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At What Temporal Scales Does Disturbance Affect Belowground Nutrient Pools?[1]

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ABSTRACT

We monitored the effects of both harvesting aboveground biomass and Hurricane Hugo on soil chemical and physical properties, and live and dead root biomass over 6 yr in a subtropical wet forest in Puerto Rico. Our goal was to determine how belowground processes changed at different temporal scales including the immediate period prior to revegetation (9 wk), the intermediate period of initial regrowth (9 mo), and the longer-term reorganization of the vegetation and biogeochemical cycling (6 yr). Harvesting resulted in temporary increases in the availability of exchangeable nutrients, but forest floor and soil nutrient pools had generally returned to pre-harvest values over a 9 wk period. Significant amounts of K moved through the soil over this time period, amounting to 29–46 kg/ha^{-1}, and resulting in a reduction in the size of the exchangeable soil K pool. The hurricane deposited approximately 845 kg/ha^{-1} of forest floor mass and considerable nutrients on the soil surface, and increased soil NO_3-N and exchangeable K pools, but in all cases, pool sizes had returned to pre-hurricane values within 9 mo. Examination of the data on an annual time step over the 6 yr period revealed an increase in soil cation pools and a significant decrease in soil pH. No change in soil organic matter was detected at any time step following the disturbances. Live fine root biomass was dramatically reduced as a result of the hurricane, and was only beginning to show signs of recovery near the end of the 6 yr experiment.

RESUMEN

Se evaluó el efecto de dos perturbaciones: recolección de la biomasa y Huracán Hugo sobre las propiedades físico-químicas del suelo y la biomasa de raíces viva y muerta durante 6 años en un bosque húmedo subtropical en Puerto Rico. Nuestro objetivo era determinar el cambio en los procesos bajo el suelo a distintas escalas temporales: periodo inmediatamente antes de la revegatación (9 semanas), periodo de crecimiento inicial (9 meses) y biogeoquímicos (6 años). La recolección de la biomasa implica un aumento inicial en la disponibilidad de nutrientes intercambiables pero los depósitos de nutrientes en el suelo vuelven a valores pre-recolección en un periodo de 9 semanas. Hasta 29–46 kg·ha^{-1} de potasio se suceden en el suelo durante este periodo, resultando en uno reducción de la cantidad de potasio intercambiable en el suelo. El huracán depositó aproximadamente 845 kg·ha^{-1} de biomasa en el suelo y una cantidad de nutreintes muy considerable. También se produjo un incremento de N03-N y de los depósitos intercambiables de potasio pero en todos los casos los depósitos de nutrientes volvieron a niveles pre-huracán en 9 meses. El examen anual de los datos durante el periodo de 6 años reveló un incremento en los depósitos de cationes en el suelo y una disminución del pH. A nivel anual no se detectaron cambios en los niveles de materia orgńica del suelo. La biomasa de pequeñas raíces vivas se redujo de manera dramática como resultado del huracán y empezó a mostrar signos de recuperación al final de los 6 años de duración del experimento.

Key words: forest floor; harvesting; hurricane; nutrient availability; root biomass; soil organic matter; tropical forest.

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SEVERAL CHANGES OCCUR FOLLOWING DISTURBANCE to the aboveground biomass in tropical forests that may lead to nutrient losses from the soil. Canopy removal raises soil temperature, and increases decomposition and nutrient mineralization rates. Decreased plant nutrient and water uptake lead to greater nutrient concentrations in the soil and soil solution, enhancing the potential for leaching losses (Uhl & Jordan 1984, Matson *et al.* 1987). On the other hand, rapid plant regrowth through stump and root sprouting, and recolonization from seedlings adapted to germinate under high light or disturbed soil conditions (see review by Clark 1990) may reduce nutrient losses. Furthermore, several nutrient conservation mechanisms may operate in the soil including the ability of microbial communities to rapidly immobilize nutrients (Vitousek & Matson 1984, Luziao *et al.* 1992, Henrot & Robertson 1994), and the augmentation of cation exchange capacity through increased soil organic matter (SOM) content, which has a high affinity for plant nutrient cations per unit volume (Sanchez 1976, Tiessen *et al.* 1994).

Processes that result in nutrient accumulation or loss from ecosystems occur simultaneously, but not necessarily at the same rates or temporal scales. For example, a rapid reduction or cessation in root activity might be expected when the canopy is destroyed, reducing the uptake of nutrients from the soil. Conversely, nutrient resupply to the soil through decomposition of organic matter may take months or years (Vogt *et al.* 1986, Bloomfield *et al.* 1993, Silver & Vogt 1993), although mobile elements such as K may be leached out relatively rapidly, on the scale of days or weeks (Ewel *et al.* 1981). These interacting processes, occurring simultaneously and at varying rates, add considerable complexity to the interpretation of patterns in nutrient cycling following disturbance.

In this study, we were interested in determining the effects of disturbances of different sizes and intensities on nutrient availability and belowground processes in a subtropical wet forest in Puerto Rico. We addressed the following three questions to estimate the temporal scales most appropriate for nutrient dynamics following disturbance. (1) How does soil nutrient availability change following severe disturbance to the aboveground biomass? (2) At what temporal scale do these changes occur relative to secondary succession? (3) How long does it take for tropical forest soils and belowground processes to reorganize following disturbance?

In the context of nutrient cycling, we consider a "reorganized" ecosystem as one where nutrient pools are not significantly different from pre-disturbance values. Nutrients measured included total Ca, Mg, K, P, and N in the forest floor, and exchangeable Ca, Mg, K, extractable P, NO_3-N, and NH_4-N in the soil. Changes in live and dead root biomass were also monitored, as were the changes in SOM content, pH, and exchangeable Al.

STUDY SITE AND EXPERIMENTAL DESIGN

The study site was located in the tabonuco (*Dacryodes excelsa* Vahl; Burseraceae) forest zone of the Bisley Research Area in the Luquillo Experimental Forest (LEF), Puerto Rico (18° 18′ N, 65° 50′ W). The area is the location of the Long Term Ecological Research project studying the effects of disturbance on ecosystem structure and function (Walker *et al.* 1991, Waide & Lugo 1992). The Bisley Research Area is classified as subtropical wet forest (sensu Holdridge *et al.* 1971) and occurs at approximately 250–450 m above sea level. The forest receives approximately 3500 mm of rain per year with most months receiving at least 200 mm (Scatena 1989).

The parent material underlying the watersheds is volcanoclastic sandstone rich in ferromagnesium minerals, which weathers to a soil high in clay, free Fe and Al, but low in silica and free bases (Bonnet 1939, Scatena 1989). Soils are mapped as part of the Humatus-Zarzal-Cristal complex (Johnston 1992), and are classified as clayey, mixed isothermic, Epiaquic Tropohumults or Palehumults (Ultisols) (Beinroth 1982). The dominant silicate clays are degraded illites which have lost a large portion of K (Jones *et al.* 1982). Silver *et al.* (1994) reported detailed analyses of soil chemical and physical properties, and spatial patterns in nutrient availability at a watershed scale for the Bisley Watersheds.

The study was originally designed as a controlled experiment to (1) determine if soil nutrient losses occur over short time periods (within the first few days or weeks) following disturbance to aboveground biomass, and (2) monitor changes in nutrient cycling over longer time intervals (months to years). In late June 1989 two 32 × 32 m gaps were created in the Bisley Research Area by carefully removing all aboveground biomass from two experimental plots (Scatena et al. 1993, Silver & Vogt 1993). The size of the areas disturbed was equivalent to medium or large landslides in the Luquillo Forest (Lugo & Scatena 1995); this allowed for the degree of sample replication necessary for an intensive sampling regime, but limited us to only 2 treatment replications. One experimental plot, hereafter referred to as the lower plot, was located just below the monitored portion of the Bisley Watershed 2. The other experimental plot, referred to here as the upper plot, was located adjacent to Bisley Watershed 1 and approximately 400 m from the lower plot. Slope, aspect, geomorphology, and forest structure were similar on the two experimental plots. The initial pre-disturbance nutrient capital (exchangeable soil nutrients + forest floor nutrients + nutrients in plant biomass) differed between the two plots, but were well within the inherent spatial heterogeneity of nutrient pools of the 13 ha Bisley watershed ecosystem (Scatena *et al.* 1993, Silver *et al.* 1994), and are used here to test process-level questions within sites and over time. Several authors have reported on tropical forest soil nutrients which vary significantly over relatively small spatial scales (Ewel *et al.* 1981, 1991; Proctor *et al.* 1983; Silver *et al.* 1994), suggesting that the heterogeneity of soil chemical properties is a reflection of the considerable biotic and functional diversity expressed in these ecosystems due to both natural processes and human use.

