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# HURRICANE DAMAGE TO A HAWAIIAN FOREST: NUTRIENT SUPPLY RATE AFFECTS RESISTANCE AND RESILIENCE

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*Abstract.* Hurricane Iniki damaged a forest in which we had previously studied nutrient limitation to productivity. We had measured the response of aboveground net primary productivity (ANPP) to fertilizer applications and had found phosphorus to be limiting. Reductions of leaf area index (LAI) after the hurricane's passage ranged from 3% to 59%, were correlated with prehurricane LAI, and were greatest in P-amended treatments (+P). LAI recovered to near prehurricane levels by 9 mo after passage, and rates of recovery were unaffected by treatment. Mortality of fine roots ranged from 35 to 48% following the hurricane and recovered in 2 yr. Stem damage was largely branch removal, but some stems were partially uprooted or decapitated. Large trees were damaged with greater frequency than small trees, and severity of damage increased in +P treatments. Fine litterfall caused by the storm was 1.4 times the annual input, and nutrient transfers to the forest floor approximated that of a typical year. Stem diameter increment and aboveground net primary productivity (ANPP) declined but returned to prehurricane values 2 yr later in +P treatments while remaining low in −P treatments (i.e., those without P supplementation).

Rates of recovery to prehurricane stem growth and ANPP were greater in +P treatments and were accompanied by a much greater ANPP per unit leaf area ($E$). The results support hypotheses that ecosystem resistance and resilience are inversely related and that resistance decreases and resilience increases as supply rates of limiting resources increase. However, they also suggest that structural and functional components of resistance and resilience should be considered separately.

*Key words: decomposition; fertilization; hurricane; Kauai, Hawaii; leaf area; montane tropical forest; nitrogen; phosphorus; productivity; resilience; resistance; roots.*

## Introduction

Hurricanes affect forest structure and productivity, and it is likely that ecosystem resistance to and recovery from such disturbances are altered by nutrient availability. On 11 September 1992, Hurricane Iniki struck the island of Kauai in the Hawaiian Islands. The storm passed directly over a montane native rain forest in Kokee dominated by *Metrosideros polymorpha* (Gaud.) in which we were measuring the response of aboveground net primary productivity (ANPP) to fertilizer applications. In that experiment, phosphorus additions in particular had modified foliar characteristics, and they had increased leaf area index (LAI) and ANPP in treatment plots (Herbert and Fownes 1995). We used our background information on ANPP, nutrient cycling, and stand structure to assess the resistance and resilience of this system to hurricane damage.

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A more resistant system may be defined as one that undergoes smaller change in a state or flux variable as a result of disturbance, while a less resistant system changes more. Conversely, resilience refers to the rate of return to the reference state following disturbance (Webster et al. 1975, DeAngelis et al. 1989, Grimm et al. 1992; see also Holling 1973). It has been hypothesized that ecosystem resistance is inversely related to resilience (Webster et al. 1975, Fisher et al. 1998) and that resistance decreases and resilience increases as supply rates of limiting nutrients increase (DeAngelis et al. 1989). Following hurricane disturbance, we predicted that changes arising from earlier P fertilization would decrease resistance and increase resilience of *M. polymorpha* forest.

Our specific objectives were to (i) assess damage in relation to stand structure; (ii) determine the relationship between aboveground and belowground structural damage and recovery processes; (iii) evaluate hurricane-induced litterfall, the associated transfer of nutrients from the canopy to the forest floor, and nutrient mineralization and immobilization processes through 2 yr of decomposition; (iv) measure the functional impact of damage on subsequent stem growth and ANPP; and (v) examine the role of nutrient availability in recovery.

Studies of hurricane damage elsewhere have related the severity of tree damage to exposure as a consequence of tree size (Foster 1988, Gresham et al. 1991, Reilly 1991, Walker 1991, Harrington et al. 1997), local topography (Bellingham 1991, Foster and Boose 1992, Boose et al. 1994), and differences among species in susceptibility (Basnet et al. 1992, Foster and Boose 1992). Large trees may sustain damage as a result of a greater exposed profile. Topographic features such as valleys may effectively increase the force of the storm locally. Because local topography, aspect, and distance to the storm at the site was uniform and the tree canopy was dominated by a single species, we hypothesized that crown damage would be proportional to tree size and leaf area. The experimental design established in Kokee prior to the hurricane, a randomized complete block ANOVA, removes most spatial variability from the analysis, including possible spatial variability of storm effects on the landscape. Therefore, the increased LAI in P fertilized plots prior to the hurricane allowed for a direct comparison of canopy reduction relative to exposed canopy area.

Fine root mortality was high following disturbance caused by Hurricane Hugo in Puerto Rico (Parrota and Lodge 1991). Although an earlier small-scale experimental disturbance caused mortality in 40% of fine roots, the hurricane caused >70% mortality in both control and experimental plots (Silver and Vogt 1993), which began to show signs of recovery after 6 yr (Silver et al. 1996). Fine root mortality may have been a consequence of crown damage and leaf area reduction. Fownes and Anderson (1991) found that fine root mass was sensitive to changes in leaf area in two fast-growing tree species. We predicted that fine root mortality following Hurricane Iniki would be proportional to the reduction of LAI and that regrowth of fine roots would be proportional to LAI recovery.

Directly associated with canopy damage was a large transfer of fine litter to the forest floor, much of which was green or incompletely senesced. Earlier studies have described an associated large flux of nutrients from the canopy to soil and increased nutrient availability (Lodge et al. 1991, Whigham et al. 1991, Silver et al. 1996, Harrington et al. 1997). However, the proportionately large mass of low quality wood debris in hurricane-caused litter can increase microbial immobilization and substantially reduce both available nutrient pools and ANPP (Zimmerman et al. 1995). Nutrient concentrations are relatively low in both green and senesced leaves of *M. polymorpha*, and decomposing senesced leaves immobilize both N and P at the Kokee site (Crews et al. 1995). Because of the low nutrient status of *M. polymorpha* leaves we expected a net immobilization effect in the first year of decomposition. Moreover, hurricane-removed twigs and branches should increase nutrient immobilization. The net effect may be to limit recovery of damaged trees because of reduced nutrient availability.

