Nitrogen Immobilization by Decomposing Woody Debris and the Recovery of Tropical Wet Forest from Hurricane Damage
Author(s): J. K. Zimmerman, W. M. Pulliam, D. J. Lodge, V. Quinones-Orfila, N. Fetcher, S. Guzman-Grajales, J. A. Parrotta, C. E. Asbury, L. R. Walker, R. B. Waide
Source: *Oikos*, Vol. 72, No. 3 (Apr., 1995), pp. 314-322
Published by: Blackwell Publishing on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3546116
Accessed: 15/04/2009 16:54

OIKOS 72: 314–322. Copenhagen 1995

Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage

J. K. Zimmerman, W. M. Pulliam, D. J. Lodge, V. Quiñones-Orfila, N. Fetcher, S. Guzmán-Grajales, J. A. Parrotta, C. E. Asbury (†), L. R. Walker, and R. B. Waide

Zimmerman, J. K., Pulliam, W. M., Lodge, D. J., Quiñones-Orfila, V., Fetcher, N., Guzmán-Grajales, S., Parrotta, J. A., Asbury, C. E., Walker, L. R. and Waide, R. B. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. – Oikos 72: 314–322.

Following damage caused by Hurricane Hugo (September 1989) we monitored inorganic nitrogen availability in soil twice in 1990, leaf area index in 1991 and 1993, and litter production from 1990 through 1992 in subtropical wet forest of eastern Puerto Rico. Experimental removal of litter and woody debris generated by the hurricane (plus any standing stocks present before the hurricane) increased soil nitrogen availability and above-ground productivity by as much as 40% compared to unmanipulated control plots. These increases were similar to those created by quarterly fertilization with inorganic nutrients. Approximately 85% of hurricane-generated debris was woody debris >5 cm diameter. Thus, it appeared that woody debris stimulated nutrient immobilization, resulting in depression of soil nitrogen availability and productivity in control plots. This was further suggested by simulations of an ecosystem model (CENTURY) calibrated for our site that indicated that only the large wood component of hurricane-generated debris was of sufficiently low quality and of great enough mass to cause the observed effects on productivity. The model predicted that nutrient immobilization by decaying wood should suppress net primary productivity for 13 yr and total live biomass for almost 30 yr following the hurricane. Our findings emphasize the substantial influence that woody debris has upon nutrient cycling and productivity in forest ecosystems through its effects on the activity of decomposers. We suggest that the manner in which woody debris regulates ecosystem function in different forests is significantly affected by disturbance regime.

J. K. Zimmerman, D. J. Lodge, J. A. Parrotta and R. B. Waide, Terrestrial Ecology Div., Univ. of Puerto Rico, San Juan, PR 00936, USA (present address of DJL: USDA Forest Serv., Center for Forest Mycology Research, Forest Products Lab, Palmer, PR 00721, USA; present address of JAP: International Inst. of Tropical Forestry, USDA Forest Serv., Río Pedras, PR 00928, USA). – W. M. Pulliam, Natural Resource Ecology Lab, Colorado State Univ., Fort Collins, CO 80523, USA. – V. Quiñones-Orfila, N. Fetcher, S. Guzmán-Grajales and L. R. Walker, Dept of Biology, Univ. of Puerto Rico, Río Pedras, Pr 00931, USA (present address of SGG: Dept of Ecology, Evolution, and Organismal Biology, Tulane Univ., New Orleans, LA 70118, USA; present address of LRW: Dept of Biological Sciences, Univ. of Nevada, Las Vegas, NV, USA).

Large inputs of litter with low nutrient contents are commonly known to temporarily limit production in agricultural systems because of nutrient immobilization by microbial decomposers (Stevenson 1986). This effect, well described by the 1930's (Paul and Juma 1981), occurs because microbes decomposing poor quality litter must draw upon plant-available forms of nitrogen in the soil in order to raise the nitrogen content of the decomposing material to that of their own biomass. As decomposition proceeds, the decomposing material becomes exhausted,

Accepted 9 September 1994

ISSN 0030-1299

microbial populations decline, and nitrogen is once again released to plant-available soil pools. These effects are only caused by litter with an N concentration less than about 2% (Stevenson 1986). Decomposition of litter with higher N concentrations either has no effect on the system or provides increased nutrient availability to plants throughout the decomposition process. In agricultural systems, the transient loss of productivity during decomposition of low quality litter typically lasts only 4–6 weeks (Anderson and Swift 1983, Stevenson 1986).

Nutrient immobilization by soil microbes has important implications for understanding patterns of nutrient cycling in forested ecosystems as well. In experimental studies it has been shown that decomposing leaves and twigs will immobilize nitrogen and other nutrients (e.g., Bocock 1964, Gosz et al. 1973, Aber and Melillo 1982) and microbes have recently been shown to be important for retaining nutrients in temperate forests during spring melt (Zak et al. 1990, Groffman et al. 1993). In many forested ecosystems, microbial biomass immobilizes much more added nitrogen than does plant uptake (Vitousek and Matson 1984, Schimel and Firestone 1989, Preston et al. 1990, Zak et al. 1990, Groffman et al. 1993). Adding sugar or sawdust to soils has been used to stimulate the growth of microbes to reduce nitrogen availability to forest trees (e.g., Turner and Olson 1976). For wet tropical forests, Lodge (1993) has recently argued that the tendency for populations of fungal decomposers to wax and wane in response to changes in soil moisture causes fluctuations in nutrient mineralization and immobilization and prevents the system from reaching a steady state.

In forested ecosystems, emphasis has sometimes been given to deposition and decomposition of green leaf material, particularly following disturbances such as treefalls (Vitousek and Denslow 1986) and hurricanes (Lodge et al. 1991, Whigham et al. 1991). Because the relatively high nutrient content of green litter should result in a shorter period of nutrient immobilization as compared to normal litter, green litter produced by disturbance was predicted to be an important source of nutrients early during recovery from disturbance.