Unmanipulated control sites were located in intact forest near the plots, but in areas which were not affected by the harvest or by run-off from the harvested plots. Because of the highly dissected topography of the area, it was not possible to establish 32 × 32 m plots in the nearby forest and control for factors such as slope and aspect which have been shown to have a very strong influence on biogeochemical cycling in this ecosystem (Scatena *et al.* 1993, Silver *et al.* 1994). Instead, we stratified our sampling in two 16 × 32 m forest areas (one near each harvested plot) and pooled the data into one unreplicated control treatment, allowing us to control for slope and aspect, and maintain a similar sample size and soil sampling density per unit area as in the experimental plots.

On 17–18 September 1989 Hurricane Hugo swept through the LEF imposing a landscape level disturbance on the Bisley Watersheds (Scatena & Larsen 1991). The hurricane devastated the forest control plots, but resulted in no mortality of the regeneration in the harvested plots where the vegetation had grown to <1 m in height. Percent cover of plants on the ground, and the number of live sprouts on stumps all increased during the first 3 mo following Hugo (Silver 1992). The few trees that were blown into the harvested plots by the storm were removed within 2 wk of the hurricane, such that the ultimate impact of the storm on these plots was the deposition of forest floor and a reduction of the edge effect. At the time of Hugo, we had completed eight of the initial twelve proposed sampling periods, and were able to document the short-term changes in belowground processes on the scale of days (N = 65) or weeks (N = 9). Having done this, we embarked on a new study to document the effects of a hurricane on gap versus forest environments, and to follow reorganization over time. The "control forest" plots became "forest plots" with pre- and post hurricane samples. After the hurricane there were no intact areas that could serve as reference areas (*i.e.* controls) for evaluating hurricane impacts.

SAMPLING SCHEDULE.—We measured a total of 35 plant and soil parameters over time from the harvested plots and the forest plots (Table 1). Samples were collected at three relative time scales: the period prior to substantial regrowth following harvesting (65 d); the initial period of revegetation following harvesting and the hurricane (9–12 mo); and the longer-term reorganization of the vegetation and nutrient cycling processes (6 yr). The time between sample collections increased as the time interval increased. Not all parameters were measured during each sampling period. Parameters where change resulted from decomposition or growth, including root biomass, forest floor, and SOM were not expected to vary significantly over short time scales (*i.e.*, 5–10 d) at the given sampling intensity, so some of the initial sampling periods were omitted. Bulk density did not vary significantly during the first 5 mo of the study, nor did it differ from pre-harvest values so sampling was discontinued and a mean value was used. Forest floor and bulk density were sampled only in the harvested plots since other studies were characterizing these or related parameters in detail nearby (Silver *et al.* 1994, Scatena *et al.* in press). Forest floor was measured prior to harvesting and for 1 yr following the harvest, at which time the canopy closed approximately 1.5 m above the ground, making quantitative sampling difficult without creating more disturbance. Mineral N was also sampled during the first year of the study.

Initial soil cation and pH samples were collected prior to the beginning of the experiment from the intact, forested plots in June 1988 (lower plot) and March 1989 (upper plot). It is generally assumed that these soil properties are fairly stable over time periods of several months in an undisturbed aseasonal environment. However, to avoid potential bias from comparing soil processes at

TABLE 1. *Sampling schedule for soil chemical and physical properties and root biomass. Sampling can be divided into 3 intervals: Short-term (65 d), Intermediate-term (9 mo), and Long-term (6 yr). All samples for a given date were collected within 1 wk of that date, but each category was collected within 1 day (i.e., roots, forest floor, or soils). Roots include live, dead, and total (live + dead) fine root biomass. Forest floor and root samples were all analyzed for biomass, Ca, Mg, K, Al, P, and N content.*

				Soil characteristics									
	Days following disturbance	Roots	Forest floor	Ca	Mg	K	Al	pH	P	SOM	NO_3-N	NH_4-N	Bulk density
SHORT	Precut (1988–1989)	X	X	X	X	X	X	X			X	X	X
	28 June 1989: 0			X	X	X	X	X	X		X	X	X
	6	X		X	X	X	X	X	X	X	X	X	
	11			X	X	X	X	X	X	X	X	X	
	16	X		X	X	X	X	X	X	X	X	X	
	26	X	X						X	X	X	X	X
INTERMEDIATE	46	X		X	X	X	X	X	X	X	X	X	
	65	X	X	X	X	X	X	X	X		X	X	X
	(Hurricane Hugo)												
	106	X	X	X	X	X	X	X	X		X	X	X
	146	X	X	X	X	X	X	X	X	X	X	X	X
LONG	257	X	X	X	X	X	X	X	X	X	X	X	
	352	X	X	X	X	X	X	X	X		X	X	
	592	X		X	X	X	X	X	X	X			
	723	X		X	X	X	X	X					
	1083			X	X	X	X	X	X	X			
	1224	X											
	1453	X		X	X	X	X	X	X	X			
	1818	X		X	X	X	X	X	X	X			

largely contrasting time scales (e.g., 9–12 mo versus 65 d) we compared pre-harvest soil cations and pH only to the immediate post-harvest samples (June 28 1989) at the shorter temporal scale, and then to the larger data set at the annual time step. Mineral N, forest floor, and root samples were collected 1 wk prior to the beginning of the harvest in June 1989. Initial samples of soil P were extracted fresh from the field and yielded values below detection of the analytical instrumentation, and therefore are not reported here. We refer to the day the last tree was felled in the harvested plots (28 June 1989) as the start of the experiment.

MATERIALS AND METHODS

SAMPLING AND ANALYSES OF FOREST FLOOR AND SOILS.—Forest floor was sampled using a 15 × 15 cm template (inside area) at 13 systematically located sites, spaced along the contour and along elevational bands within the harvested plots. These samples contained recent litter and humified organic matter. Samples were dried at 70° C, weighed, ground in a Wiley mill and redried. Ground samples were digested in Li_2SO_4 (Parkinson & Allen 1975), and analyzed for Ca, Mg, K, Al, and P on a Thermal-Jarrel Ash ICP, and on a Technicon auto analyzer for N. Standard reference material (citrus leaves), procedural blanks, and replicate samples were run for quality assessment at the rate of 1 per 34 samples, and yielded results within 5 percent of the expected values.

Soil was collected from 15 random sites stratified by latitudinal and longitudinal bands in each harvested plot using a 2.5 cm diameter corer. Multiple core samples were taken from both the 0–10 cm and 10–35 cm depths, and placed in separate plastic bags yielding 15 aggregate samples per depth per plot ($N = 60$ samples/date). Few changes occurred in the 10–35 cm depth, so we report only data from the 0–10 cm depth here. In the control forest, 14 aggregate samples were collected using the same technique as the treatment plots (seven aggregate samples per control forest plot; four aggregate samples were collected in the control area prior to 13 August 1989).