Defoliation can cause short term reductions in stem growth (Harrington et al. 1997). However, growth rates of surviving stems may later increase, as was true following hurricane Gilbert in Yucatan (Whigham et al. 1991) and hurricane damage at the Hubbard Brook Experimental Forest in 1938 (Merrens and Peart 1992). Increased growth rate of surviving stems in the latter cases was probably the result of increased availability of light and other resources to survivors. Hurricane Iniki caused partial defoliation, and mortality appeared to be low immediately following the storm. We expected a negative effect of the hurricane on stem diameter growth, and predicted that stem growth would recover only after LAI recovered. Furthermore, because of the low mortality, we did not expect to see increased growth by survivors.

Studies elsewhere have reported high rates of tree mortality continuing ≥5 yr after a hurricane and having large impacts on demography (Fu et al. 1996, Lugo and Scatena 1996). The occurrence of continued mortality highlights possible physiological impacts related to the loss of photosynthetic area and fine roots. *M. polymorpha* forests on the younger Hawaiian islands, particularly Hawaii, are established as cohorts that mature and senesce synchronously (Mueller-Dombois 1987). A possible mechanism underlying senescence of mature *M. polymorpha* trees is an increase in the respiratory sink relative to leaf biomass (Gerrish 1990). Removal of leaf area from large trees already close to such a respiratory debt could increase mortality. Because *M. polymorpha* forests in Kokee are not even-aged we expected greater posthurricane mortality among large trees, an effect that could alter stand demography.

Finally, phosphorus was the nutrient element most limiting to productivity at the site prior to the hurricane (Herbert and Fownes 1995), and we expected that the increased P availability in P fertilized plots would enhance recovery rates.

## Site Description

The study site is located in the Na Pali–Kona Forest Reserve in Kokee State Park, island of Kauai, Hawaii (22°08′ N and 159°38′ W) at 1134 m elevation. The site is on a broad ridge top, a remnant of a shield volcano surface (Fig. 1), with a geologic age estimated to be $3.9–4.3 \times 10^6$ yr (Clague and Dalrymple 1988). The soil is mapped as a clayey ferritic isomesic Plinthic Acrorthox (Soil Survey Staff 1972) revised to an Acrudox (Soil Survey Staff 1992), and P availability is low (Crews et al. 1995). Mean annual precipitation is ~2500 mm (Giambelluca et al. 1986). The site has a slope of ~2–3° and a SSW aspect, and there is little topographic variation.

Vegetation is composed predominantly of *Metrosideros polymorpha* Gaud. var. *glaberrima* (H. Lev.) St. John, which accounts for 88% of the stem basal area. Other tree species include *Syzigium sandwichensis* (A. Gray) Nied., *Cheirodendron trigynum* (Gaud.) A. Hell-

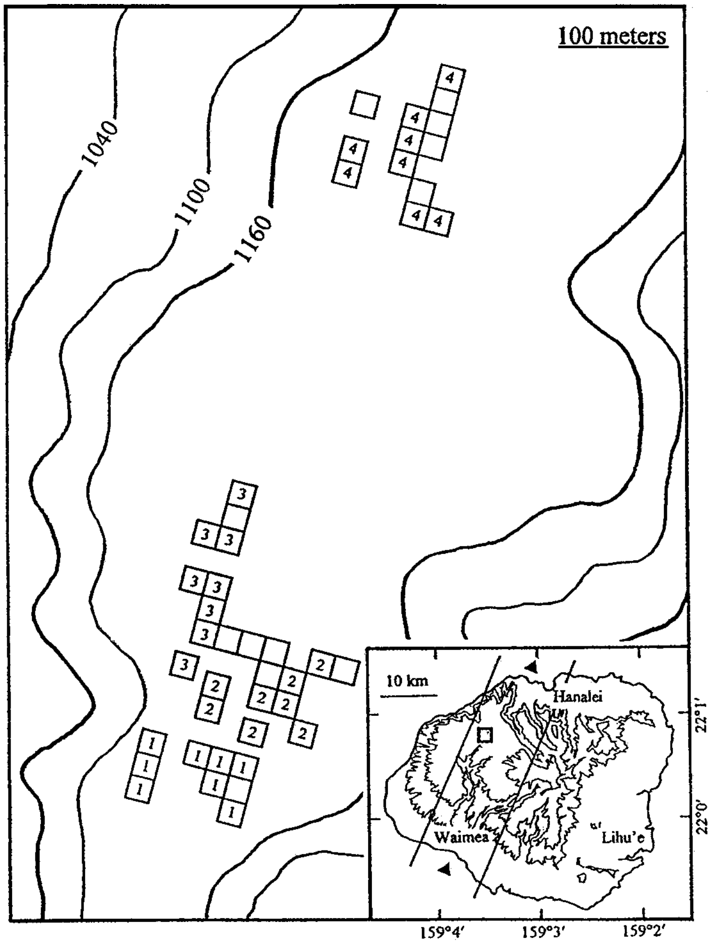


FIG. 1. Plot layout and local topography at the Kokee study site; elevation contours are in meters. Plots are numbered to indicate blocking of the fertilizer experiment. Plots without numbers were surveyed in 1991 but were not used in the fertilizer experiment. Inset shows width, track, and direction of the storm eye of Hurricane Iniki in September 1992, relative to the study site (□). Inset contour lines are at 600-m intervals.

er, and *Cheirodendron platyphyllum* (Hook. and Arnott) Seem. ssp. *kauaiense* (Kraj.) Lowry (Kitayama and Mueller-Dombois 1995). The understory is primarily dominated by ferns, with alien *Hedychium gardnerianum* and *Rubus* spp.

An ongoing fertilization experiment at the site had modified vegetation characteristics in treatment plots (Table 1). Phosphorus additions in particular had altered foliar characteristics, and had increased LAI and ANPP in treatment plots (Herbert and Fownes 1995).

