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Hurricane Effects on Soil Organic Matter Dynamics and Forest Production in the Luquillo Experimental Forest, Puerto Rico: Results of Simulation Modeling[1]

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ABSTRACT

The forests and soils at Luquillo Experimental Forest (LEF), Puerto Rico, are frequently disturbed by hurricanes occurring at various frequencies and intensities. We have derived a forest version of the Century soil organic matter model to examine the impact of hurricanes on soil nutrient availability and pool sizes, and forest productivity in the tabonuco forest at Luquillo. The model adequately predicted aboveground plant production, soil carbon, and soil nitrogen levels for forest conditions existing before Hurricane Hugo. Simulations of Hurricane Hugo and of an historical sequence of hurricanes indicated a complex pattern of recovery, especially for the first 10 yr after the hurricanes. After repeated hurricanes, forest biomass was reduced, while forest productivity was enhanced. Soil organic matter, and phosphorus and nitrogen mineralization stabilized at higher levels for the LEF than for hurricane-free tabonuco forest, and organic soil phosphorus was substantially increased by hurricanes. Results from these simulations should be regarded as hypotheses. At present there is insufficient data to validate the results of hurricane model simulations.

RESUMEN

Los bosques y suelos en el Bosque Experimental de Luquillo (BEL), Puerto Rico, son frecuentemente perturbados por huracanes que ocurren a varias frecuencias e intensidades. Nosotros hemos derivado una versión para bosques del modelo "Century" para materia orgánica de suelos para examinar el impacto de huracanes en la disponibilidad de nutrimentos en el suelo y el tamaño de las fuentes, y la productividad del bosque de tabonuco en Luquillo. El modelo predijo adecuadamente la producción sobre el suelo de plantas, el carbono en el suelo, y los niveles de nitrógeno en el suelo para las condiciones existentes en el bosque antes del huracán Hugo. Las simulaciones del huracán Hugo y de una secuencia histórica de huracanes indican un patrón complejo de recuperación, especialmente para los primeros diez años después de huracanes. Luego de repetidos huracanes, se redujo la biomasa del bosque, a la vez que se aumentó la productividad. La materia orgánica del suelo, y la mineralización de fósforo y nitrógeno se estabilizó a niveles más altos para BEL que para el bosque de tabonuco libre de huracanes, y el fósforo del suelo orgánico aumentó sustancialmente luego de los huracanes. Los resultados de estas simulaciones podrían considerarse como hipótesis. Al presente los datos son insuficientes para validar los resultados de las simulaciones del modelo de huracanes.

THE BIOGEOCHEMICAL CYCLES of carbon, phosphorus, and nitrogen are important factors for assessing the productivity and resiliency of tropical forest ecosystems, and for investigating interactions with abiotic factors, such as temperature and rainfall. The complex interactions that arise from inter-element linkages and abiotic driving variables have been examined in a conceptual framework that encompasses primary production, decomposition, and nutrient cycling (Stewart *et al.* 1983). This conceptual framework was subsequently developed into the

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Century simulation model for grassland ecosystems (Parton *et al.* 1988). The Century model has been used to examine soil organic matter dynamics for cultivated and uncultivated grassland soils (Parton *et al.* 1983a, b, 1987, 1988) and to simulate regional patterns of grassland production (Parton *et al.* 1989a). We used a variation of the Century model developed for forest ecosystems to examine the effects of hurricanes on tropical forest production and nutrient cycling processes. The model offers a means of testing ecosystem concepts by providing a tool for integrating available quantitative data on carbon, phosphorus, and nitrogen interactions and their driving variables. The data necessary to set the parameters for most forest simulation models for nutrient cycling in a tropical forest environment are rarely available for a single site, and the capability of simulating a massive disturbance in tropical forest has been rarely demonstrated. Here we report simulation results from the Century simulation model for repeated hurricanes in LEF. The objective of our modeling approach was to generate and test hypotheses concerning the controls on nutrient cycling in a tropical forest within the context of repeated disturbances by hurricanes and to compare these results against simulations of undisturbed (hurricane-free) forest. The three specific hypotheses that we address follow: (1) Forest biomass is lower in the hurricane-affected tropical forests than in hurricane-free tropical forests because the forest never fully recovers before it is blown down again. (2) Soil organic carbon is maintained at higher levels in hurricane-affected tropical forests than in hurricane-free forests because of periodic massive inputs of forest litter. This results in several nutrient and production feedbacks with important consequences for forest production. (3) Net forest productivity in hurricane-affected forests is higher than for hurricane-free forests. Although it is very unlikely that any hurricane-free areas exist in LEF, these comparisons serve as an heuristic device and also provide insight on the effects of hurricanes in this tropical forest ecosystem.