Less well appreciated in the nutrient dynamics of forested ecosystems is the decomposition of coarse woody debris (Anderson and Swift 1983, Harmon et al. 1986). Typically of low quality and often quite abundant in forested ecosystems (Harmon et al. 1986), decomposing wood should have a large impact on patterns of nutrient availability. Decomposing logs often increase in nutrient content during decomposition (Harmon et al. 1986), suggesting nutrient immobilization in decaying wood is common. Potential sources of nutrients in decomposing wood include rainfall and throughfall, nitrogen fixation (Harmon et al. 1986), and translocation of nutrients from soil and litter to decomposing wood by cord-forming decomposer fungi (Wells et al. 1990). Depending on the size and intensity of a disturbance, coarse wood is often a dominant component of the resulting debris and might be expected to govern subsequent nutrient dynamics. For example, following a hurricane in the Yucatan Peninsula of Mexico, almost 70% of debris was coarse wood >1 cm in diameter in contrast to a typical nonhurricane year in which 90% of litter was leaf material (Whigham et al. 1991). Even in less severe disturbances, such as local tree- or branchfall, the decomposing woody debris can be expected to have a strong effect on nutrient availability in the area of the disturbance because of its great mass and low nutrient concentration (Anderson and Swift 1983). The importance of decomposing woody debris becomes greater when it is realized that its decomposition, and related effects on nutrient availability, can potentially last for decades (Harmon et al. 1986).

We studied soil nitrogen availability and components of forest productivity for over three yr in a Puerto Rican wet forest that was severely disturbed by Hurricane Hugo in September 1989. Comparison of the effects of removal of hurricane-generated debris and regular nutrient additions to unmanipulated forest plots indicated that hurricane-generated debris depressed nitrogen availability and caused a reduction in forest productivity following the hurricane. Using CENTURY, a linked decomposition-production model (Parton et al. 1987, 1988) parameterized for our site (Sanford et al. 1991), we show that the effects were very likely the result of nitrogen immobilization during decomposition of woody debris. We use the model to further predict that the effects of decomposing woody debris will influence forest biomass for almost 30 yr following the hurricane. We conclude that, in a long-term perspective, pulses of woody debris produced by hurricane disturbance governs the tempo of nutrient cycling in our forests and, depending on disturbance regime, should have similar and dramatic effects on nutrient cycling in other forested ecosystems.

Material and methods

Study site

We studied subtropical wet forest (Ewel and Whitmore 1973) at elevations between 340 and 460 m elevation in the Luquillo Experimental Forest in eastern Puerto Rico (18°20'N, 65°49'W). Our sites were on the northwest flank of Luquillo Mountains in an area marked by deeply dissected drainages and steep northeast and southwest facing slopes. At the nearby El Verde Field Station, annual precipitation is approximately 350 cm per year (Brown et al. 1983) with rainfall distributed more or less evenly throughout the year. Soils of the area are a complex of upland Ultisols and Oxisols (Zarzal-Cristal complex; Huffacker 1994) and are mostly well-drained silty clay loams. Locally, the vegetation is referred to as tabonuco forest after the dominant tree species *Dacryodes excelsa* Vahl. Additional common species include *Manilkara bidentata* (A.DC.) A. Cher., *Sloanea berteriana* Choisy, *Prestoea montana* (R. Grah.) Nichols, and *Cecropia schreberiana* Miq.

Field studies

In June of 1989, we established four blocks of five plots, placing the plots along ridges to avoid exchange of nutrients in water flow among plots. Each plot was 20 × 20 m with an interior 10 × 10 m measurement plot. The center of Hurricane Hugo passed within 15 km of our site on 18 September 1989 (Walker et al. 1992), generating winds from the north and northwest which, near the path of the hurricane, were in excess of 200 km/h (Scatena and Larsen 1991). Using non-destructive methods, it was estimated that the hurricane removed 99% of leaf biomass, 70% of fine branches (<5 cm diameter), and 35% of coarse wood, depositing them on the forest floor (Sanford et al. 1991, Walker 1991). In addition, the storm and subsequent drought caused fine root biomass in the upper 10 cm of soil to decline to zero during a three-month period following the storm (Parrotta and Lodge 1991, see also Silver and Vogt 1993).

Originally, the experimental design was meant to accommodate a factorial fertilization study, but this was abandoned after the hurricane. After the hurricane, one plot from each block was randomly selected for each of three treatments: one-time removal of litter and woody debris; quarterly nutrient amendments; or an unmanipulated control. Debris removal included standing stocks present before the hurricane and was completed within one month of the hurricane. Inorganic fertilization treatments were applied every three months throughout the study at the following rate: 30 g N, 10 g P, 10 g K, 1.9 g Mg, 2.5 g Mn, 2.6 g Zn, 1.5 g Cu, 0.2 g Fe, and 0.8 g B m^{-2} yr^{-1}. Nitrogen was added as both ammonium nitrate and urea at a rate approximately 3 times the normal amount of N added annually as litterfall (Lodge et al. 1991). Additional details on the species composition and hurricane damage received by these plots are described in Parrotta and Lodge (1991) and Walker (1991).

During one fertilization treatment (March 1991), fertilizer was mistakenly placed on all treatment plots in two of the four blocks. Fertilizer was applied at 1.33 the normal rate to the interior 10 × 10 m measurement plots. This one time error damaged some small seedlings as normally observed following fertilization (S. Guzmán-Grajales, pers. obs.), but otherwise had no apparent long-term effects on the understory. Subsequent to the error there were no significant differences in leaf litter production (collection method described below) between affected and unaffected blocks (J. K. Zimmerman, pers. obs.). Beginning in October 1991 additional control plots in the affected blocks, randomly selected from among those remaining from the original experimental design, were monitored for leaf litter production. These data also showed that there was no detectable effect of one-time fertilization on leaf litter production (J. K. Zimmerman, pers. obs., methods described below). These results are available from the senior author upon request.