TABLE 1. Prehurricane productivity and canopy characteristics at the experimental field site in Kokee, Hawaii. Values are arithmetic means ± 1 SE.

| Variable | Fertilizer treatment† | | | | ANOVA *P* statistic | |
|---|---|---|---|---|---|---|
| | −N,−P | +N,−P | −N,+P | +N,+P | +N | +P |
| ANPP ($g \cdot m^{-2} \cdot yr^{-1}$) | 879 (81) | 983 (68) | 1121 (81) | 1350 (162) | NS | 0.006 |
| Litterfall ($g \cdot m^{-2} \cdot yr^{-1}$) | 453 (19) | 526 (32) | 515 (23) | 634 (30) | 0.003 | 0.006 |
| DBH increment (mm/yr) | 2.0 (0.34) | 2.0 (0.28) | 2.0 (0.21) | 3.1 (0.40) | NS | 0.027 |
| Fine live root mass ($g/m^2$)‡ | 261 (20) | 280 (16) | 332 (29) | 278 (26) | NS | NS |
| LAI ($m^2/m^2$) | 2.4 (0.19) | 2.5 (0.14) | 2.9 (0.18) | 3.4 (0.20) | NS | 0.001 |
| *E* ($g/m^2$)§ | 385 (55) | 402 (41) | 399 (33) | 401 (42) | NS | NS |
| LMA ($g/m^2$)‖ | 193 (11) | 194 (7) | 186 (9) | 162 (12) | NS | 0.046 |
| Foliar P (%) | 0.061 (0.003) | 0.059 (0.003) | 0.102 (0.006) | 0.106 (0.010) | NS | <0.001 |
| Foliar N (%) | 0.829 (0.033) | 0.859 (0.040) | 0.845 (0.017) | 0.935 (0.049) | NS | NS |

*Notes:* Prehurricane treatment effects were largely in response to P fertilization, and there were no significant N × P interactions. ANOVA was performed on log-transformed data. Fixed model *F* tests were used to analyze the three main treatments (N, P, and OE) and all interactions (Herbert and Fownes 1995).

† Treatments: +P = P addition, −P = no P addition; +N and −N have analogous meanings.

‡ Sampled 2 wk after Hurricane Iniki.

§ ANPP/leaf area.

‖ Leaf mass/ leaf area.

## Physical Characteristics of Hurricane Iniki

Hurricane Iniki was classified as a category 4 storm on the Saffir-Simpson scale; it crossed the island on 11 September 1992, with wind speeds measured at 48–53 m/s (210–233 km/h) and gusts to 64 m/s (280 km/h) (National Weather Service 1992). Iniki had a high speed of passage estimated at 7.3–9.1 m/s (32–40 km/h), which may have reduced its impact. Hawaii Civil Defense authorities estimated that major damage covered 75–80% of the Island of Kauai, making it the most powerful storm to have struck the Hawaiian Islands in at least 90 yr. The storm path took the eye directly over our study site in Kokee (Fig. 1).

## Methods

### *Experimental design and statistical analyses*

In March 1991, 18 mo prior to the hurricane, a fertilization experiment was initiated on the site (Herbert and Fownes 1995). A stem inventory had been completed in forty-four 10 × 10 m plots, 32 of which had been selected for use in the experiment on the bases of similarity in species composition, total basal area, and diameter distribution of stems. A 20 × 20 m area encompassing each 10 × 10 m plot and a 5 m border around it was fertilized. The three main treatments were (1) N and (2) P applied at the annual rate of 100 kg/ha each, and (3) a mix of other essential (OE) nutrients (excluding N and P), including K, Ca, Mg, S, Fe, Mn, Zn, Cu, and B as described elsewhere (Herbert and Fownes 1995). Treatments were applied on 6-mo intervals at two levels, zero or plus, in eight factorial combinations of N, P, and OE, randomly assigned to eight plots in each of four blocks.

Earlier analyses (Herbert and Fownes 1995) show little influence of the OE treatment on measured responses, and there was no measurable effect of OE in the present analyses. Therefore, data from the OE treatments including either N or P were pooled with data from the N or P treatments lacking OE. Control plot data were pooled with those from OE treatments lacking both N and P. The combining of treatments effectively reduced the number of treatments to four (N, P, N × P, and control) but doubled the treatment sample size.

Treatment effects on plot-level damage and recovery were analyzed by randomized complete block ANOVA with 31 degrees of freedom. The design removes most spatial variability from analyses. A split-plot ANOVA with fertilizer treatment as the main plot and two stem diameter classes as subplots (63 degrees of freedom) was used to determine the influence of both tree size and treatment (Snedecor and Cochran 1980). Data were log transformed when appropriate to homogenize variance and meet the assumptions of ANOVA. Arcsine square-root transformations were applied when analyses were performed on proportions between 0 and 1 derived from categorical data sets (Snedecor and Cochran 1980). An alpha of 0.05 was used to determine significance in all cases, but possible trends indicated by an alpha near 0.05 were also noted. For clarity, all results are presented as arithmetic means or fractions thereof.

Measures of resistance were based on absolute loss of mass, structure, or function, and when possible as fractional loss relative to prehurricane conditions. Resilience was measured as the fractional rate of return to prehurricane structure and function.

### *Leaf area index (LAI)*

LAI was estimated optically by a LI-COR LAI-2000 plant canopy analyzer (LI-COR, Lincoln, Nebraska), which uses gap fraction analysis of diffuse radiation transmittance to estimate LAI indirectly (Welles and Norman 1991). The method is known to underestimate LAI where canopy elements are aggregated in space, but corrections can be determined allometrically (Gower and Norman 1991, Smith et al. 1993). We report uncorrected optical values as a measure of relative change throughout this paper but provide the correction [multiplication] factor 2.4 (Herbert and Fownes 1997), for purposes of comparison with reports elsewhere. Prehurricane LAI was measured in August and October 1991, and in March 1992. Posthurricane LAI measurements were made in 3-mo intervals beginning in September 1992. In all cases LAI-2000 measurements were based on six samples, each from a separate permanent sampling point. Differences between March 1992 measurements and posthurricane September 1992 measurements were used as the best estimate of LAI losses caused by the hurricane.

### *Fine roots*

Fine roots (<2.0 mm diameter) were sampled with a 51 mm diameter soil corer to a depth of 10 cm. The sample depth included 90% of the fine roots in the upper 50 cm of the soil profile (Herbert 1995). Initial fine root biomass was determined from six cores per plot collected 2 wk after the hurricane (coefficient of variation [expressed as a percentage] = 16 – 40% by plot, 25–45% by treatment at first sampling). Subsequent biomass measurements were determined from five to six samples per plot and were collected at 3, 6, 12, and 24 mo posthurricane. The sampling frequency was designed to capture both the short-term disturbance responses and the longer-term recovery dynamics. Soil cores were refrigerated at ~6°C within 24 h of collection and fine roots were separated within 4 wk (10 wk for the 18-mo samples). Cores were washed in tap water and roots <2 mm diameter were separated from the washed sample in a water bath. Roots were classified as live or dead based on color and texture and then oven dried to constant mass at 70°C.

