) as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by the Forest Service (US Department of Agriculture) and the University of Puerto Rico.

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