Soil samples were collected from each plot twice in 1990. Soil samples, four replicates per plot, were collected using 8.5 cm diameter plastic cores driven to a 10-cm soil depth. Soil samples were immediately sieved (5 mm and then a 2 mm mesh) and extracted with 2N KCl for 1 h on a wrist-action shaker. Ammonium and nitrate concentrations in extracts were determined spectrophotometrically using the phenate and cadmium reduction methods, respectively (Technicon 1985). Some soil extracts were misplaced during processing such that data were not recovered for all plots. However, there was at least one replicate plot per treatment.

In tabonuco forest, leaf litterfall accounts for 47% of aboveground net primary productivity (NPP; Weaver and Murphy 1990) and was considered to be a sensitive indicator of short-term changes in NPP, therefore we present data on the production of leaf litter only. Litter production was monitored in litter baskets (10 per plot, 1.6 m^2 total surface area) randomly placed in each 10 × 10 m inner measurement plot beginning in March 1990. Litter was collected fortnightly, dried at 60°C, sorted, and weighed.

Leaf area index (LAI) was measured in each inner treatment plot in July August 1991 and May – June 1993. LAI was measured using a LI-COR LI-2000 Plant Canopy Analyzer at 30 randomly selected locations in each plot.

Analysis of variance for treatment and block effects (ANOVA) were performed using the general linear models procedure of SAS (SAS 1987) on plot means. Soils and LAI data collected on different dates were analyzed separately. ANOVA's on extractable soil N were consistent with respect to the occurrence of missing data (SAS 1987; i.e., there was at least one replicate per treatment). Comparison of means was conducted using the REGWF procedure (SAS 1987) when means had identical sample sizes (LAI) and the Tukey-Freeman procedure when there were unequal sample sizes (extractable soil N). Data on mean leaf litter production per plot per quarter were analyzed using repeated measures ANOVA and analyzed separately for the years 1990, 1991, and 1992.

Modelling

We used the CENTURY model (Parton et al. 1987, 1988, Sanford et al. 1991) to simulate forest responses to hurricane damage and litter inputs. CENTURY simulates flows and standing stocks of C, N, and P among biomass, litter, woody debris, and soil organic matter (SOM) pools. We used the version of CENTURY for tabonuco forest described by Sanford et al. (1991) with several small modifications (all model parameters are provided in Appendix): litter decomposition controls were calibrated against field measurements of C and N mass loss of leaf litter (La Caro and Rudd 1985, Bloomfield et al. 1993, X. Zou, R. Waide, and C. Zucca, unpubl.); initial leaf litter C/P ratio was adjusted to 700 (X. Zou et al., unpubl.); and biomass allocation was adjusted to better reflect observed patterns (Odum and Pigeon 1970). In

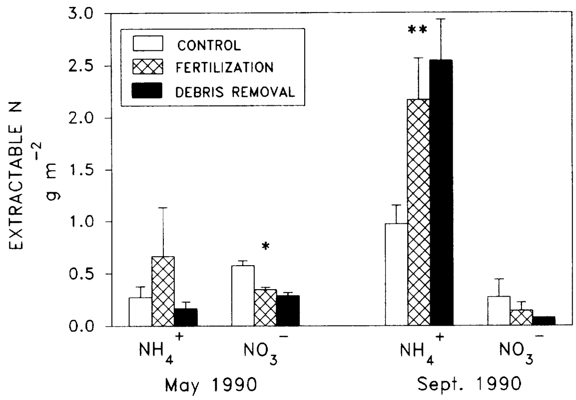

Fig. 1. Comparisons of ammonium and nitrate availability (KCl extractions) in soils collected (to a depth of 10 cm) from each of three plot treatments in Puerto Rican subtropical wet forests on two dates in 1990. Means + 1 SE (N = 1–4 replicates). Significance levels are *: P<0.05; **: P<0.01.

CENTURY, simulated rates and patterns of leaf and fine root litter decomposition are controlled by initial lignin and N content (Vitousek et al. 1994).

Woody debris decomposes in CENTURY by a simple exponential model modified by temperature and moisture controls (Sanford et al. 1991). The effective mean decay rate was 0.5 yr^{-1} for small aboveground wood and 0.1 yr^{-1} for large wood. The latter is not much different from a decomposition rate of 10.9% yr^{-1} measured at El Verde over a 2-yr period using stumps of four freshly cut tree species representing the range of wood densities at the site (Odum 1970). As wood in the model decomposes, N is immobilized from available pools in order to bring the C/N ratio down to that of newly formed microbial biomass and soil organic matter (SOM). Thus, in the model, the N which is immobilized by decomposing woody debris is not available for plant growth until it is later remineralized by decomposition of SOM.

CENTURY simulations of forest responses to hurricane damage between September 1989 and December 1992 were conducted to ascertain the effects of hurricane-generated debris on nutrient availability and forest production and to directly complement the results of debris removal in field studies. A simulated hurricane transferred 99% of leaves and fine roots, 70% of fine branches, and 35% of large wood (large branches and tree boles) to necromass, based on measured hurricane effects in our plots (Parrotta and Lodge 1991, Walker 1991). Loss of coarse roots was not measured in any study and was estimated to be 35%, same as that for coarse wood (Sanford et al. 1991). In control simulations all hurricane-generated debris remained within the forest; in removals, all hurricane debris and preexisting woody debris were removed. Belowground debris remained within the system in all simulations. Simulations were driven by observed climate at El Verde for 1989–1993 (Luquillo Long-Term Ecological Research Program, unpubl.).