Samples were stored at 4°C until they were extracted, generally within 24 h of collection. Approximately 4 g of fresh soil was extracted with approximately 55 ml 1*M*-NH_4Cl using a vertical vacuum extractor (Johnson 1989) and analyzed for Ca, Mg, K, and Al on a Thermal-Jarrell Ash ICP. Soil samples of approximately 10 g were extracted immediately upon collection with 2*M*-KCl and analyzed for NO_3-N and NH_4-N on a Technicon auto analyzer (Keeney & Nelson 1982). Soil pH was determined in a 10: 1 slurry of deionized H_20 (McLean 1982). To measure extractable P and SOM, five random samples were selected from each harvested plot and from the control area. Samples were air-dried and ground to pass through a 2 mm sieve prior to extraction. For P, approximately 5 g of soil were extracted with 50 ml of a modified Olsen solution (0.01 *M* NH_4-0.01 *M* EDTA-0.25 *M* $NaHCO_3$) using a vertical vacuum extractor (Wilde *et al.* 1979, Hunter 1982). Samples were analyzed on a DCP Spectraspan V spectrophotometer. Soil organic matter was determined in approximately 0.25 g samples using the Walkley-Black procedure (Nelson & Sommers 1982). Blanks, replicate samples and a reference soil were included in all extract runs for quality control and yielded results within 5 percent of the expected values. Subsamples of all soils were dried at 105°C to determine moisture content. All data reported here is on an oven dry soil basis.

Bulk density was sampled with a known-volume bulk density corer at eight systematically located sites along the contour and elevational bands within the harvested plots. Samples were weighed fresh, dried at 105°C to a constant weight and reweighed for bulk density determinations.

Root biomass.—Roots were sampled with a root corer of 4.1 cm inside diameter using standard techniques (Vogt & Perrson 1991, Silver & Vogt 1993). In each harvested plot, root cores (0–10 cm depth) were taken from nine randomly located sites stratified by five 32 × 8 m transects parallel to the contour during each sampling period. Care was taken to sample at least 4 m in from the edge of the plots. In the control forest, four sites (two per plot) were sampled 8 m apart. Cores were stored at 4° C until processed.

Roots were sorted by size (<2 mm and 2–5 mm) and by dead and live categories. Only data on fine roots <2 mm in size are presented here. Sorted roots were dried at 70° C and weighed. Chemical analyses were performed on live and dead roots during the first year of the study, and are reported in Silver and Vogt (1993).

Litterfall.—To estimate the short-term changes in litterfall carbon and nutrient inputs associated with disturbance, litterfall was measured in the gaps for 2 mo prior to Hurricane Hugo. Nine 25 × 25 cm litterfall baskets were randomly placed approximately 10 cm above the soil surface in each gap. Fine litterfall, consisting of leaves, twigs, fruits, flowers, and miscellaneous material was collected from each basket at 2 wk intervals prior to the hurricane. Litterfall was dried at 70°C and weighed. To estimate nutrient inputs via litterfall, we used nutrient concentrations taken from 60 baskets collected every 2 wk in the Bisley Watersheds during the same sampling periods and using the same sampling protocol (Scatena *et al.*, in press). Concentrations were multiplied by mass to obtain estimates of nutrient inputs from litterfall.

Vegetation.—Aboveground biomass and nutrient content were sampled in the harvested plots 1 yr from the start of the experiment. Ten randomly located 1 × 1 m quadrats were established in each of the harvested plots. Percent cover of the ground (0–100%) was determined by visual estimation, and then all live aboveground biomass was harvested. Plant material was dried at 70°C, weighed to determine mass and ground using a Wiley mill. Samples were digested in $LiSO_4$ (Parkinson & Allen 1975), and analyzed for Ca, Mg, K, and P on an ICP and for N on an auto-analyzer. Standard reference material (citrus leaves), procedural blanks, and replicate samples were run for quality assessment at the rate of 1 per 34 samples, and yielded results within 5 percent of the expected values.

Statistical analyses.—Statistical analyses were performed using Systat 5.0 (Wilkinson 1990). Data were log transformed when appropriate to meet the assumptions of analysis of variance (ANOVA). Residuals from all analyses were checked for normality and homogeneity of variances (Steel & Torrie 1980). ANOVA's were performed (using a factorial design) to determine: (1) if live and dead root biomass, forest floor mass and nutrients (harvested plots only), or soil nutrients changed significantly over time within the harvest-

TABLE 2. *Comparison of exchangeable cations (kg ha^{-1}), mineral N (kg ha^{-1}), and pH in top 10 cm of mineral soil prior to cutting and immediately following the removal of the aboveground biomass in two experimental plots in the Bisley Research Watersheds, PR. Lower case letters indicate statistically significant differences between dates and within plots. Upper case letters indicate statistically significant differences between plots and within dates. Significance was determined as* P < *0.05 unless otherwise noted. Values are means* ± *1 SE.*

Soil property	Pre-harvest lower plot	Post-harvest lower plot	Pre-harvest upper plot	Post-harvest upper plot
Ca	81.4 (15.4)aA	143.7 (19.5)bA	51.9 (10.3)B	66.6 (11.5)B
Mg	90.5 (12.3)aA	116.1 (9.0)bA	53.7 (6.7)B	58.8 (5.3)B
K	12.1 (3.2)a	43.9 (7.3)b	19.3 (5.7)a	35.1 (13.7)b
NO_3-N	0.6 (0.1)a	1.1 (0.1)b*	0.4 (0.1)a	1.1 (0.1)b*
NH_4-N	3.2 (0.2)aA	7.4 (0.7)bA	2.3 (0.2)aB	1.5 (0.3)bB
Al	169.8 (13.9)a	119.2 (12.9)b	152.3 (9.2)	145.5 (12.7)
pH	4.9 (0.2)A	5.0 (0.2)A	5.0 (0.2)aB	4.8 (0.2)bB

* $P = 0.07$.

ed plots and within the control forest (TIME); (2) if live and dead root biomass, forest floor mass and nutrients (harvested plots only), or soil nutrients differed between the two harvested plots and/or between the harvested plots and the control forest (LOCALE); and (3) if there were significant interactions between time and locale in live and dead root biomass, forest floor mass and nutrients, or soil nutrients (TIME·LOCALE). Regression analyses were conducted to determine if plant and soil parameters were correlated. Significance was determined as $P < 0.05$ unless otherwise noted. Mean values reported in the text are followed by standard errors.

RESULTS

Response to biomass removal: 65 days.—Soil pools of exchangeable Ca, Mg, and K were significantly greater in the lower plot at the end of the felling period relative to pre-harvest samples (Table 2). Similar trends occurred in the upper plot soil, but only exchangeable K pools increased significantly. Exchangeable Al decreased significantly in the lower plot after felling (Table 2). Nitrate-N increased significantly in both plots immediately following the harvest relative to samples collected 1 wk earlier, while NH_4-N increased significantly in the lower plot, but decreased significantly in the upper plot (Table 2). Nitrate-N did not change during the next 65 d (Fig. 1). Ammonium-N decreased in the lower plot by day 6 following the harvest to levels that were not significantly different from the upper plot or control.

The harvesting was done carefully to minimize soil disturbance. Most of the trees were felled with their crowns outside the plots and all harvest debris was removed. One month following the harvest, there were no statistically significant differences in forest floor mass compared to samples collected 1 wk prior to the harvest (Table 3). Small and significant declines in forest floor K (0.3 and 0.7 g m^{-2} in the lower and upper plots respectively) and P content (0.2 g m^{-2} in the upper plot) occurred during the first month following the harvest due to declines in forest floor K and P concentrations. Litterfall into the plots was low following the harvest (mean = 1.2 g m^2 day^{-1}). This represented a reduction of 85 and 78 percent in the lower and upper plots, respectively, of the litterfall in the nearby intact forest for the same period (Scatena *et al.* in press).

Within 65 d after the harvest, exchangeable soil K pools had declined significantly by 34 and 25 kg ha^{-1} in the lower and upper plots respectively, representing a loss of 71–78 percent since the start of the experiment (Fig. 1). Furthermore, when the input to the soil from root mortality, the change in forest floor nutrient content, and the amount added in aboveground litterfall are considered, there was a loss of 105 percent of the initial exchangeable soil K pool in the lower plot (46 kg ha^{-1} K) and 83 percent of the initial exchangeable soil K pool in the upper plot (29 kg ha^{-1} K) over this period (Fig. 2). Pools of exchangeable Ca and Mg followed similar trends, but results were only statistically significant for Mg in the lower plot (Fig. 1). Extractable soil P increased by approximately 3 kg ha^{-1} in the harvest plots during the first 6 wk, but returned to values not significantly different from the start of the experiment by day 65 (Fig. 1).