### *Litterfall collections*

Monthly fine litterfall collections (including twigs <1 cm diameter) began at the end of September 1991, 6 mo after initial fertilization, and continued through October 1994. Collections were made from four $0.2-m^2$ frame traps per plot. Hurricane-caused litterfall was separated into senesced and green fractions of *M. polymorpha* leaves, other miscellaneous leaves, and twigs. Fallen large wood was not collected or estimated. Prehurricane fine litterfall collections had not been separated into green and senesced components.

### *Litterfall nutrients*

Tissue nutrient concentrations were determined for the main components of hurricane-caused litter from control plots. Samples were dried at 70°C, ground, and acid-digested in a block digester using a semimicro-Kjeldahl procedure with a mercuric oxide catalyst. Total N concentration (Alpkem method A303S071, 1990) and total P concentration (Alpkem method A303S050, 1990) were determined by an Alpkem autoanalyzer (Alpkem Corporation, Wilsonville, Oregon). Samples for K, Ca, and Mg analysis were dry-ashed at 500°C for 4 h, then dissolved in nitric acid and analyzed by atomic absorption spectrophotometry. Blanks and plant tissue standards were used to check digesting efficiency and spectrophotometer calibration, and random duplicates were used to check the constancy of results.

### *Litter decomposition and nutrient transfer*

The rates of mass loss, nutrient immobilization, and mineralization of green and senesced *M. polymorpha* leaves and twigs, the main components of hurricane-caused fine litter, were measured over a 24-mo period for hurricane-caused litter collected from control plots. Thirty-five samples of each tissue type were air-dried for 8 wk, weighed to the nearest 0.01 g, and sewn into 15 × 15 cm nylon bags of 1.0-mm mesh. Samples consisted of ~3 g of leaves or 5 g of twigs. A subsample of each tissue type was oven dried at 70°C to constant mass to determine an air-dry-to-oven-dry conversion. These subsamples were then ground and analyzed for N, P, K, Ca, and Mg concentration by the methods described in the preceding paragraph. Values obtained were used to estimate initial oven-dry mass and nutrient content of the decomposition samples.

Litter bags were placed in a common nonfertilized location on the forest floor at the field site in December 1992. Five randomly selected bags of each tissue type were collected at 1, 3, 6, 12, 18, and 24 mo. At the 24-mo collection, only three twig litter bags were collected. Samples were oven dried at 70°C to constant mass (recorded to nearest 0.001 g) and analyzed for nutrient content.

Estimates of nutrient flux from decomposing hurricane-caused litter were made for control plots after each litter bag collection and nutrient analysis. Nutrient flux was calculated as the product of fractional nutrient gains or losses from each decomposed litter type and the initial nutrient mass of that hurricane-caused litter type.

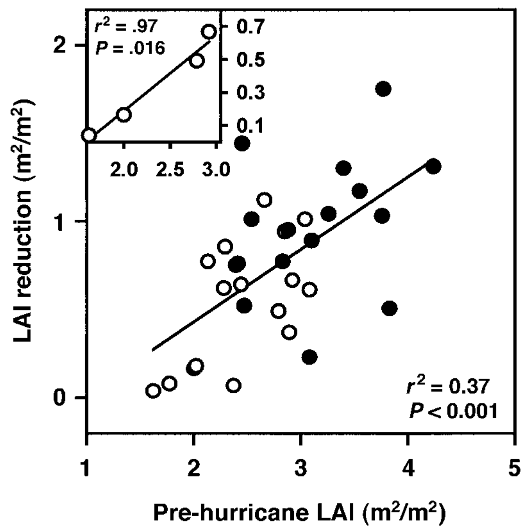


FIG. 2. Reduction in LAI vs. prehurricane LAI for all treatment plots. Inset uses untreated control plots only. Symbols: ●, +P (P supplementation) treatments; ○, −P (no supplementation) treatments.

### *Stem growth, allometric equations, and biomass estimation*

Spring-loaded dendrometer bands were installed on six *M. polymorpha* trees per plot in February 1991. Because the initial experiment was designed for the analysis of a fertilizer treatment response, trees were selected for codominance in the canopy and understory trees were avoided. Diameter increment was measured at 6-mo intervals through September 1994. Because diameter increments were small (<1 mm), yearly increments were analyzed and are reported here.

Wood biomass ($W$), including boles, branches, and twigs, was estimated by an allometric equation generated from the destructive sampling of 45 *M. polymorpha* trees ranging in size from 1.0 to 38 cm basal diameter ($D$), harvested from several different sites on the Island of Hawaii (Gerrish 1988; J. Raich and G. Aplet, *unpublished data*). Regression of ln $W$ vs. ln $D$ produced the equation $\ln W = 2.619 + 3.034 \ln D$ ($r^2 = 0.977$, $P < 0.001$, $S_{y \cdot x} = 0.548$). The correction factor $\exp(S^2_{y \cdot x}/2)$ was applied to counteract bias from logarithmic transformation (Baskerville 1972, Sprugel 1983). The final equation was $W = 15.945 \times D^{3.034}$, where $D$ is measured in centimeters and $W$ is predicted in grams.

### *Estimates of production*

Aboveground net primary production (ANPP) was estimated as the sum of the change in wood biomass and fine litterfall. The change in wood biomass was estimated by applying the allometric equation for biomass, as described in the preceding paragraph, to stem diameters at the beginning and end of each measurement interval. Mean growth increment of measured

TABLE 2. Fractional reduction of LAI after the passage of Hurricane Iniki over Kauai Island, Hawaii, by fertilization treatment. Values are arithmetic means ± 1 SE.

| LAI reduction | Fertilizer treatment† | | | |
|---|---|---|---|---|
| | −N, −P | +N, −P | −N, +P | +N, +P |
| Fractional | 0.210 (0.054) | 0.209 (0.042) | 0.262 (0.039) | 0.363 (0.039) |
| Absolute | 0.553 (0.151) | 0.525 (0.105) | 0.721 (0.101) | 1.208 (0.111) |

*Notes:* The fraction of prehurricane LAI lost was larger for +P treatments ($P = 0.022$). Absolute reductions in LAI were larger for +P treatments ($P = 0.001$), and there was a positive interaction with N ($P = 0.033$).