Additional CENTURY simulations were designed to isolate the potential effects of particular components of hurricane debris on forest productivity during 1989 through 1992. In these simulations, either leaves, fine branches, or coarse wood were returned separately to the forest floor after a simulated hurricane and the remaining components were removed from the system. These simulations were compared to ones in which, as done previously, none or all of the debris components were removed following the hurricane. To differentiate between the effects of the quantity and quality of debris components, two additional sets of simulations were conducted. In one, the actual estimated biomass of each component was returned to the forest floor. In a second set of simulations, each component was returned at the same mass of 300 g m^{-2}. The combined effect of all components together was achieved by returning each at a mass of 100 g (for a total of 300 g m^{-2}).

Long-term CENTURY simulations (1989–2039) of the effect of debris removal on forest productivity and biomass following hurricane damage were also conducted. These simulations utilized the mean El Verde climate for 1976 – 1992 (Luquillo LTER Program, unpubl.).

Results

Field studies

In May 1990, soil extractable ammonium and nitrate concentrations were low but with a significant trend towards higher nitrate availability in the control plots (P = 0.026; Fig. 1). Treatment differences for ammonium were not significant (P = 0.36). In September 1990, soil nitrate availability remained low and their were no significant treatment effects (P = 0.773). However, extractable ammonium was much higher and was significantly greater in debris removal and fertilizer plots than in control plots (P = 0.008).

Leaf litterfall in 1990 (Fig. 2) was much reduced from

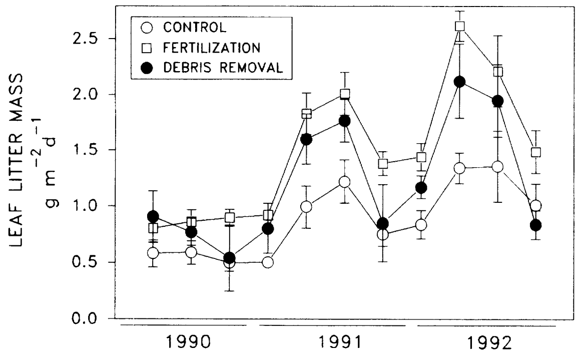

Fig. 2. Comparisons of leaf litter production in control plots, in regularly fertilized plots, and in plots in which hurricane-generated debris was removed following Hurricane Hugo. Litter collections began six months after the hurricane (September 1989).

Table 1. Mean leaf area index (± SE; N = 4) in forest plot treatments measured July – August 1991 and April – June 1993. Means with same letter were not significantly different at $P < 0.05$.

Treatment	1991	1993
Control	3.45^{A} (0.49)	3.96^{A} (0.56)
Fertilization	4.29^{B} (0.17)	4.74^{B} (0.18)
Litter removal	4.56^{B} (0.32)	4.98^{B} (0.28)

measured rates at El Verde (1.4 g m^{-2} d^{-1}; measured >30 yr post-hurricane, Wiegert 1970) with little apparent difference among treatments ($P = 0.097$). Leaf litter production increased in 1991 in all treatments and resumed its normal seasonal cycle (Wiegert 1970). Treatment differences were significant in both 1991 ($P = 0.034$) and 1992 ($P = 0.023$), with leaf litter production increasing as: control < debris removal < fertilization. In August 1991 leaf area index (LAI) in debris removal and fertilized plots was significantly elevated compared to control plots (Table 1; $P = 0.016$). An a posteriori comparison of means indicated that debris removal and fertilization plots were statistically indistinguishable but significantly greater than control plots ($P < 0.05$). Similar results were obtained in 1993 (Table 1) and differences among means were again significant ($P = 0.035$).

CENTURY model

Simulated live leaf biomass increased more rapidly following hurricane damage when debris was removed from the system than in control simulations (Fig. 3A). CENTURY predicted that removal plots would have 40% greater leaf biomass than control plots at the end of 1992, quite similar to observed differences in leaf litter production and LAI (Fig. 2, Table 1). In the model, available soil N (ammonium and nitrate combined) was at times substantially higher in removal simulations than in controls (Fig. 3B), a pattern reflected in field data (Fig. 1). Direct comparison of model results and field measurements are not possible because of differences in depth of soil represented by the two studies (20 vs 10 cm), but the amounts of available N predicted by the model were less, overall, than the amounts of extractable N measured in the field. In CENTURY, simulated N-mineralization rates (Fig. 3C) were greater in the debris removal treatment in comparison to the control simulations. Conversely, predicted microbial C (not shown) and N (Fig. 3D) were elevated in control vs removal simulations. Overall, the CENTURY simulations indicated that there should be less nitrogen capital in plant-available forms and more in microbial biomass in the control treatments compared to the debris removal treatments.

CENTURY simulations in which individual litter/woody debris components were separately returned to the forest (Table 2) indicate that suppression of net primary productivity (NPP) by hurricane-generated litter and woody debris is influenced most strongly by decomposition of coarse wood. The mass of hurricane debris inputs is dominated by large wood (Table 2A). When equal masses of individual components were returned to the model system (Table 2B), leaves increased simulated NPP slightly, while small branches depressed production more than did coarse wood. However, because the actual mass of coarse wood inputs is so much greater than that of the small wood, the large wood component was predominately responsible for the suppression of post-hurricane NPP in the model.