Soil pH decreased significantly by an average of 0.6 pH units 5 d following the harvest in both the gaps and in the control forest, and then grad-

TABLE 3. *Mean forest floor mass and nutrient content (g m^{-2}) before and after harvesting and Hurricane Hugo in the Bisley Research Watersheds (± 1 SE). Different lower case letters indicate statistically significant differences among dates and within plots (P < 0.05). There were no statistically significant differences between plots within dates.*

Days after harvest	Mass	Ca	Mg	K	*P*	*N*
			Lower Plot			
Precut (9 June 1989)	1040 (471)ab	6.6 (2.4)ab	1.6 (0.7)a	1.2 (0.6)ab	0.4 (0.1)ac	12.3 (4.4)abc
32	1359 (311)ab	10.6 (2.6)ab	3.2 (1.1)a	0.9 (0.8)a	0.7 (0.2)ab	20.6 (5.4)ab
61	655 (146)ab	4.8 (1.4)ab	0.3 (0.2)b	0.0 (0.0)a	0.3 (0.1)abc	7.9 (2.0)a
106	1929 (541)a	12.2 (4.1)a	2.9 (1.2)a	2.8 (1.2)b	1.2 (0.5)b	24.8 (7.0)b
146	1393 (355)a	10.6 (3.2)a	1.8 (0.6)a	1.2 (0.6)b	0.9 (0.2)ab	21.6 (6.1)ab
257	1188 (396)ab	8.9 (3.1)ab	2.7 (1.0)a	0.0 (0.0)a	0.7 (0.3)abc	16.2 (6.0)ac
352	595 (179)b	4.6 (1.4)b	1.0 (0.2)a	0.4 (0.2)a	0.4 (0.1)c	8.4 (2.4)c
			Upper Plot			
Precut (9 June 1989)	682 (89)ab	3.4 (0.5)ab	0.6 (0.1)a	0.7 (0.1)ab	0.3 (0.0)ac	8.7 (0.8)abc
32	935 (144)ab	4.3 (0.8)ab	1.3 (0.3)a	0.0 (0.0)a	0.1 (0.1)ab	11.4 (1.7)ab
61	1119 (158)ab	4.9 (0.7)ab	0.4 (0.1)b	0.3 (0.2)a	0.4 (0.1)abc	12.3 (1.7)a
106	1536 (254)a	8.2 (1.5)a	1.8 (0.4)a	3.4 (1.0)b	0.8 (0.1)b	18.4 (3.0)b
146	1911 (471)a	12.0 (4.3)a	2.0 (0.6)a	4.7 (2.1)b	1.0 (0.3)ab	22.6 (7.0)ab
257	1383 (403)ab	9.4 (2.7)ab	2.0 (0.5)a	1.0 (0.6)a	0.7 (0.2)abc	14.2 (3.5)ac
352	1056 (398)b	7.9 (3.7)b	1.8 (0.9)a	0.5 (0.2)a	0.5 (0.2)c	10.6 (4.0)c

ually increased over the next 20 d (Fig. 1). Re-analysis of the same soils within 48 h on a different pH meter and with a different clean water source assured us that we had not made a systematic error in the analysis of these samples. In the harvested plots exchangeable Al increased significantly 5–10 d following the harvest, then dropped by day 16 to levels not significantly different from day 1 (Fig. 1). A similar, but non-significant trend occurred for exchangeable Al in the control forest.

RESPONSE TO HURRICANE HUGO: NINE MONTHS.—The hurricane deposited a large amount of litter on the soil surface in the harvested plots and adjacent forest. There were no significant differences in the amount of mass and nutrients added to the gaps as a result of Hurricane Hugo so the data from the two gaps were pooled for analyses. Forest floor mass approximately doubled in the gaps as a result of the hurricane, increasing the mean mass from 887 ±115 kg ha^{-1} to 1732 ± 296 kg ha^{-1} and adding a mean value of 52, 19, 30, 6, and 116 kg ha^{-1} of Ca, Mg, K, P, and N respectively. These values represent between 58–116 percent of the exchangeable soil Ca pool, 22–41 percent of the exchangeable soil Mg pool, 300 percent of the exchangeable soil K pool, and 100–150 percent of the extractable soil P pool prior to the hurricane. By June 1990, 9 mo following the hurricane, forest floor mass and nutrient content had returned to levels not significantly different from pre-Hugo values (Table 3, Fig. 2).

Within 4 wk of the hurricane, exchangeable soil K pools increased by 37, 14, and 35 kg ha^{-1} in the lower plot, upper plot, and forest plot, respectively. Nine mo later, soil K pools had returned to levels not significantly different from the start of the experiment prior to Hurricane Hugo. Soil P pools increased slightly but significantly until November 1989, 146 d after the start of the experiment and 64 d following the hurricane, and then returned to preharvest levels. Soil organic matter content did not change significantly during the first year of the experiment. There was significantly more SOM in the upper plot (6.92 ± 0.23%, N = 35) and forest (7.90 ± 0.39%, N = 30) than in the lower plot (5.68 ± 0.18%, N = 35). Soil P was significantly correlated with SOM in the gaps and forest plots (r^2 = 0.62, $P < 0.001$, N = 33) during this time period. Mineral N exhibited dramatic changes following Hurricane Hugo. Nitrate-N increased significantly by a factor of 2–3 in the gaps and by a factor of 8 in the forest following the hurricane (Fig. 1). Ammonium-N pools fluctuated over time, increasing significantly in all plots during the first 64 d following the hurricane, then declining significantly after 175 d (257 d from the start of the experiment).

There were no statistically significant effects of the harvest or the hurricane on gravimetric soil