† Defined in Table 1 treatment footnote.

trees in each treatment plot was applied to all trees within the plot to estimate wood production on a stand basis. Although radial growth rate can vary with stem diameter we assumed that the mean increment of the six measure trees from each plot adequately represented the mean increment for all *M. polymorpha* trees in the plot because the range of stem diameters was small. The assumption was supported by a large prehurricane data set in which there was no clear relationship between radial stem growth and initial stem diameter (Herbert and Fownes 1995; D. Herbert, *unpublished data*). Production per unit leaf area ($E$) was calculated as the quotient of ANPP divided by LAI.

### *Structural stem and crown damage*

Structural damage to stems and crowns and tree survival were assessed 2 yr after the hurricane. We visually rated structural crown reduction (branch loss) and partial uprooting of all stems >3.0 cm dbh as follows: Crowns were considered to be relatively undamaged if branch loss resulted in less than a 25% reduction in crown volume and damaged if branch loss was greater. Severity of crown loss was further separated into two categories; 25–50% crown loss, and >50% loss including decapitation. Partial uprooting was also separated into two severity categories; ≤45° and >45° stem angle. To determine the effect of tree size on damage, stems were separated into two dbh size classes; >10 cm and ≤10 cm. Only two size classes were used because of the limited size distribution. The proportion of all trees damaged in each plot was analyzed by ANOVA for treatment and size-class interactions.

TABLE 3. Structural stem damage frequencies synthesized for all plots and fertilization treatments. Thirteen of the 1007 stems surveyed are included in more than one damage category.

| Damage form | dbh < 10 cm | | dbh > 10 cm | |
|---|---|---|---|---|
| | Freq. | % | Freq. | % |
| Uproot < 45° | 21 | 3.3 | 15 | 4.1 |
| Uproot > 45° | 24 | 3.8 | 11 | 3.0 |
| Crown loss < 50% | 72 | 11.3 | 139 | 37.6 |
| Crown loss > 50% | 70 | 11.0 | 46 | 12.4 |
| Decapitation | 11 | 1.2 | 9 | 2.4 |
| No damage | 446 | 69.8 | 156 | 42.2 |

## RESULTS

### *Hurricane-caused damage*

LAI reductions ranged from 3% to 59% and were positively correlated with prehurricane LAI (Fig. 2). Although the relationship explains only 37% of the variance there is strong evidence that much of the unexplained variance is due to treatment effects (Fig. 2 inset). Prior to the hurricane, LAI in plots receiving P additions was 1.3 times greater than that in plots without P additions (Herbert and Fownes 1995). After the hurricane there was no significant difference between treatments. Both absolute and fractional LAI reduction was significantly greater for +P treatments and there was a P × N interaction for absolute but not fractional losses (Table 2).

Structural damage to individual tree crowns (25% to complete crown loss) occurred in 34% of the 1007 trees surveyed in the 32 treatment plots (Table 3). Analysis by split-plot ANOVA shows that the proportion of all large trees having crown damage was twice that of small trees (Table 4). Generally, the frequency of crown-damaged trees in plots without N or P fertiliza-

TABLE 4. Structural crown reduction after passage of Hurricane Iniki, by tree size class and fertilization treatment.

| Size class (dbh) | Treatment† | Crown reduction category | | |
|---|---|---|---|---|
| | | 25–50% | >50% | Pooled |
| <10 cm | −N, −P | 0.08 (0.01) | 0.10 (0.01) | 0.18 (0.01) |
| | +N | 0.13 (0.02) | 0.11 (0.02) | 0.24 (0.02) |
| | +P | 0.12 (0.01) | 0.14 (0.01) | 0.27 (0.02) |
| | +N, +P | 0.12 (0.02) | 0.18 (0.01) | 0.30 (0.02) |
| | Pooled | 0.11 (0.02) | 0.13 (0.02) | 0.25 (0.02) |
| >10 cm | −N, −P | 0.28 (0.01) | 0.06 (0.01) | 0.34 (0.02) |
| | +N | 0.46 (0.02) | 0.17 (0.01) | 0.63 (0.01) |
| | +P | 0.32 (0.02) | 0.18 (0.01) | 0.50 (0.01) |
| | +N, +P | 0.43 (0.02) | 0.18 (0.02) | 0.60 (0.02) |
| | Pooled | 0.37 (0.03) | 0.15 (0.02) | 0.52 (0.03) |

*Notes:* Decapitated trees are included in the >50% category. The proportions of trees damaged are presented as arithmetic means ± 1 SE. ANOVA was performed on arcsine square-root transformed values. Large stems incurred more damage than small stems ($P < 0.001$). N increased the occurrence of crown reduction ($P = 0.002$) primarily in the <50% category ($P = 0.037$). P also appeared to affect losses ($P = 0.054$) and increased the occurrence of severely damaged crowns ($P = 0.019$).

† Defined in Table 1 treatment footnote.

TABLE 5. Hurricane-caused fine litterfall mass (Mg/ha) by treatment. Values are arithmetic means ± 1 SE.

| Litter type | Fertilizer treatment† | | | |
|---|---|---|---|---|
| | −N,−P | +N,−P | −N,+P | +N,+P |
| Senesced leaf | 0.68 (0.06) | 0.75 (0.06) | 0.84 (0.05) | 0.92 (0.08) |
| Green leaf | 1.34 (0.19) | 1.60 (0.13) | 1.79 (0.20) | 2.50 (0.27) |
| Senesced twig | 3.03 (0.20) | 3.17 (0.29) | 3.60 (0.12) | 3.46 (0.32) |
| Green twig | 0.71 (0.09) | 0.77 (0.16) | 1.02 (0.20) | 1.60 (0.22) |
| Total | 5.76 (0.43) | 6.29 (0.25) | 7.25 (0.43) | 8.48 (0.63) |

*Notes:* ANOVA by treatment was performed on log-transformed data. Total hurricane-caused litter was greatest in P ($P < 0.001$) and N ($P = 0.036$) treatments. P increased senesced leaf ($P = 0.003$), green leaf ($P = 0.001$), and green twig ($P = 0.017$) litter. N increased green leaf litter ($P = 0.010$), and there was an N × P interaction increasing green leaf ($P = 0.021$) and green twig ($P = 0.040$) litter.