Long-term simulations suggest that suppression of forest NPP by hurricane-generated woody debris will have a prolonged effect. After 13 yr NPP becomes lower in debris removal than control simulations (Fig. 4A), and total forest biomass in control simulations exceeds removal simulations after 29 yr (Fig. 4B). These CEN-

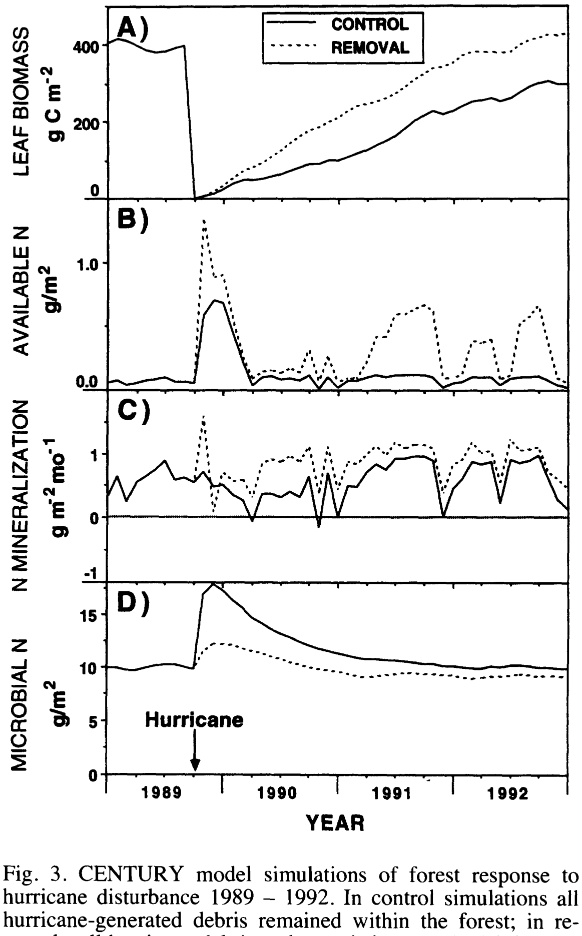

Fig. 3. CENTURY model simulations of forest response to hurricane disturbance 1989 – 1992. In control simulations all hurricane-generated debris remained within the forest; in removals, all hurricane debris and preexisting woody debris were removed. Belowground debris remained within the system in all simulations. Simulations were driven by observed climate at El Verde for 1989–1992: (A) leaf biomass; (B) nitrogen available to plants in the soil to a depth of 20 cm; (C) the rate of N-mineralization in soil (20 cm depth); and (D) nitrogen present in microbial fraction of SOM (20 cm depth).

Table 2. Results of CENTURY model simulations to show predicted effects of individual hurricane litter components on forest NPP expressed as three-yr total (1990 – 1992). In each simulation single debris components were returned to the system; all other debris was removed. Simulations with no litter added ("none") is equivalent to debris removal treatment and "combined" refers to control situation. Difference is NPP relative to debris removal treatment ("none").

Debris component(s) added	none	leaf	small wood (< 5 cm)	large wood (> 5cm)	combined
A. Components of hurricane debris added using actual (estimated) masses.					
Mass (g m^{-2})	0	397.7	360.1	2793.4	3554.2
NPP (gC m^{-2})	2262.4	2377.4	2075.6	1616.7	1493.1
Difference	–	+115.0	−186.6	−645.7	−769.3
B. Debris components added using constant amounts.					
Mass (g m^{-2})	0	300.0	300.0	300.0	300.0[1]
NPP (gC m^{-2})	2262.4	2346.3	2169.9	2226.1	2244.2
Difference	–	+83.9	−92.8	−36.3	−18.2

[1]100 g m^{-2} of each component.

TURY simulations indicate that nutrients immobilized in wood early in decomposition should be released to plant-available pools during subsequent decades.

Discussion

Microbial immobilization of plant-available nutrients during decomposition of low quality litter, and its short-term negative effects on plant productivity, is a well established phenomenon in agricultural soils (Stevenson 1986). Our results indicate that woody debris can also have dramatic but more prolonged effects on production in forested ecosystems. Removal of hurricane-generated debris from forest plots increased above-ground forest productivity by up to 40% during three yr following the hurricane. These increases in productivity were almost as great as those observed in plots subject to repeated fertilization with inorganic nutrients. While this study demonstrates large effects of the forest plot treatments on above-ground productivity, there have been no detectable effects of the treatments on the biomass of live fine (<3 mm diameter) roots (Parrotta and Lodge 1991, Parrotta, Lodge, and Zimmerman, unpubl.).

In describing the tabonuco forest version of CENTURY, Sanford et al. (1991) predicted that the decomposition of hurricane-generated debris would cause a suppression of forest productivity for a period of time following a hurricane. Our field studies have confirmed the basic prediction that decomposition of hurricane-generated debris suppresses productivity and the model appears to mimic closely the actual magnitude of the effect during the first three yr following hurricane damage. However, assessing the validity of the match between empirical observations and model results is dependent on the mechanism(s) by which decaying woody debris, the largest component of the hurricane debris, can immobilize nitrogen otherwise available for plant growth.

There are two potential mechanisms for woody debris to bring about nitrogen immobilization at our site. First, the addition of organic matter to the soil via wood decomposition may stimulate immobilization of nitrogen by soil microbial biomass. In CENTURY, woody debris enters the soil with a relatively low N concentration (0.3%) and is then transferred to microbial SOM pools with much higher concentrations (3–4%). This transfer results in net nutrient immobilization because N is removed from available pools and added to decomposing litter and woody debris to bring its nitrogen content up to that of SOM. The decomposition rate used in the model, 10% per year, is similar to the relevant early decay rate value measured by Odum (1970), indicating a high potential for