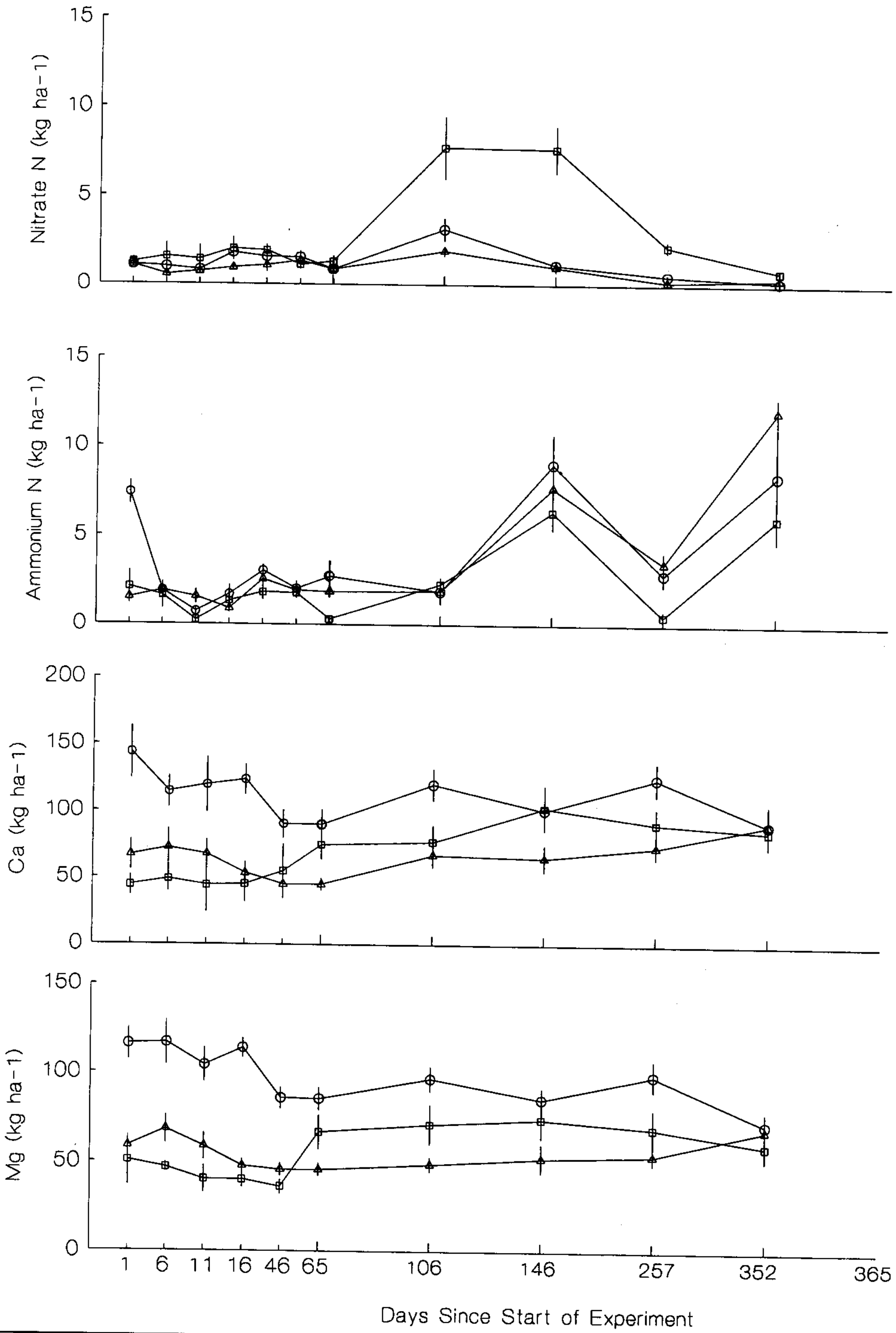

FIGURE 1. Soil nutrient pools (kg ha^{-1}) and soil pH during the first year following harvesting and Hurricane Hugo in the Bisley Research Watersheds, Puerto Rico. Day 1 is the day the last tree was felled in the harvested plots (29 June 1989); Hurricane Hugo struck on day 82. The X axis is scaled for shorter term (1–65 d) and intermediate term (66–365 d) sampling intervals (see text). ○ = lower harvested plot; △ = upper harvested plot; □ = control/forested plots. Vertical lines are standard errors. Samples for pH on day 106 from the lower harvested plot were lost due to equipment failure associated with the hurricane.

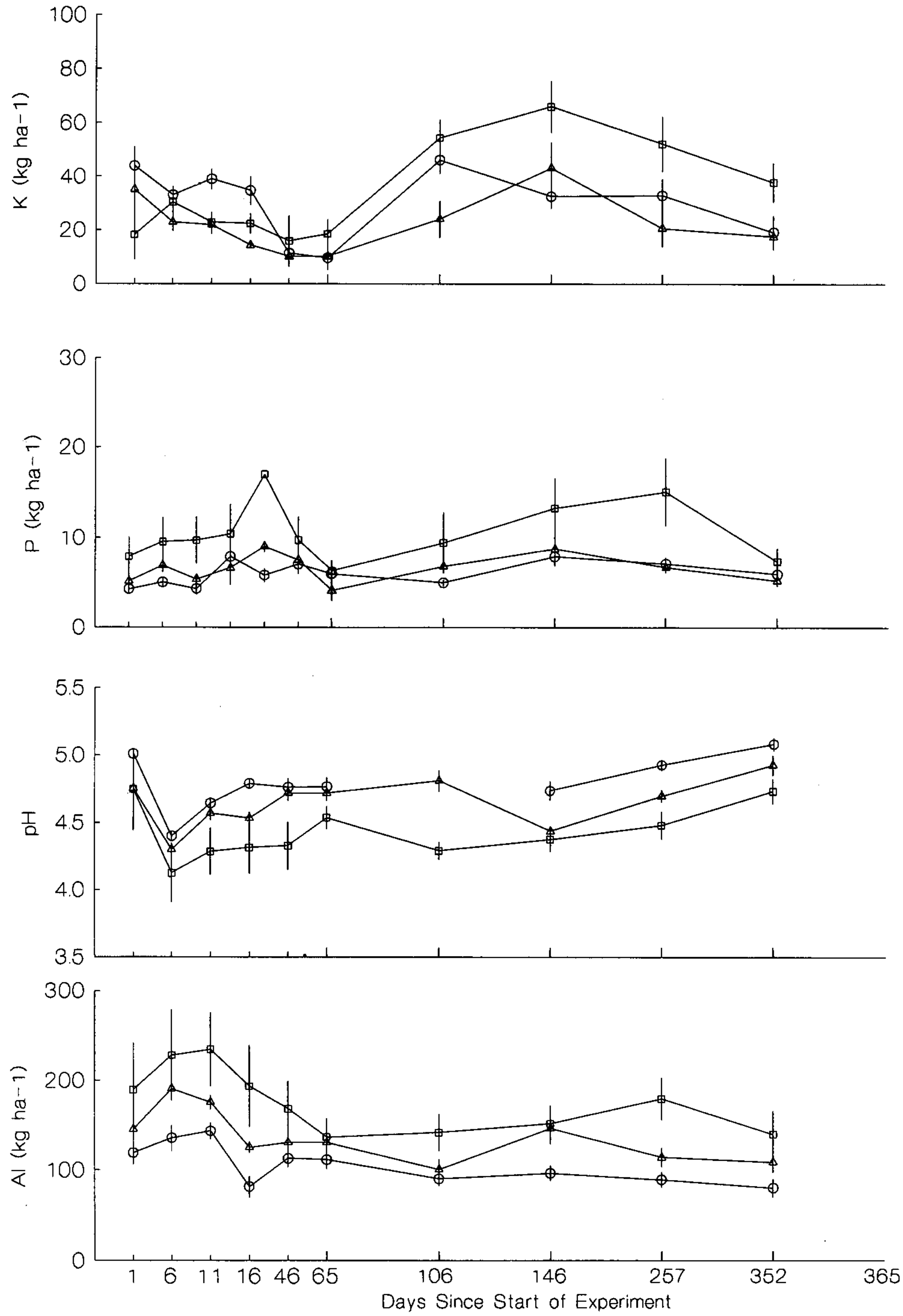

FIGURE 1. Continued.