† Defined in Table 1 treatment footnote.

tion was low, while a greater proportion of N fertilized trees showed some form of damage, primarily as moderate rather than severe (>50%) crown reduction ($P = 0.037$). P supplementation (+P) treatments also appeared to increase crown damage, but not significantly ($P = 0.054$), and a larger proportion of P fertilized trees incurred severe crown reductions ($P = 0.012$). Seventy-one trees, equally split between size classes, were either moderately or severely uprooted. No pattern was detected for this form of damage by either tree size or fertilizer treatment.

In total, 53 trees died in the 2 yr following the storm. Only three of these cases involved partial uprooting without the added influence of structural crown loss. The remaining 50 deaths were associated with crown reductions and included 34.6% of large trees and 38.3% of small trees with structural crown loss >50%.

### *Litterfall, decomposition, and nutrient transfer*

Fine litterfall caused by the hurricane (excluding hanging dead branches and leaves) was 5.76 Mg/ha in control plots and 8.48 Mg/ha in +N+P treatments, with significant positive +N and +P treatment effects (Table 5). Treatment effects generally corresponded with those measured for LAI reductions, and litter deposition was significantly correlated with absolute reductions in LAI ($P < 0.001$, $r^2 = 0.34$). Hurricane-caused litter measured in control plots was 1.4× the previous year's total, but twig and fine wood debris input was >3× that of the previous year.

TABLE 6. Nutrient concentration in hurricane-caused fine litter components after passage of Hurricane Iniki over Kauai Island, Hawaii. Values represent percentage concentration for composite samples of each tissue type.

| Litter type | N | P | K | Ca | Mg |
|---|---|---|---|---|---|
| Metrosideros leaves | | | | | |
| Senesced | 0.70 | 0.035 | 0.17 | 0.51 | 0.15 |
| Green | 0.78 | 0.043 | 0.33 | 0.47 | 0.12 |
| All other leaves | | | | | |
| Senesced | 1.11 | 0.070 | 0.33 | 1.27 | 0.31 |
| Green | 1.23 | 0.050 | 0.75 | 1.22 | 0.32 |
| Twigs | | | | | |
| Senesced | 0.35 | 0.011 | 0.06 | 0.88 | 0.12 |
| Green | 0.56 | 0.036 | 0.32 | 0.70 | 0.09 |

Relative to hurricane-caused litter from rain forests elsewhere (Lodge et al. 1991), nutrient concentrations in all litter components were low (Table 6). However, nutrient concentrations in hurricane-caused senesced *Metrosideros polymorpha* leaf litter were substantially elevated relative to prehurricane measures from control plots (Crews et al. 1995), suggesting that the bulk of leaves we had classified as senesced were incompletely senesced. Specifically, N concentration was elevated by the factor 1.9, and P by 1.6. A much greater proportion of leaf litter was classified as green, and this further increased nutrient concentrations in the bulk of hurricane-caused leaf litter. By component, nutrient concentrations were elevated, and the mass of hurricane-caused litter was greater than annual deposition rates. However, the proportionately large mass of senesced twigs diluted nutrient concentrations in the bulk litterfall mass so that nutrient transfer from the canopy to forest floor was comparable to that in the previous year's litterfall but with slightly higher K and Ca and smaller P loads (Table 7).

Mass loss during decomposition was linear and slow for both green and senesced *M. polymorpha* leaves and twigs (Fig. 4). After the first month there was little difference in mass loss rates of green and senesced materials. By 24 mo, mass loss in both green and senesced twigs was 26%, while mass loss in green and senesced leaf litter was 41% and 37%, respectively.

The fraction of N and P remaining in most litterfall types was substantially decreased in the first 6 mo, presumably due to leaching (Fig. 3). From six to 12 mo, N, and proportionately more P, were immobilized in most tissue types. Increased N immobilization was measured at 18 and 24 mo, while P losses generally followed tissue mass losses from 12 to 24 mo. The net result was a small flux of N and P from the bulk of hurricane-caused litter, a trend of increased P immo-

TABLE 7. Fine litterfall nutrient deposition in control plots of a fertilization study in Kauai, Hawaii, after passage of Hurricane Iniki.

| Litter type | N | P | K | Ca | Mg |
|---|---|---|---|---|---|
| Hurricane-caused (kg/ha) | | | | | |
| Senesced leaf | 5.34 | 0.26 | 1.38 | 4.51 | 1.24 |
| Green leaf | 11.22 | 0.62 | 5.12 | 7.55 | 1.94 |
| Senesced twig | 10.60 | 0.34 | 1.83 | 26.77 | 3.65 |
| Green twig | 4.00 | 0.26 | 2.26 | 5.59 | 0.64 |
| Total | 31.16 | 1.48 | 10.59 | 44.42 | 7.47 |
| Annual, pre-hurricane ($kg \cdot ha^{-1} \cdot yr^{-1}$) | | | | | |
| Senesced leaf | 24.49 | 1.32 | 7.23 | 24.22 | 6.55 |
| Senesced twig | 2.93 | 0.09 | 0.50 | 7.35 | 1.01 |
| Total | 30.42 | 1.91 | 7.73 | 31.59 | 7.56 |

*Note:* The lower part of the table represents 12-mo litterfall nutrient deposition prior to the hurricane (September 1991 through August 1992).

bilization from six to 12 mo, and increased P mineralization and N immobilization in the second year (Fig. 4).

### *Changes in growth and productivity*

The first sampling of fine root mass was made 2 wk after the hurricane and does not account for mortality that may have occurred by that time. At 3 mo, mass of fine live roots had declined by an average 28% from the initial sample, and it declined an average 44% by 6 mo, with a range of 35–48%. As was the case for LAI reductions, fine live root mass losses were greatest in +P treatments (absolute $P = 0.057$, fractional $P = 0.053$) (Fig. 5), but there was no relationship between fine root and LAI reductions when regressed against each other ($r^2 = 0.01$, $P = 0.58$). Increases in fine root mass were measured by 12 mo and a return to the initially measured levels had occurred by 24 mo, whereupon fine live root mass was the greatest in +P treatments ($P = 0.034$). Rate of fine root mass recovery was not dependent on treatment, although there may have been a somewhat elevated rate of recovery in +P treatments ($P = 0.081$).

The initial increase of LAI following the hurricane was rapid (Fig. 6A). Earlier differences in LAI between treatments had been removed by the hurricane, but P fertilized plots had again accumulated greater LAI by 3 mo ($P = 0.016$). However, the fractional recovery rate toward prehurricane LAI was not affected by treatment. Subsequent high wind events in August 1993 and March 1994 reduced LAI to levels similar to those measured immediately after the hurricane. By 21 mo LAI had again increased and was significantly greater in +P treatments ($P = 0.012$). Recovery after 2 yr approached but did not reach prehurricane LAI.