METHODS

MODEL DESCRIPTION.—The Century (grassland) model was modified to examine processes that control soil formation in the tropics and to simulate tropical forest, grassland and agricultural soil organic matter processes (Parton *et al.* 1989b). These modifications did not include any specific forest compartmentalization, but rather involved altering flows, rates, and ratios to emulate forest biomass.

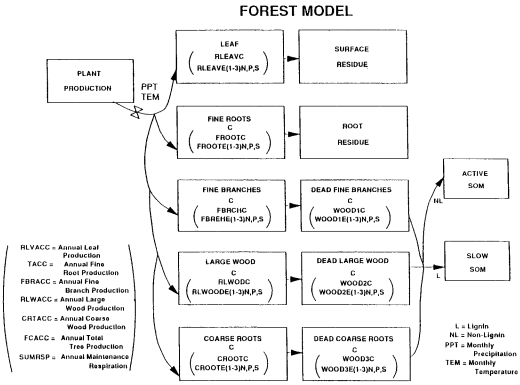

FIGURE 1. Forest production submodel compartments that were used to simulate hurricane disturbances in the tabonuco forest of the Luquillo Experimental Forest, Puerto Rico.

Results from that work indicated that modifications were required to better approximate tropical forest nutrient cycling patterns and a forest production and decomposition model was developed to interface with Century. The soil processes in the forest model remain basically unaltered from the grassland model; we have no reason to suspect that the abiotic controls on soil organic matter formation and cycling are substantially altered between different terrestrial ecosystems. However, we have substantially modified the production and decomposition components to correspond to forest ecosystems. These changes are described below.

The forest production submodel divides trees into five parts: leaves, fine branches (<5 cm diameter), large wood, fine roots (<2 mm diameter), and coarse roots (Fig. 1) with each part further partitioned into live and dead components. Carbon (C) is allocated to the different plant parts using a fixed allocation scheme and maximum monthly production is calculated as a function of the available moisture (*i.e.,* current available soil water plus rainfall input), soil temperature, and tree respiration. Monthly rates of maintenance respiration (g C m^{-2}) for the five tree components are calculated using a modification of the equations for daily maintenance respiration that were presented by Running and Coughlan (1988). Average monthly air temperature is used to calculate maintenance respiration for leaves, branches, and large wood. Average soil temperature is used to calculate rates of maintenance respiration for fine and coarse roots. These rates are sensitive to temperature changes and have a temperature response such that rates are increased by a factor of 2.3 per 10°C increase in the controlling temperature (*i.e.,* Q10 of 2.3).

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TABLE 1. *Soil, forest, and climate input parameters for tabonuco forest in the Luquillo Experimental Forest, Puerto Rico.*

Description		Value	Reference
Soils			
% Sand, silt, clay		29.2, 21.2, 49.6	Odum 1970a
Bulk density g/ml		0.77	Odum 1970a
pH		5.1	Odum 1970a
Soil organic matter g/m^2	0–2 cm	5960	
	2–15 cm	7540	
	15–30 cm	1130	Odum 1970b
Forest			
Production carbon to element ratios			
Leaf C/N, C/P		40, 2122	Odum 1970b
Fine root C/N, C/P		76, 765	Odum 1970b
Branch C/N, C/P		84, 1366	Odum 1970b
Stem C/N, C/P		155, 2260	Odum 1970b
Coarse root C/N, C/P		84, 1366	Odum 1970b
Decomposition rates g dry mass m^{-2} d^{-1}			
Dead branch		?	
Dead stem		0.44	Odum 1970b
Dead coarse roots		?	
Death rates for forest components/			
Fine and coarse roots		0.57	Odum 1970b
Branch		?	
Stem		0.54	Odum 1970b
Leaf litter C/N, C/P		26, 2592	Odum 1970b

Month	Precipitation (cm/mo^1)	Temperature (°C) Maximum	Temperature (°C) Minimum
Climate[a]			
J	26	26	16
F	20	26	16
M	16	27	17
A	23	28	18
M	38	29	19
J	25	29	19
J	27	30	20
A	35	30	20
S	31	30	20
O	31	29	19
N	40	28	18
D	38	27	17

[a] Mean monthly values from 1976–1989 (Luquillo LTER, pers. comm.).