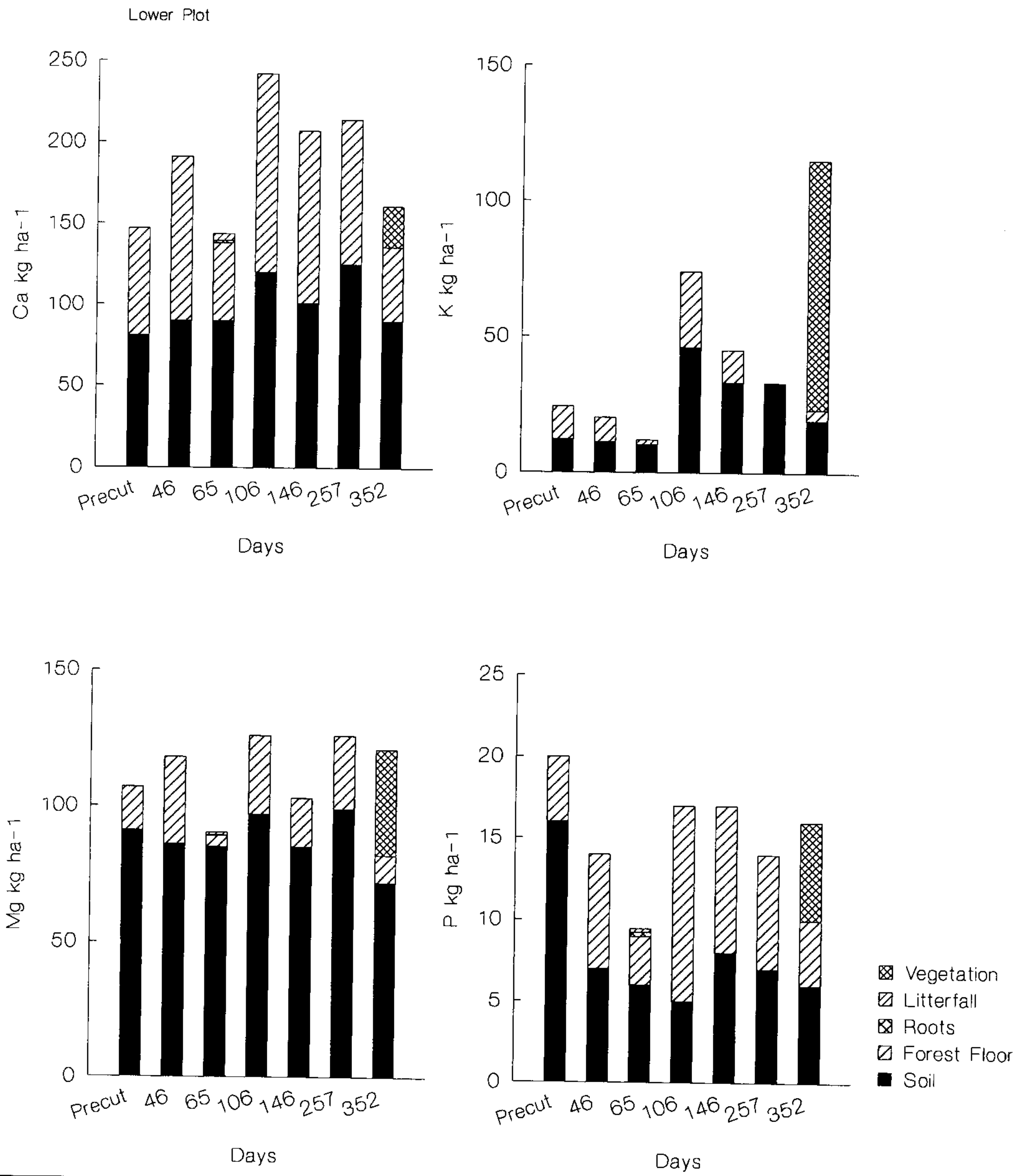

FIGURE 2. The distribution of plant and soil nutrient pools (kg ha^{-1}) during the first year following harvesting and Hurricane Hugo in the Bisley Research Watersheds, Puerto Rico. Litterfall and root nutrient inputs are shown for the period culminating on day 65. Nutrients stored in the 1 yr old regrowth are shown for day 352.

moisture. Soil moisture differed significantly among the harvested and forest plots in the following order: upper plot (49 ± 0.5%, N = 165) > lower plot (46 ± 0.3%, N = 164) > forest (44 ± 0.3%, N = 104).

The harvested plots each accumulated approximately 5 ± 1 Mg ha^{-1} of aboveground biomass by the end of the first year of the experiment. There were some interesting patterns in the distribution of labile nutrients between plant tissues and soil exchange sites. Pools of exchangeable Ca and Mg were greater in the soil than the amounts of these nutrients stored in the vegetation (Fig. 2). The vegetation in the lower plot contained approximately four times as much K (92 ±20 kg ha^{-1}) as the exchangeable soil pool (19 ± 6 kg

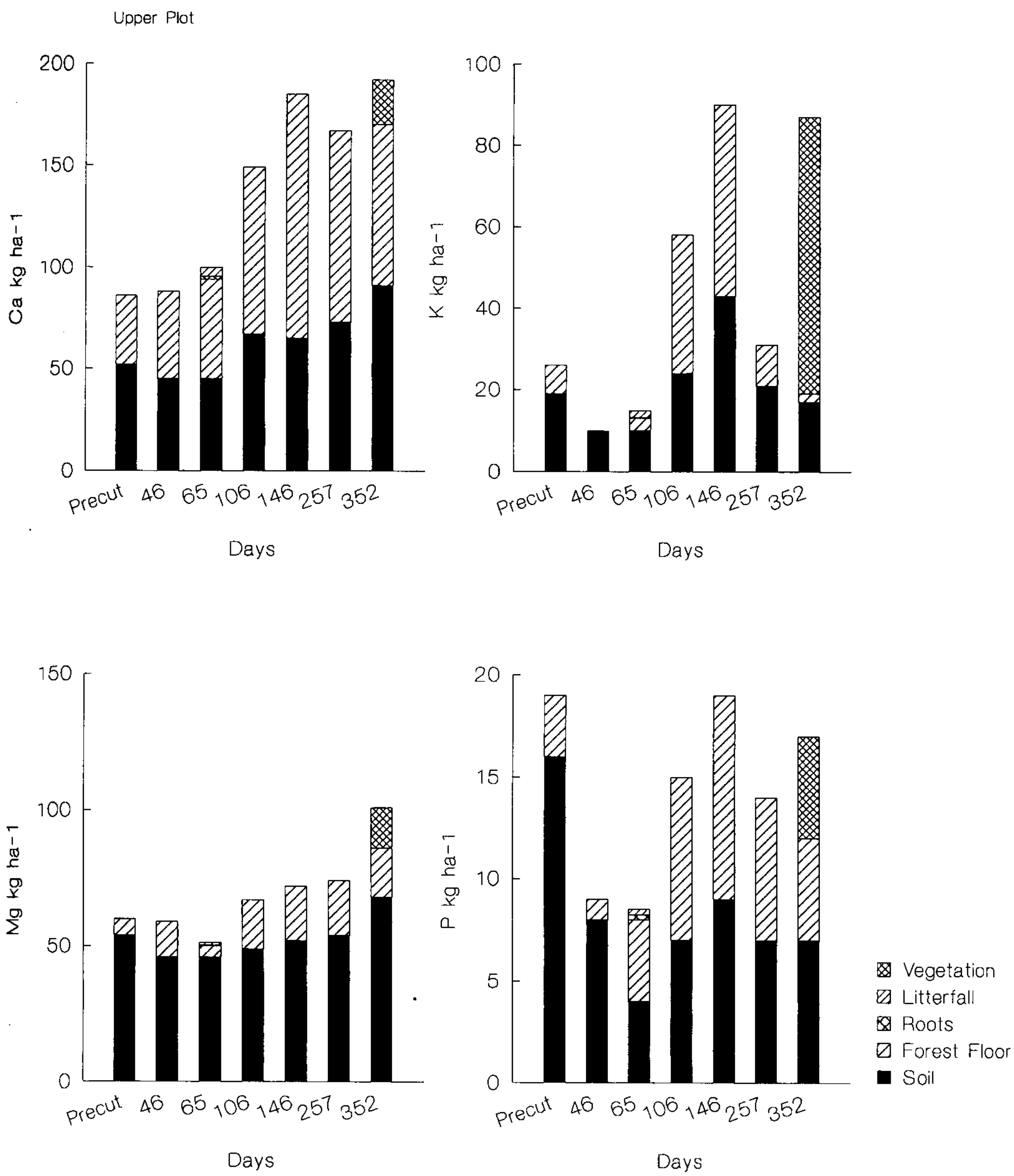

FIGURE 2. Continued.

ha^{-1}) (Fig. 2). In the upper plot, exchangeable K in the soil was 17 ± 4 kg ha^{-1} at the end of the first year while the vegetation stored 68 ± 11 kg ha^{-1}. Labile P was relatively evenly distributed between plants and soil in the harvest plots at the end of the first year (Fig. 2).

RECOVERY FROM DISTURBANCE: THE FIRST SIX YEARS.— Soil exchangeable Ca, Mg, and K pools reached a low point in 1990 following the hurricane, and were significantly greater during 1991–1994 (Fig. 3). Soil P pools peaked from 1991–1993 in the harvested plots, but by 1994 were not significantly different from 1989 values (Fig. 3). The extractable P pool in the forest soils did not change significantly at an annual time step over the 6 yr period. Soil P in all plots was significantly correlated with SOM at this level of resolution (r^2 = 0.55, P <

0.001, $N = 59$). Soil organic matter averaged 6–7 percent and did not vary significantly within or among plots over the six year period using an annual time step.