Litterfall did not decrease substantially in the months following the hurricane, probably because of sustained inputs from hanging dead branches and leaves, but significant differences between treatments had been removed (Fig. 6B). Posthurricane pulses of increased litterfall coincided with high wind events and large decreases in LAI. However, by 13 mo there were small but significant increases in monthly litterfall in +N and +P treatments (Fig. 6B). By 22 mo, the effect was greater ($P < 0.001$), and the response to P alone was much greater than to N alone.

Prior to the hurricane, mean stem diameter increment had increased in +P treatments (Table 1). In the year following the hurricane diameter increment had declined to 73% of prehurricane rates in +P treatments and to 62% in −P treatments. However, declines were not statistically different between fertilizer treatments

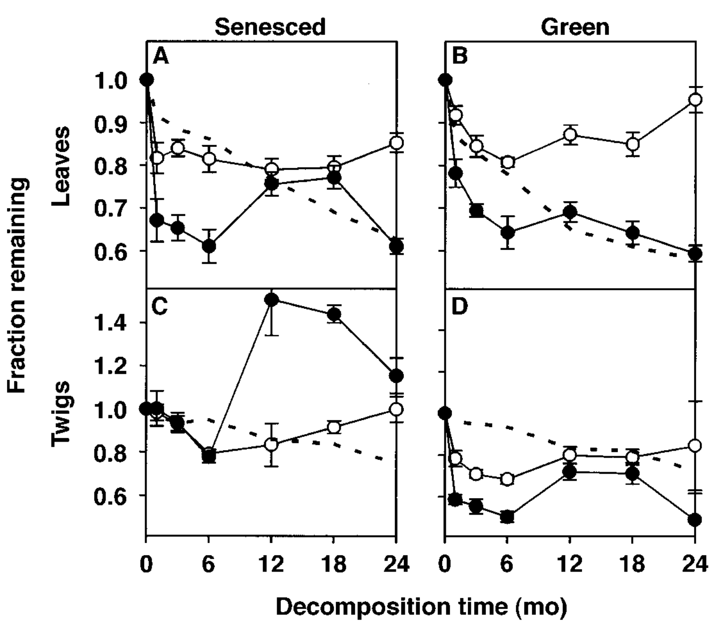


FIG. 3. Fraction of initial dry mass and nutrient mass in decomposed (A) senesced leaves, (B) green leaves, (C) senesced twigs, and (D) green twigs. Symbols: ●, P; ○, N; – – –, tissue mass.

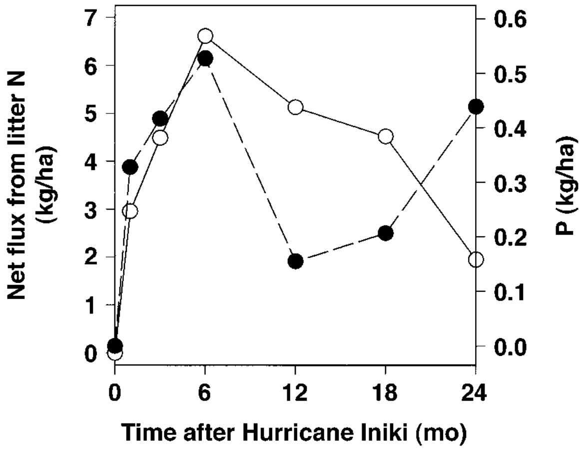


FIG. 4. Estimated N and P flux from decomposing hurricane-caused litter in control plots. Values are the product of nutrient mass in hurricane-caused litter and the fraction of nutrient mass lost from decomposed litter. Increasing trends = net flux from litter; decreasing trends = net immobilization. Symbols: ●, P; ○, N.

(Fig. 7A). By the end of 2 yr, diameter increment in +P treatments had returned to prehurricane rates and were greater than those in −P treatments ($P = 0.003$), which remained low at 76%. The rate of recovery to prehurricane diameter growth increment was also greatest in +P treatments ($P = 0.007$).

ANPP was similarly increased in +P treatments prior to the hurricane ($P = 0.006$), and declines relative to prehurricane ANPP were similar for all treatments (Fig. 7B). By the end of 2 yr, ANPP in +P treatments had recovered to 105% of prehurricane levels and was significantly greater than in −P treatments ($P < 0.001$), which remained low at 88%. Increased ANPP in the +P treatments was accompanied by increased production per unit leaf area, $E$, while −P treatments showed little change in $E$ ($P = 0.022$, Fig. 7C).

## DISCUSSION

### *Comparison with hurricane effects on forests elsewhere*

Defoliation is reported to be the most common type of damage caused by hurricanes (Brokaw and Walker 1991, Whigham et al. 1991). In Kokee, large decreases in LAI were measured in the present study and in six nearby *Acacia koa* (Gray) stands having a range in stature and LAI (Harrington et al. 1997). In the *A. koa* forests, defoliation was proportional to prehurricane LAI, but the effect could not be separated from site or topographic variation. LAI reductions in the *Metrosideros polymorpha* forest were similarly proportional to prehurricane LAI, and here the differences among plots were due to fertilizer treatments and not topography or species differences in susceptibility to damage. These results support the hypothesis that increased leaf area, which may be associated with increased aerodynamic drag, made trees more susceptible to wind damage (Foster 1988, Brokaw and Grear 1991, Reilly 1991, Harrington et al. 1997). Reduced leaf mass per unit leaf area (LMA) reported earlier in +P treatments (Herbert and Fownes 1995) may have also been a contributing factor in LAI reductions (Bellingham et al. 1996).

Fine live root mass declined in the 6 mo following Hurricane Iniki but remained relatively intact by comparison with the 70% to nearly 100% fine root mass losses reported from Puerto Rico following Hurricane Hugo (Parotta and Lodge 1991, Silver and Vogt 1993). Fine root mortality may be related to defoliation (Fownes and Anderson 1991), but in Kokee, plot-level reductions in fine roots and LAI were not correlated. Parrota and Lodge (1991) suggest that fine root mortality following hurricanes may result from physical disturbance to tree root systems caused by swaying and partial uprooting of stems during the storm. We had predicted that rates of fine root and leaf recovery would be temporally similar. However, root recovery was slow, taking >1 yr, while initial recovery of LAI was rapid. Whigham et al. (1991) measured similar rapid foliage recovery in a completely defoliated forest. Silver et al. (1996) measured the beginnings of root recovery 6 yr after Hurricane Hugo. Canopy recovery in the same forest required 2 yr (Scatena et al. 1996). Canopy recovery was relatively slow in the Puerto Rico case because it required the establishment of new individuals.