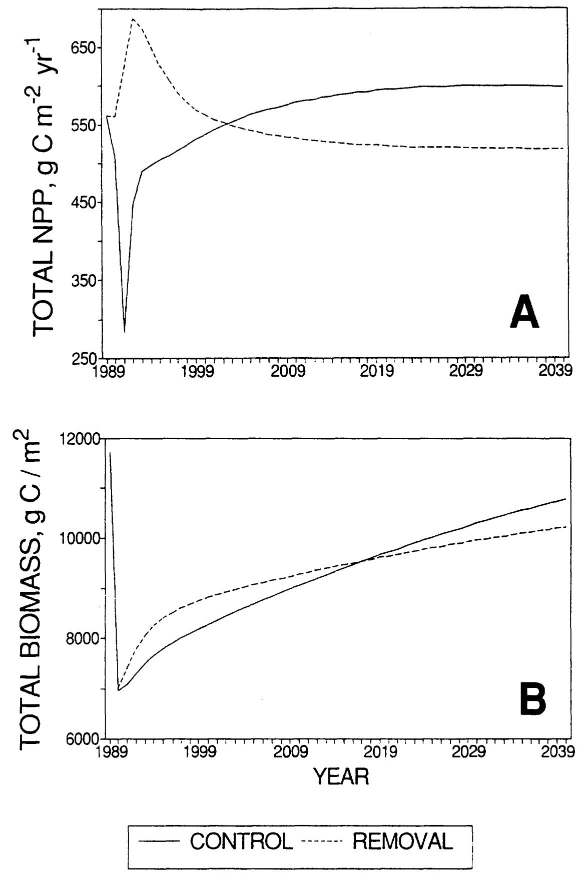

Fig. 4. CENTURY model simulations of net primary productivity (NPP) and live biomass for 50 yr following Hurricane Hugo. "Removal" simulation is one-time removal of hurricane-generated debris and pre-existing standing debris); "control" simulation is for all debris left in system. A) NPP expressed in units of carbon, total for each calendar year. B) Total biomass in units of carbon at end of each calendar year. Simulations utilized the mean El Verde climate for 1976–1992.

microbial immobilization of nitrogen via decaying woody debris. Initially, much of the organic matter from wood probably enters the soil as frass from wood-boring insects (e.g., termites, MacMahon 1970, Torres 1994).

The second potential mechanism for nitrogen immobilization is translocation of nitrogen from soil and fine litter into decaying wood by cord-forming fungi. These fungi can translocate large quantities of nutrients (including nitrogen) long distances between pieces of decaying wood (Watkinson 1984, Thompson 1984) and, at least for phosphorus, it has been shown that cord-forming fungi will translocate nutrients from soil into wood (Wells et al. 1990). This process is not explicitly represented in CENTURY, but would be included as an unresolved portion of the general immobilization of N by decomposers during decay of woody debris. Fungal mycelial cord systems and high fungal biomass are common in soils near decaying wood at El Verde (Lodge 1993), but tracer experiments have not been conducted which demonstrate that the fungi translocate significant amounts of nitrogen or other nutrients into decomposing logs. In order for this mechanism to be important, it would require that the wood be initially in contact with the soil and not be completely suspended. While we have no detailed measurements of this, our field observations indicate that much of the coarse woody debris was in contact with the soil after the storm. By the second and third years after the storm initial decomposition had caused some suspended logs and most of the small woody debris to fall to the forest floor.

Decaying wood may immobilize some nitrogen directly from rainfall, but inputs of nitrogen in precipitation are rather small at El Verde (0.21 g m^{-2} yr^{-1}; McDowell et al. 1990). There is a large potential for input of nitrogen in throughfall via N-fixation by epiphylls (Edmisten 1970), which could be intercepted by fallen logs on the forest floor, but the biomass of epiphylls should have been severely reduced for several years following the defoliation caused by the hurricane. Thus we do not feel that fluxes of nitrogen in precipitation and throughfall during this study represent an important source of nitrogen for fallen logs following the hurricane. Again, this process is not explicitly simulated in CENTURY. In the model, N input with precipitation is not separated from that derived from decomposition, and both will be equally available for uptake by microbes or vegetation.

Some studies have emphasized the large amount of green leaf litter on the forest floor following hurricanes and the implications of this for subsequent nutrient cycling (Lodge et al. 1991, Steudler et al. 1991, Whigham et al. 1991). By showing that a greater than normal annual amount of litter nutrients are deposited on the forest floor in a single day, these studies proposed that subsequent leaf litter decomposition should have strong effects on patterns of soil nutrient availability, trace gas emissions, and fluxes of nutrients into forest streams. In the short term (2–6 months) this is undoubtedly true. Using CENTURY, we have resolved the potential effects of the individual debris components on productivity and the model indicated that the deposition of leaves alone should fertilize the system slightly. However, because hurricane-generated debris is predominately coarse wood, its decomposition should have a strong negative effect on long-term nutrient availability. In contrast to agricultural systems where nutrient immobilization has transient effects on net primary productivity, CENTURY predicts that wood decomposition can be expected to suppress forest productivity at El Verde for well over a decade.

While a severe hurricane unquestionably represents an extreme case of coarse wood deposition among forested ecosystems (Foster 1988, Foster and Boose 1992, Harmon et al. 1994), we believe that the relationships we have demonstrated for this wet tropical forest site has important implications for understanding patterns of nutrient cycling and productivity in many forested ecosystems. Windstorms, fire, and pest and disease outbreaks are common in most forests (Harmon et al. 1986) and cause large sudden inputs of dead wood to the forest floor. Similarly, slash left over from logging operations can be substantial (Matson and Vitousek 1981). In temperate forests, 2–25% of the soil surface is covered by decomposing wood (Harmon et al. 1986). The occurrence of woody debris in tropical forests is less well studied, but in one wet tropical forest 13–23% of aboveground organic matter, nitrogen, and phosphorus were located in fallen logs (Greenland and Kowal 1960; also see Harmon et al. 1994). The potential for woody debris to regulate nutrient cycling and productivity in forested ecosystems is thus great.