Soil pH decreased significantly in all plots after 1992, resulting in 1994 values that were significantly lower than 1988 soil pH in the gaps, but not different from 1989 values in the forest (Fig. 3). Exchangeable Al increased significantly after the hurricane in 1990, decreased significantly in 1991, then generally increased to levels similar to 1988–1989 values (Fig. 3). Soil moisture also changed significantly at this time step, although it is unclear how much soil moisture is linked to specific rainfall events versus long term soil processes in this relatively wet environment. In June 1992 soils were significantly wetter in the harvested plots (52–53 ± 1%) than other years, and in June 1994, the year of a significant drought in Puerto Rico, were significantly drier than previous years (44 ± 1%, 48 ± 2%, 41 ± 1% in the lower, upper, and forest plots, respectively).

Silver and Vogt (1993) reported a significant decline in live root biomass following the harvest and following Hurricane Hugo. Expanding the study to 6 yr, we found that fine live root biomass was still significantly reduced until 1993 in the upper plot, and had not fully recovered in the lower plot by 1994 (Fig. 4). Fine root necromass did not change over time in either the gaps or the forest sites (Fig. 4).

DISCUSSION

CHANGES IN NUTRIENT POOLS OVER DAYS AND WEEKS.—We hypothesized that soil nutrient losses would occur rapidly following disturbance to the aboveground biomass, over a period of days and weeks, due to rapid mineralization of nutrients from organic matter and high leaching losses in the warm, wet environment. Contrary to this hypothesis, most soil nutrients did not decrease dramatically during the first 9 wk of the study. The harvest resulted in a short-term increase in exchangeable nutrients in the soil (Table 2), which subsequently returned to levels not significantly different from pre-harvest values within 65 d. Nutrient additions from forest floor and litterfall inputs were lost from the exchangeable soil pools, but most soil nutrient pools never dropped below pre-disturbance levels. The exception was the soil K pool, which increased greatly as a result of the harvest, and then decreased to very low levels. When considered together with the additional losses of K from litterfall, forest floor, and root nutrient inputs, the change in K pools indicated a large and rapid flushing of K from the ecosystem.

During this time period, the gaps began to revegetate. By September 1989, plant cover remained sparse (9–15% of the ground area) and low, < 1 m above the ground (Silver 1992). Total belowground biomass did not change, but the ratio of live to dead fine roots decreased significantly as root mortality increased necromass and replacement of live root biomass lagged behind (Silver & Vogt 1993). This suggests that the majority of nutrients added as a result of the harvest were probably immobilized in the soil or lost from the ecosystem. However, with the exception of K, soil nutrient pools did not drop below pre-disturbance levels. The reduction in exchangeable K may have resulted from leaching losses and from fixation by clay particles. The Bisley soils have a high K sorption capacity, which can effectively remove K from the soil exchange complex on a scale of weeks to months (Graham & Fox 1971). Our results are similar to those reported by Ewel *et al.* (1981) for a volcanic soil in Costa Rica. They reported increases in most soil nutrients including K concentrations during the first 11 wk following cutting in a premontane wet forest in Costa Rica. When inputs from the forest floor were considered, however, they reported a loss of 33 percent of the K pool over this time period.

Soil nutrient dynamics following disturbance are rarely studied over short time scales of days or weeks, presumably due to the assumption that soil processes occur more slowly than plant regrowth. Yet, several lines of reasoning suggest that changes can occur rapidly in tropical soils. For example, microbial processes and rainfall or drought events effect soil nutrients over short time periods (Silver & Vogt 1993, Lodge *et al.* 1994), particularly following a dramatic change in resource availability and utilization commonly associated with disturbance. This was apparent in the rapid drop in pH 5 d from the start of the experiment, which occurred in both experimental and control sites following a short-term drought. The change in pH was probably due to an increase in the electrolyte concentration of the soil solution associated with increased NO_3-N concentrations, the addition of Cl to the soil solution associated with a brief rain storm at the end of the drought, or hydrolysis associated with increased Al concentrations in the soil (Richter *et al.* 1988). All of these processes can add H ions to the soil solution and lower pH (as measured in deionized H_2O).

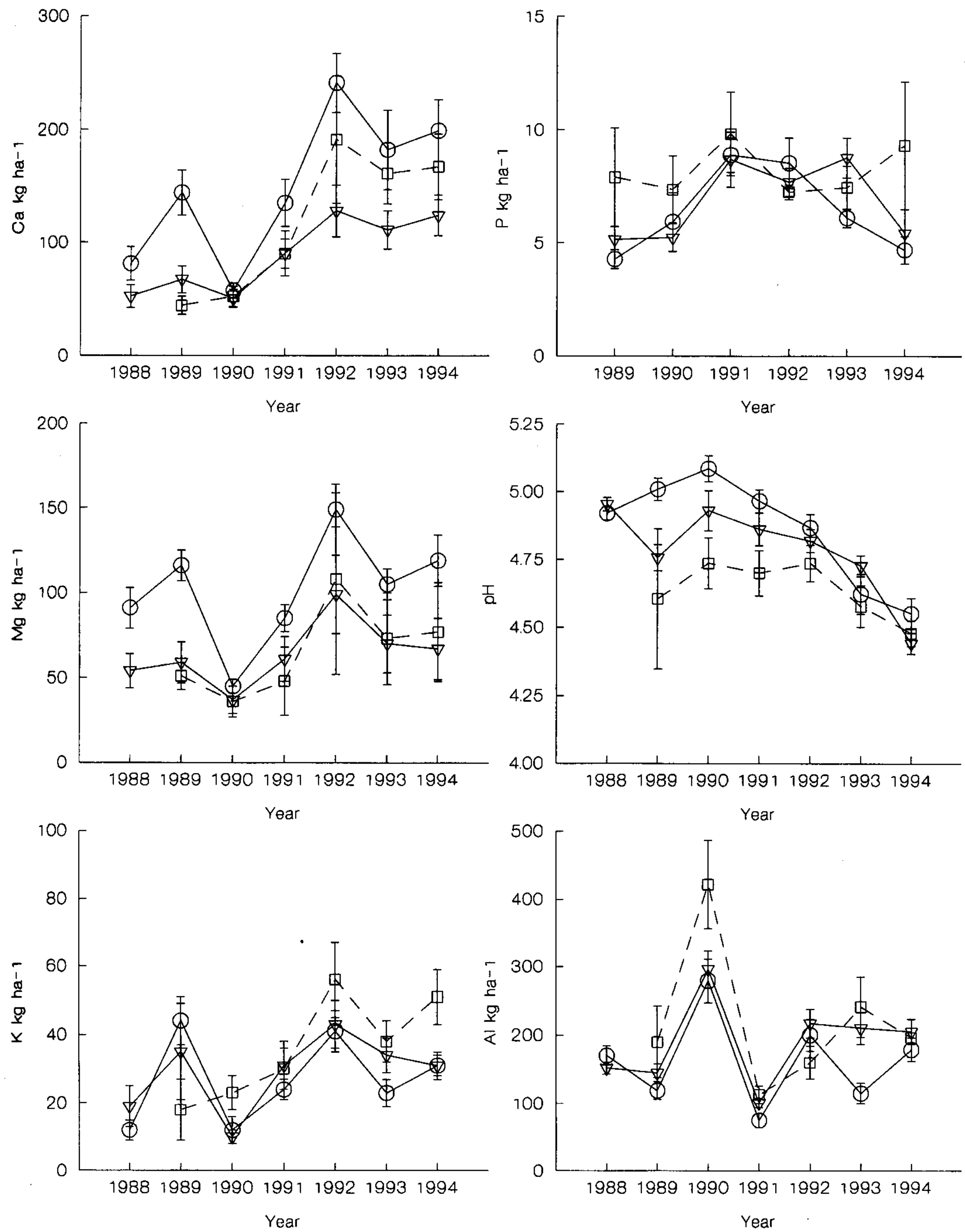

FIGURE 3. Soil nutrient pools (kg ha^{-1}) during the first six years following harvesting and Hurricane Hugo in the Bisley Research Watersheds, Puerto Rico. ○ = lower harvested plot; △ = upper harvested plot; □ = control/forested plots. Vertical lines are standard errors.