The Century forest version of the model allows for separate allocation patterns for young and mature forests and can also represent seasonally deciduous forest as well as evergreen forest. Death of the live plant parts is set equal to monthly constants for continuously growing forests. Dead leaves and fine roots are transferred into surface and root residue pools and are then allocated into pools corresponding to structural and metabolic residue which are based on the lignin to nitrogen ratio of the residual material (for a full description of the soil and decomposition submodels see Parton *et al.* 1987). The components of dead wood, *i.e.,* fine branch, large wood, and coarse root pools, have pool-specific decay rates. These pools of dead wood decay so that their lignin fraction is transfered to the slow-turnover pool of soil organic matter, while the nonlignin fraction flows to the active pool of soil organic matter. This split between the lignin and nonlignin fraction is similar to that used for the decomposition of structural residue. The decay rates of the dead wood pools are also a function of abiotic decom-

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position parameters. Nitrogen (N) and phosphorus (P) submodels are integrated with the carbon submodel such that the labile N and P supply rates are largely controlled by the C:N and C:P ratios of the plant residue, soil organic matter pools, soil texture, and climate as described by Parton *et al.* (1988).

A forest disruption subroutine has been included to simulate disturbance due to hurricane, fire events, and/or forest harvest events. For each disturbance event, the fraction of each live plant part exported (due to harvesting, for example) and the fraction of material that is returned to the soil system can be specified. Death of fine and coarse roots, branch and large wood are also specified in the disturbance subroutine. The amount of N and P concentrations of live leaves that fall to the soil surface can also be specified to simulate the effect of adding live leaves to surface residue through processes like high winds or harvesting. The scheduling of forest disturbance events is entered interactively prior to running the model, and forest management parameters are specified by interactively specifying values.

HURRICANE SIMULATION.—The values used to set the LEF parameters for the Century forest model were taken from Odum (1970a, b) (Table 1). These values included decay rates of woody material, elemental ratios of the live vegetation and soils, and production values. Within the LEF we restricted our analysis to the tabonuco forest ecosystem (described by Wadsworth 1951) located in the subtropical wet forest life zone (Ewel & Whitmore 1973). This is the forest ecosystem that has been the focus of the Long-Term Ecological Research Program (LTER) from 1988 to the present. For all of our simulations, we used monthly averages of temperature and rainfall from 1976–1989 (Luquillo LTER, pers. comm.).

We simulated hurricane events using a modification of the hurricane intensity index (HII) (Scatena & Larsen 1991). We incorporated data from an observed hurricane disturbance (Lodge *et al.* 1991, Parrotta & Lodge 1991, Scatena & Larsen 1991) to derive a relative disturbance event scale for six historical hurricanes based on the index of hurricane intensity (Table 2). The index of hurricane intensity is the normalized product of the square of maximum reported wind and storm duration for hurricanes that have passed Puerto Rico since 1899. We listed the leaf, fine branch, large wood, coarse root, and fine root inputs recorded for Hurricane Hugo which occurred in 1988 and then scaled these inputs for each hurricane according to the hurricane intensity index. We were unable to obtain a mortality value for coarse roots from Hurricane Hugo, so for the purpose of this study, we assumed that it equals large wood mortality for each hurricane event.

TABLE 2. *Hurricane years and intensity index (Scatena & Larsen 1991) with estimated inputs for five forest compartments. Inputs are scaled according to measurements taken from Hurricane Hugo litter, branch, stem and root mortality, and the hurricane intensity index.*

Year	Intensity index (0–100)	% leaf	% branch	% stem	% fine root	% coarse root
1989	19	99	70	39	99	39
1956	13	68	48	27	68	27
1932	57	99	91	82	99	82
1931	27	99	80	59	99	59
1928	100	99	99	99	99	99
1899	19	99	70	39	99	39

We simulated two types of hurricanes; type (a) was based on the historical information and simulated events based on the index of hurricane intensity, while type (b) was a repeated simulation of Hurricane Hugo at 60 yr intervals. We chose 60 yr intervals because that is the estimated average return time for a hurricane of this strength (Weaver 1986). For both types of hurricane simulation we ran the model for a 600 yr period without disturbance to approximate steady state conditions prior to initiating disturbance events.