The spatial and temporal pattern of nutrient immobilization associated with decomposing wood should be strongly tied to disturbance regimes (Waide and Lugo 1992). Large-scale intense disturbances, such as hurricanes, should result in system-wide modulation of forest productivity. At our Puerto Rican site, major hurricanes occur on average every 60 yr (Scatena and Larsen 1991). We estimated, using the CENTURY model, that the effects of wood decomposition and accompanying nutrient immobilization on live biomass should persist through much of the interstorm interval. Where disturbances are limited to isolated treefalls, the effects should be correspondingly patchy (Anderson and Swift 1983). Here, the spatial pattern of forest soil nutrient availability is expected to be a palimpsest (a parchment that has been partially erased and written upon many times; Hubbell 1979) of past disturbance events, recording the deposition and decomposition of woody debris for many years. Vitousek and Denslow (1986) tested this idea at a lowland forest site in Costa Rica using uprooted trees 2 months to 2 yr after the trees had fallen. While the predominant effect was that of the root throw zone, where the exposed subsoil has much lower nitrogen and phosphorus availability than other microsites, the amounts of nitrogen in microbial biomass were consistently greater in the crown zones of each of nine treefalls than in the adjacent forest understory. More studies, in a variety of forested sites, are needed to confirm the idea that disturbance regime and the deposition and decomposition of coarse woody debris are critical factors regulating nutrient cycling in forested ecosystems.

Acknowledgements – We give special thanks to our advisory panel: E. Cuevas, A. Lugo, E. Tanner, and P. Vitousek. We thank D. Schaefer and X. Zou for comments on the manuscript and other assistance with the project. Field and laboratory assistance were provided by R. DeLeon, S. Matta, A. L. Mendez, R. Trinidad, and L. M. Babilonia. This research was performed under the National Science Foundation Minority Research Centers of Excellence Program, Cooperative Agreement No. RII-8802961. Additional funding was provided by grant BSR-8811902 from the National Science Foundation to the Terrestrial Ecology Division, Univ. of Puerto Rico, and the International Inst. of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support provided by the Forest Service (U.S. Dept of Agriculture) and the Univ. of Puerto Rico.

References

Aber, J. D. and Melillo, J. M. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. – Can. J. Bot. 60: 2263–2269.

Anderson, J. M. and Swift, M. J. 1983. Decomposition in tropical forests. – In: Sutton, S. L., Whitmore, T. C. and Chadwick, A. C. (eds), Tropical rain forest: ecology and management, Blackwell, Oxford, pp. 287–310.

Bloomfield, J., Vogt, K. A. and Vogt, D. J. 1993. Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. – Plant Soil 150: 233–245.

Bocock, K. L. 1964. Changes in the amounts of dry matter, nitrogen, carbon, and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. – J. Ecol. 52: 273–284.

Brown, S., Lugo, A. E., Silander, S. and Liegel, L. 1983. Research history and opportunities in the Luquillo Experimental Forest. – General Technical Report No. SO-44, U.S. Dept of Agriculture Forest Service, Southern Experiment Station, New Orleans.

Edmisten, J. 1970. Preliminary studies of the nitrogen budget of a tropical rain forest. – In: Odum, H. T. and Pigeon, R. F. (eds), A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. N.T.I.S., Springfield, VA, pp. H-211–215.

Ewel, J. J. and Whitmore, J. L. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. – U.S. Forest Service Research Paper ITF-18. Inst. of Tropical Forestry, Rio Piedras, Puerto Rico.

Foster, D. R. 1988. Species and stand response to catastrophic wind in Central New England. – J. Ecol. 75: 135–151.

– and Boose, E. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. – J. Ecol. 80: 79–98.

Gosz, J. R., Likens, G. E. and Bormann, F. H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. – Ecol. Monogr. 43: 173–191.

Greenland, D. J. and Kowal, J. M. L. 1960. Nutrient content of the moist tropical forest of Ghana. – Plant Soil 12: 154–174.

Groffman, P. M., Zak, D. R., Christensen, S., Mosier, A. and Tiedje, J. M. 1993. Early spring nitrogen dynamics in a temperate forest landscape. – Ecology 74: 1579–1585.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Lattin, J. D., Anderson, N. H., Gregory, S. V., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, Jr., K. and Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. – Rec. Adv. Ecol. Res. 15: 133–302.

– , Whigham, D. F., Sexton, J. and Olmsted, I. 1994. Decomposition and stores of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. – Biotropica (in press).

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. – Science 203: 1299–1309.

Huffacker, L. 1994. Soil survey of the Caribbean National Forest and Luquillo Experimental Forest. – United States Dept of Agriculture Forest Service. (In press).

La Caro, F. L. and Rudd, R. L. 1985. Leaf litter disappearance rates in a Puerto Rico montane rain forest. – Biotropica 17: 269–276.

Lodge, D. J. 1993. Nutrient cycling by fungi in wet tropical forests. – In: Isaac, S., Frankland, J. C., Watling, R. and Whalley, A. J. S. (eds), Aspects of tropical mycology. Cambridge Univ. Press, Cambridge, pp. 37–57.

– , Scatena, F. N., Asbury, C. E. and Sanchez, M. J. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. – Biotropica 23: 336–342.

MacMahon, E. A. 1970. Radiation and the termites at El Verde. – In: Odum, H. T. and Pigeon, R. F. (eds), A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. N.T.I.S., Springfield, VA, pp. E-105–122.

Matson, P. A. and Vitousek, P. M. 1981. Nitrification potentials following clearcutting in the Hoosier National Forest, Indiana. – For. Sci. 27: 781–791.

McDowell, W. H., Gines, C. and Ramos, C. 1990. Influence of seasalt aerosols and long range transport on precipitation chemistry at El Verde, Puerto Rico. – Atmos. Environ. 24: 2813–2821.

Odum, H. T. 1970. Summary, an emerging view of the ecological system of El Verde. – In: Odum, H. T. and Pigeon, R. F. (eds), A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. N.T.I.S., Springfield, VA, pp. I-191-289.

– and Pigeon, R. F. 1970. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. – N.T.I.S., Springfield, VA.

Parrotta, J. A. and Lodge, D. J. 1991. Fine root dynamics in a subtropical wet forest following hurricane disturbance in Puerto Rico. – Biotropica 23: 343–347.