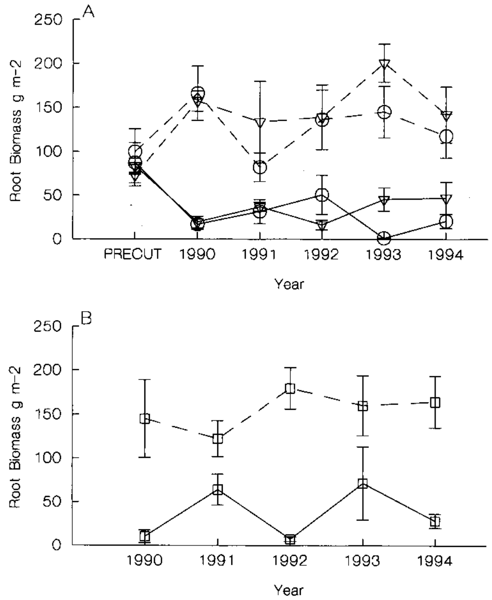

FIGURE 4. Changes in live (solid lines) and dead (dashed lines) fine root biomass over time in the harvested plot (a) and forested sites (b) in the Bisley Research Watersheds, Puerto Rico. No precut sample was taken from the forested sites. ○ = lower harvested plot; △ = upper harvested plot; □ = control/forested plots. Vertical lines are standard errors.

The changes that occurred rapidly in the soil are coupled to the biota in a number of ways. Pools of exchangeable K and NO_3-N may have swelled as a result of reduced plant uptake, increased mineralization rates, and leaching from the forest floor. Increases may have initially stimulated microbial activity, and then potentially reduced it shortly thereafter, as NO_3-N and K leached from the soil or K was sorbed. We observed rapid germination and sprouting during this period which may have been stimulated by the input of these nutrients to the soil.

Disturbance effects after 9–12 months.—Most studies looking at disturbance effects on nutrient cycling sample on the scale of 6–12 mo or longer following the event (Harcombe 1980, Uhl *et al.* 1982, Sanchez *et al.* 1983, Uhl & Jordan 1984). In this study we found that many of the changes that occurred as a direct result of either harvesting or the hurricane occurred within the first year of the study, and in many cases were no longer distinguishable at the end of that period. The hurricane added nutrients to the soil surface, although only K and NO_3-N were measurably incorporated into the soil exchange complex during the 9 mo sampling period. These pools also returned to predisturbance levels rapidly, exhibiting no significant differences from pre-hurricane values within 9 mo following the disturbance. The large nutrient input associated with the hurricane litterfall was either lost through leaching, immobilized in the soil, or incorporated into the vegetation (Fig. 2).

High fine root mortality following the hurricane was coupled with increased soil nitrate concentrations and cation leaching at this site (Silver & Vogt 1993). Increased nitrate concentrations could have resulted from nitrification stimulated by the addition of SOM and nutrients from decomposing roots, and/or from decreased uptake and immobilization. Decomposition of fine roots occurred over approximately 1.5 yr (Silver & Vogt 1993), and recovery of live root biomass was significantly slower, requiring several years of regrowth (Fig. 4). High root mortality may have contributed to the loss of some of the nutrients added to soil as a result of the disturbances. The aboveground biomass in 1 yr old regrowth was substantial (Fig. 2), suggesting that nutrient uptake and immobilization was also an important pathway for nutrients released as a result of these disturbances.

Recovery over six years.—The longer-term recovery of forest ecosystems is generally examined on annual to multi-annual time steps. For soils and belowground processes, this approach may exclude shorter-term dynamics that can have an important influence on ecosystem development and the reorganization of biogeochemical cycling. However, several factors such as the effects of changes in plant species composition on soil properties, and the inputs associated with the mineralization of organic matter, are likely to have an impact on soils at this level of resolution. For example, an examination of the 6 yr data set excluding the shorter-term samples provides some notable additions to the interpretation of the results. In the lower plot, the harvest resulted in a short-term ($\leq$ 12 mo) increase in exchangeable Ca and Mg in the soil. Calcium and Mg in the less fertile upper plot did not change at this scale. It is interesting to note that although the amount gained and subsequently lost by the more fertile lower plot was significantly more than that in the upper plot, the pool sizes of the lower plot never dropped below the level of the upper plot, suggesting that a minimum level of nutrient retention is achieved by the ecosystem (Fig. 3). Similar results were reported during 5 yr of recovery in Costa Rica, where fertile sites lost more nutrients than less fertile ones, but only approached the lower fertility level and never dropped below it (Ewel *et al.* 1991).

Some of the early work in tropical forests was conducted at sites where plant biomass accounted for most of the nutrient retention in the ecosystem and soils had low nutrient holding capacity (Nye & Greenland 1964, Cuevas & Medina 1986, Jordan 1987, Medina & Cuevas 1989). Soil nutrient losses occurred following disturbances that removed the aboveground biomass, and were particularly severe following slash and burn clearing or where soils were continuously cultivated for several years (Nye & Greenland 1964, Jordan 1987). Where soils were not cultivated, both nutrient accumulation (Uhl & Jordan 1984) and nutrient losses (Ewel *et al.* 1991) have been reported over 5 yr intervals. In most cases these changes were small, and soils returned to or approached pre-disturbance nutrient levels within 5 yr. Here, we found that some nutrient pools increased in the soil over 6 yr. Nutrient cations increased from 1990–1994, reaching a maximum level in 1992. The year 1992 was also the wettest year which could account for higher exchangeable cation concentrations in the soil either due to enhanced mineralization rates or nutrients added to the soils from plant and litter leachates. Regardless, values remained relatively higher through to the end of the six year period. The increase in base cation concentrations over time was accompanied by a drop in pH. At first glance this may seem contradictory, since higher base cation concentrations are generally associated with a corresponding increase in pH. We expect that much of the cation retention, including H ions is occurring in SOM (Tiessen *et al.* 1994), although we have no good explanation of the mechanism since no significant increase in SOM occurred. A similar pattern of increased exchangeable acid and base cation concentrations, with little or no change in soil organic matter content was observed following whole tree harvesting in a northern hardwood forest in New Hampshire, USA (Johnson *et al.* 1991). It is also possible that the reduction in pH in the mineral soil may have resulted from increased root activity or the mobilization of Al from the forest floor and mineral soil accompanied by increased water flow through the soil after disturbance (Johnson *et al.* 1991).

Perhaps the most surprising result was the lack of change in SOM pools over the 1–6 yr following the disturbances. We might expect the large amount of organic material deposited on the forest floor during the hurricane and in the soil due to root mortality to augment SOM content. While SOM fluctuated over time, there were no trends showing accumulation or loss. Ewel *et al.* (1991) reported small losses of SOM from a volcanic soil over 5 yr following cutting and burning in Costa Rica, although they added that the pool was relatively stable due to complexation of the heavy SOM fraction with allophane. The Bisley soils are unlikely to contain allophane which disappears relatively rapidly in the weathering sequence (Sánchez 1976). One possible explanation is that increased decomposition and soil respiration rates in the disturbed environments may have balanced the SOM added as a result of the hurricane, leading to no net change in the SOM pool. Alternatively, 6 yr may not yet be long enough to detect changes in SOM pools, especially when considering the potentially important inputs from coarse roots.

In this study, we show that soils in a subtropical wet forest are relatively resilient when exposed to severe aboveground disturbances. Mobile nutrient elements such as K and NO_3-N may be lost from the soil initially, but most exchangeable soil nutrient pools were either the same as or greater than pre-disturbance levels after 1–6 yr. Nutrient cycling and pools sizes in the Bisley Watershed soils are not dissimilar from other lower montane wet tropical forests (Silver *et al.* 1994) and thus we would expect that other forest soils could also have similar nutrient conservation mechanisms following disturbance, particularly in the absence of soil disturbance or burning. The results of this study also raise the question of what is the most appropriate temporal scale to use when examining the effects of disturbance on nutrient availability in tropical forests. As we have shown, soils can be relatively dynamic over short time scales and short-term variations must be viewed in the context of longer-term trends when considering their effects on the biota and ecosystem-level processes.

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