RESULTS

The hurricane *vs.* hurricane-free forest simulations reported here should be interpreted in the context of hypothesis testing. At present, data are virtually nonexistent to reject the hypotheses as stated, although post Hurricane Hugo measurements may be used for this purpose in the future. The simulated impact of hurricanes on forest carbon (Fig. 2) decreased total live carbon from 130 to ~100 Mg/ha. It took approximately 240 yr for total plant carbon to reach the new dynamic steady state. This new level was reached regardless of the type of hurricane sequence simulated, *i.e.*, historical hurricanes (Fig. 2a) and repeated–regular-interval hurricanes (Fig. 2b). In the absence of hurricane simulation, total plant carbon slowly increased by

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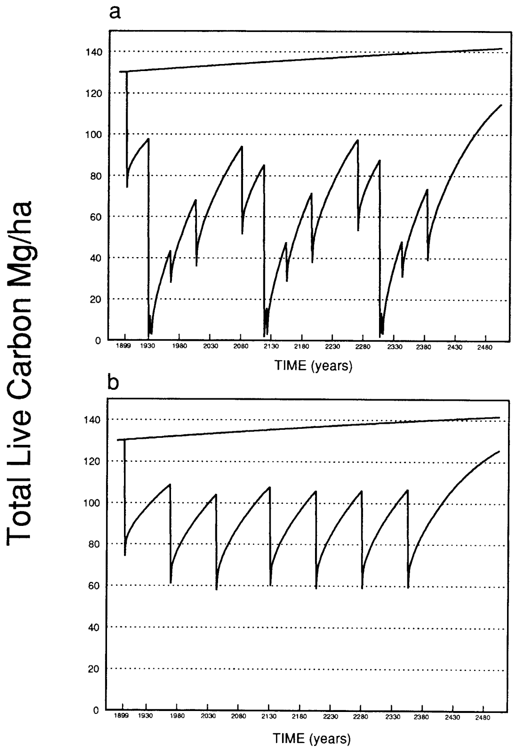

FIGURE 2. Aboveground and belowground forest carbon simulations for tabonuco forest of the Luquillo Experimental Forest, Puerto Rico. The straight lines represent nondisturbance simulations while the irregular lines indicate hurricane disturbance. (a) Historical hurricane sequence consisting of the six hurricanes that occurred from 1899–1989 shown in Table 2. (b) Hurricane sequence of repeated Hurricane Hugo events at 30 yr intervals.

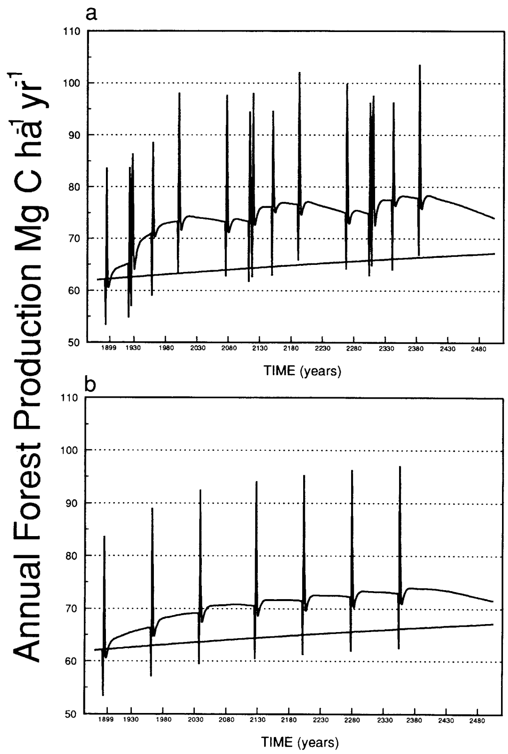

FIGURE 3. Forest production under historical (a) and repeated Hurricane Hugo (b) sequences compared with undisturbed forest production (straight lines) for tabonuco forest of the Luquillo Experimental Forest, Puerto Rico.

approximately 9 percent over the 600 yr simulation from 132 Mg/ha to 141 Mg/ha.

In contrast to forest biomass, simulated net forest productivity showed an increase in response to repeated hurricane disturbances (Fig. 3). Hurricane-free forest productivity rose slowly during the simulation, however the trend was stable and indicated annual forest productivity at approximately 650 Mg ha^{-1} yr^{-1}. The hurricane simulations suggested that a sharp and immediate drop in forest production occurred, followed by a 2 to 3 yr surge in production. Repeated hurricanes, whether historical (Fig. 3a) or at unvarying intensity and regular intervals (Fig. 3b) resulted in an overall increase in annual forest productivity.