Parton, W. J., Schimel, D. S., Cole, C. V. and Ojima, D. S. 1987. Analysis of factors controlling soil organic matter levels in the Great Plains grasslands. – Soil Sci. Soc. Am. J. 51: 1173–1179.

– , Stewart, J. W. B. and Cole, C. V. 1988. Dynamics of C, N, P, and S in grassland soils: a model. – Biogeochemistry 5: 109–131.

Paul, E. A. and Juma, N. G. 1981. Mineralization and immobilization of soil nitrogen by microorganisms. – Ecol. Bull. (Stockholm) 33: 179–194.

Preston, C. M., Marshall, V. G. and McCullogh, K. 1990. Fate of ^{15}N-labelled fertilizer applied on snow at two forested sites in British Columbia. – Can. J. For. Res. 20: 1583–1592.

Sanford, R. L., Jr., Parton, W. J., Ojima, D. S. and Lodge, D. J. 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: results of simulation modelling. – Biotropica 23: 364–372.

SAS 1987. SAS/STAT Guide for Personal Computers, Version 6 ed. – SAS Inst., Inc., Cary, NC.

Scatena, F. N. and Larsen, M. C. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. – Biotropica 23: 317–323.

Schimel, J. P. and Firestone, M. K. 1989. Nitrogen incorporation and flow through a coniferous forest soil profile. – Soil Sci. Soc. Am. J. 53: 779–784.

Silver, W. L. and Vogt, K. A. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. – J. Ecol. 81: 729–738.
Steudler, P. A., Melillo, J. M., Bowden, R. D., Castro, M. S. and Lugo, A. E. 1991. The effects of natural and human disturbance on soil nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. – Biotropica 23: 356–363.
Stevenson, F. J. 1986. Cycles of soil: carbon, nitrogen, phosphorus, sulfur, micronutrients. – Wiley, New York.
Technicon Instrument Corp. 1985. AutoAnalyzer II. – Tarrytown, NY.
Thompson, W. 1984. Distribution, development, and functioning of mycelial cord systems of decomposer basidiomycetes of the deciduous woodland floor. – In: Jennings, D. H. and Rayner, A. D. M. (eds), The ecology and physiology of the fungal mycelium. Cambridge Univ. Press, Cambridge, pp. 185–214.
Torres, J. 1994. Wood decomposition of *Cyrilla racemiflora* in a tropical montane forest. – Biotropica 26: 124–140.
Turner, J. and Olson, P. R. 1976. Nitrogen relations in a Douglas fir plantation. – Ann. Bot. 40: 1185–1193.
Vitousek, P. M. and Matson, P. A. 1984. Mechanisms of nitrogen retention in forest ecosystems: a field experiment. – Science 225: 51–52.
– and Denslow, J. S. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. – J. Ecol. 74: 1167–1178.
– , Turner, D. R., Parton, W. J. and Sanford, R. L. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms, and models. – Ecology 75: 418–429.
Waide, R. B. and Lugo, A. E. 1992. A research perspective on disturbance and recovery of a tropical montane forest. – In: Goldammer, J. G. (ed.), Tropical forests in transition, Birkhäuser, Basel, pp. 173–190.
Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. – Biotropica 23: 379–385.
– , Voltzow, J., Ackerman, J. D., Fernández, D. S. and Fetcher, N. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. – Ecology 73: 691–694.
Watkinson, S. C. 1984. Morphogenesis of the *Sepula lacrimans* colony in relations to its function in nature. – In: Jennings, D. H. and Rayner, A. D. M. (eds), The ecology and physiology of the fungal mycelium. Cambridge Univ. Press, Cambridge, pp. 165–184.
Weaver, P. L. and Murphy, P. G. 1990. Structure and productivity in Puerto Rico's Luquillo Mountains. – Biotropica 22: 69–82.
Wells, J. M., Hughes, C. and Boddy, L. 1990. The fate of soil-derived phosphorus in mycelial cord systems of *Phanerochaete velutina* and *Phallus impudicus*. – New Phytol. 114: 595–606.
Whigham, D. F., Olmsted, I., Cabrera Cano, E. and Harmon, M. E. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. – Biotropica 23: 434–441.
Wiegert, R. G. 1970. Effects of ionizing radiation on leaf fall, decomposition, and litter microarthropods of montane rain forest. – In: Odum, H. T. and Pigeon, R. F. (eds), A tropical rainforest. National Technical Information Service, Springfield, VA, pp. H89-H100.
Zak, D. R., Groffman, P. M., Pregitzes, K. S., Christensen, S. and Tiedje, J. M. 1990. The vernal dam: plant-microbe competition for nitrogen in northern hardwood forests. – Ecology 71: 651–656.

Appendix

Parameter values used for CENTURY model simulations. See Sanford et al. (1991) for further details on model structure. A. Initial soil organic matter (SOM) and detritus pools.

Pool	C (g m^{-2})	C/N	C/P
Active SOM, surface	30	12	150
Active SOM, soil	100	13	110
Slow SOM	2500	16	320
Passive SOM	4000	8	114
Leaf litter	92	100	1100
Fine root litter	130	100	1100
Fine branch litter	220	84	1366
Large woody debris	2200	155	2260
Dead coarse roots	1200	155	2478

B. Live biomass initial pools and chemistry.

Component	C (g m^{-2})	C/N	C/P	Lignin
Leaves	375	40	700	15
Fine branches	500	84	1366	35
Large wood	7500	155	2260	35
Coarse roots	2700	155	2478	35
Fine roots	450	76	765	35

C. Allocation and turnover.

Component	NPP allocation (%)	Turnover (% month^{-1})
Leaves	34	4.0
Fine branches	11	1.0
Large wood	22	0.1
Coarse roots	8	0.2
Fine roots	25	3.0