The increase in forest soil organic carbon (SOC) due to simulated hurricane disturbance was one of the most striking results of our model (Fig. 4) and it was this increase that may be the main cause of increased forest production. The effect of hurricane disturbance was to increase soil organic carbon substantially above hurricane-free levels and to maintain very high amounts of carbon in the soil. This pattern was evident for both type (a) and type (b) simulated hurricanes.

One effect of increased SOC was a measurable and persistent increase in mineralized P in the forest soils (Fig. 5). Phosphorus mineralization appears to have been very sensitive to hurricane disturbance for 3 to 10 yr following each hurricane. An abrupt decrease in P mineralization rates was quickly followed by a spike in mineralization that roughly doubled the amount of mineralized P for a several year period. After approximately 4 to 10 yr (depending on hurricane intensity), our simulations showed a rapid decrease in rates of P mineralization to near prehurricane levels, but still markedly elevated above the hurricane-free rate. After approximately three 60 yr hurricane disturbances, the hur-

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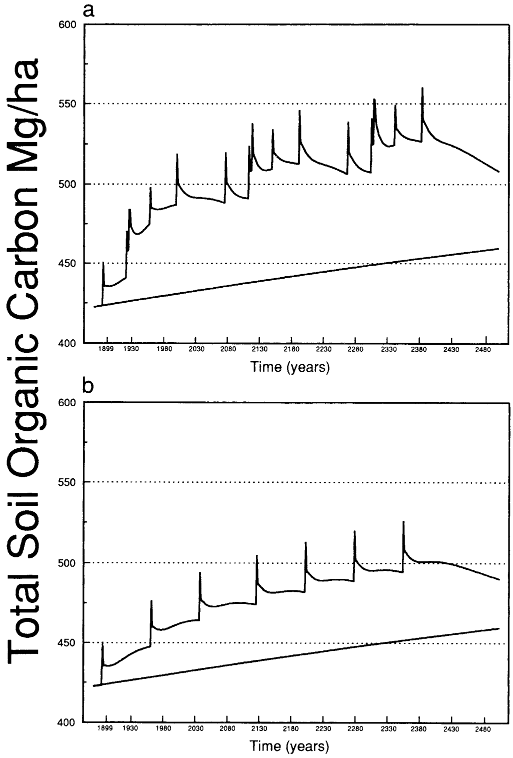

FIGURE 4. Forest soil organic carbon under historical (a) and repeated Hurricane Hugo (b) sequences compared with undisturbed forest SOC (straight lines) for tabonuco forest of the Luquillo Experimental Forest, Puerto Rico.

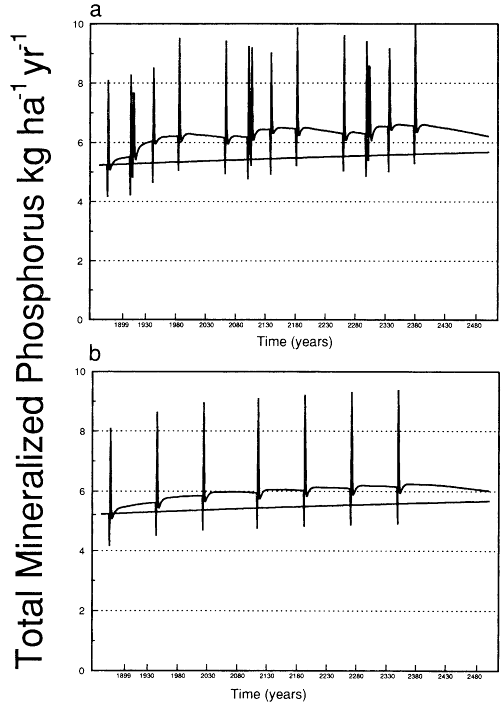

FIGURE 5. Phosphorus mineralization under historical (a) and repeated Hurricane Hugo (b) sequences compared with undisturbed forest SOC (straight lines) for tabonuco forest of the Luquillo Experimental Forest, Puerto Rico.

ricane-maintained level of mineralized P stabilized at a higher rate than without hurricanes. A closer look at the dynamics of P cycling revealed a trend toward large increases in organic P and sorbed P while labile, inorganic P was little affected by hurricanes (Fig. 6). The increase in simulated organic P was expected due to the increase in SOC, and it was the increase in the organic P pool that caused P mineralization rates to increase so much after each hurricane event. The increase in sorbed P (Fig. 6) limited P availability to plants, and reduced the potential increase in plant production because a large proportion of the P that was mineralized after each hurricane was sequestered in the pool of sorbed P. This result was intriguing but because there are almost no P fractionation data for LEF, the simulated values presented here can not be validated.

Nitrogen mineralization rates were also increased due to hurricane disturbances (Fig. 7), and this increase was also probably due to the increase in SOC. For the type (a) simulated hurricane disturbance sequence there was an overall increase of 12 to 15 kg ha^{-1} yr^{-1}. Similar to P mineralization, N mineralization was initially reduced following a hurricane and subsequently elevated to levels as high as 115 kg ha^{-1} yr^{-1} before decreasing again.

DISCUSSION

FOREST BIOMASS.—The biomass in the tabonuco forest ecosystem is 300 Mg/ha which is approximately 135 Mg/ha of carbon (Odum 1970a, Jordan 1971). This value is among the lowest reported for neotropical lowland forests (Vitousek & Sanford 1986, Jordan 1989). Our simulation results indicate that LEF tabonuco forest biomass was reduced below what could be sustained in this ecosystem by repeated hurricane disturbances. Forest biomass never fully recovered to nonhurricane, steady state levels because of the frequency and intensity of hurricanes. Simulation of the historical hurricane sequence reduced the forest biomass below the 60 yr interval sequence because the hurricane with a hurricane intensity index (HII) of 100 caused such a large

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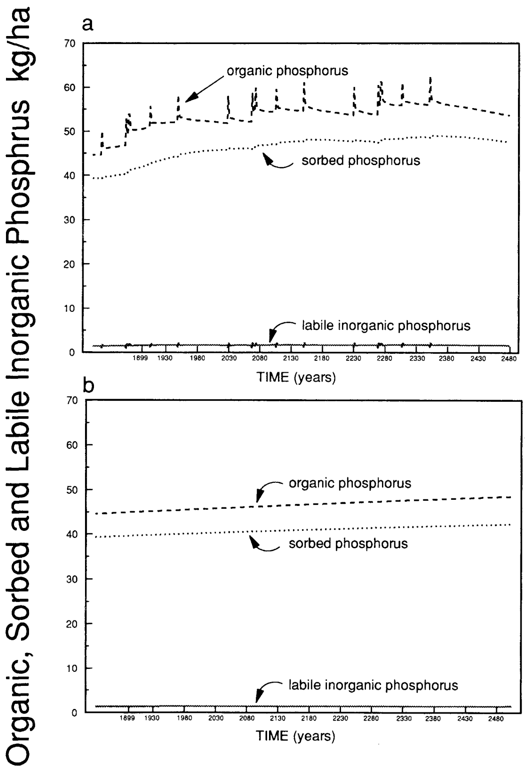

FIGURE 6. Organic, sorbed, and labile inorganic phosphorus pools under an historical simulation compared with undisturbed forest SOC (straight lines) of hurricane simulation sequence (a) and a nonhurricane simulation (b) for tabonuco forest historical sequence of the Luquillo Experimental Forest, Puerto Rico.

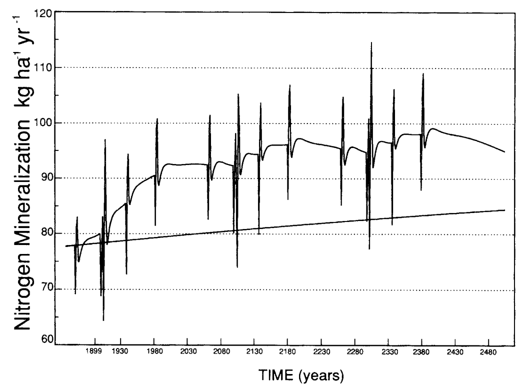

FIGURE 7. Nitrogen mineralization rates under an historical hurricane sequence compared with undisturbed forest (straight line) for tabonuco forest of the Luquillo Experimental Forest, Puerto Rico.

decrease in biomass that the forest never recovered to more than 95 Mg/ha. If the index of hurricane intensity is correctly calibrated and HII 100 events recur at 90 yr intervals then forest biomass should remain well below steady state levels. However, it is interesting to note that even an HII 19 event repeated at 60 yr intervals still resulted in forest biomass values that were never more than 75 percent of the nonhurricane steady state. In the absence of hurricanes, approximately 400 yr were required for total forest biomass to return to nonhurricane, steady state levels regardless of the type of hurricane sequence.

Forest soil organic carbon.—We hypothesized that SOC would be maintained at high levels due to frequent inputs from hurricanes. Forest SOC increased dramatically with each simulated hurricane and there was an overall increase in SOC in the forest. Although there are as yet no observed data to compare with our simulations, it appears that the large increase in SOC provided a source for increased P mineralization. We predict that most of the phosphorus in this forest was mineralized from organic sources of P. There was, however, a noticeable drop in P (and N) mineralization rates immediately following each hurricane. We attribute this drop to microbial immobilization of N and P in the forest floor debris. The model results were consistent with observed reductions in stream water nitrate concentrations to near zero for several weeks following the hurricane in tabonuco forests in the LEF (C. Asbury & F. N. Scatena, pers. comm.; see Lodge *et al.* 1991).

The questions pertaining to the effects of SOC and associated P cycling on forest production are very intriguing for this forest. However, validation of the model simulations that are presented here was not possible due to insufficient P fractionation data. These simulations were based on several assumptions that are unavoidable at present, including that sorbed P was less than but near to organic P levels; that net losses of P from the forest were always very low; and that occluded phosphorus (Fe and Al hydroxide P) were stable pools that remained unaffected by hurricane events. It would be very useful to obtain additional information on the status of phosphorus in LEF soils so that we could dispense with these assumptions.

Forest productivity.—The overall increase in forest productivity due to hurricane disturbance was probably due to several factors including the re-

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peated establishment of young, fast growing forests following hurricanes and an increase in available nutrients, especially phosphorus. Previous work indicates that LEF may be a P-limited ecosystem; the C:P ratio for tabonuco forest foliage is exceptionally high (Odum 1970a), and falls well within the range of tropical forest ecosystems that are expected to be P-limited (Vitousek & Sanford 1986). The reduction of total biomass was accompanied by an increase in forest productivity. The increased production was matched by an even more pronounced increase in SOC and elevated rates of N and P mineralization. After decomposition proceeded to a point where mineralization exceeds immobilization, we showed an abrupt increase in mineralization rates that coincided with the peak in forest production, regardless of the fact that P sorption occurs. We hypothesize that posthurricane successional vegetation responded to the increase in mineralization rates with increased production. The peaks and subsequent decreases in organic P, along with a similar pattern for SOC, suggest that the source for the short-term increases in production as well as the long-term trend in elevated forest productivity were due to amplified nutrient cycling rates via augmentation of the SOC pool in addition to elevated mineralization from those pools. Higher mineralization rates were also probably responsible for the high productivity of the disturbed forest, and the specific timing of the spikes in mineralization rates is important to understanding the recovery process for this forest. Data of Steudler *et al.* (1991) indicate that N mineralization rates in tabonuco forest were highest at the time of their first sampling 4 mo after the hurricane and declined gradually over the following 7 mo. Unfortunately, there are no comparable data available for comparison with P mineralization simulations.

Hurricane disturbances periodically return masses of plant material to the soil surface. In effect this process takes elements (especially phosphorus) that are usually bound up in wood and maintains those elements in a more active form, cycling through SOC at higher long-term rates than for hurricane-free tropical forests. We hypothesize that tabonuco forest production is maintained at an elevated rate as a result of the large amounts of SOC in tabonuco forest soil. We propose that the large amounts of SOC result in comparably larger pools of organic P and ultimately in high P mineralization rates. Hence the long-term, hurricane-driven maintenance of P in organic form is the key to understanding the apparent anomaly of high productivity in the comparatively low biomass tabonuco forest. Our hypotheses and simulated results call for rigorous testing and validation in the field and through corollary laboratory measurements. Such an approach requires systematic measurements and analysis of P, N, and C soil pools and consistent measurements of P and N mineralization rates both before and after hurricane disturbance. Empirical measurements that are coupled with simulation modeling to integrate and extrapolate the results provides a very powerful approach to understanding tropical forest ecosystems, and should yield considerable insight in tropical soil chemistry, controls on productivity, and tropical forest resiliency.

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