By optical methods, LAI in Kokee had not fully recovered in 2 yr, but because litterfall rates had returned to prehurricane levels we suspect that LAI may have been underestimated. Optical methods underestimate LAI when leaves are clustered (Gower and Norman 1991, Smith et al. 1993, Herbert and Fownes 1997). In Kokee, removal of branches from tree crowns promoted

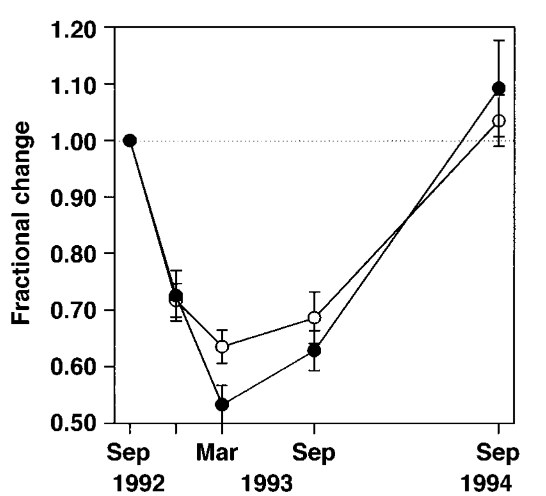


FIG. 5. Fractional change in fine live root mass. Values are means ± 1 SE. Symbols: ●, +P (P supplementation) treatments; ○, −P (no supplementation) treatments.

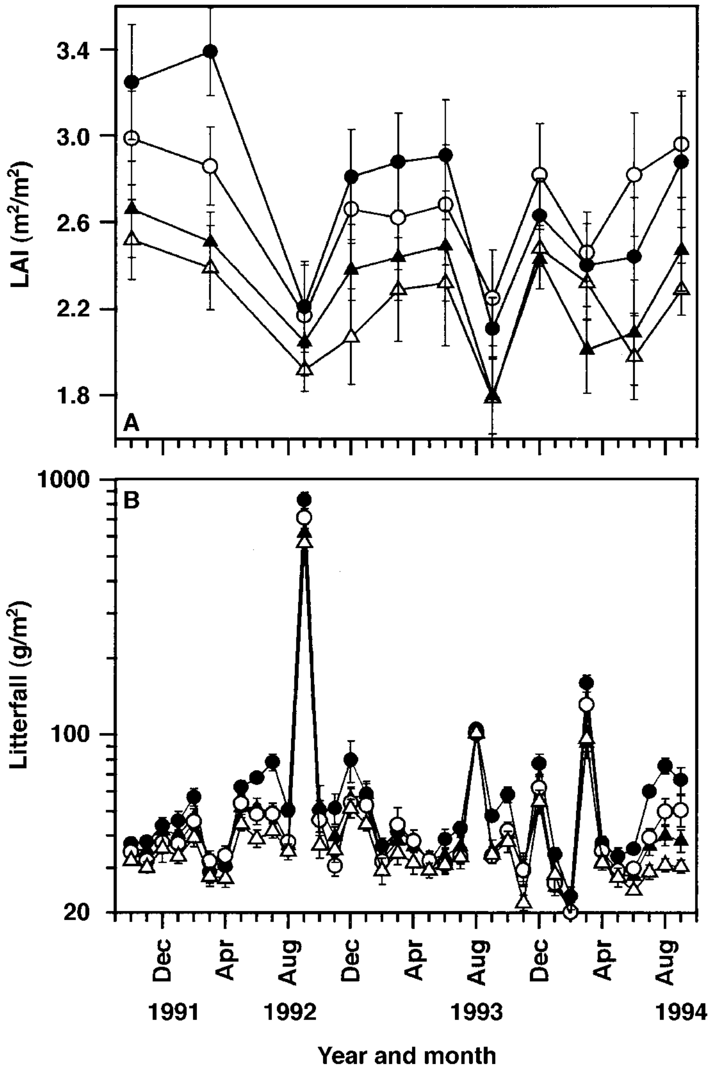


FIG. 6. Patterns of (A) LAI and (B) litterfall beginning 1 yr prior to hurricane Iniki. Values plotted are means ± 1 SE. Symbols: ●, +P,+N; ○, +P,−N; ▲, −P,+N; △, −P,−N.

epicormic sprouting, which may have increased clustering of new leaves around remaining branches, leading to underestimates of posthurricane LAI relative to prehurricane LAI.

We also noted reductions in LAI at 12 and 18 mo that were associated with high wind events and accompanied by litterfall pulses. These posthurricane events and associated LAI reductions suggest an increased susceptibility of new leaves and shoots to repeated disturbances which may remove a substantial amount of leaf area with substantially less force. *M. polymorpha* leaves are sclerophyllous and typically persist ≥2 yr (Porter 1972). Prior to the hurricane, leaf turnover in control plots was estimated at 2.8 yr and LMA 2.11 g/m$^2$ (Herbert and Fownes 1995). Two years after the hurricane, leaf turnover was estimated to be 2.6 yr and LMA 1.84 g/m$^2$ (D. A. Herbert and J. H. Fownes, *unpublished manuscript*). The rapid production of less sclerophyllous, less durable leaves following defoliation may involve a trade-off between rapid recovery of photosynthetic area and resistance to defoliation.

Partial uprooting of stems was infrequent and observed equally in both large and small size classes, but large stems sustained a greater frequency of structural crown damage than did small stems as observed elsewhere (Putz and Sharitz 1991, Reilly 1991, Walker 1991). It was also observed that those trees in +N treatments had a greater frequency of crown damage but that trees in +P treatments received more severe damage. This latter relationship may be due to increased aerodynamic drag caused by the increased LAI in +P treatments.

The impact of Hurricane Iniki on stand demography in the study area appeared to be minimal. After 2 yr, mortality had occurred in only 20 of the large trees >10 cm dbh (63 individuals/ha) and few large canopy gaps were formed. Low mortality following the category 4 Hurricane Iniki suggests that most hurricanes

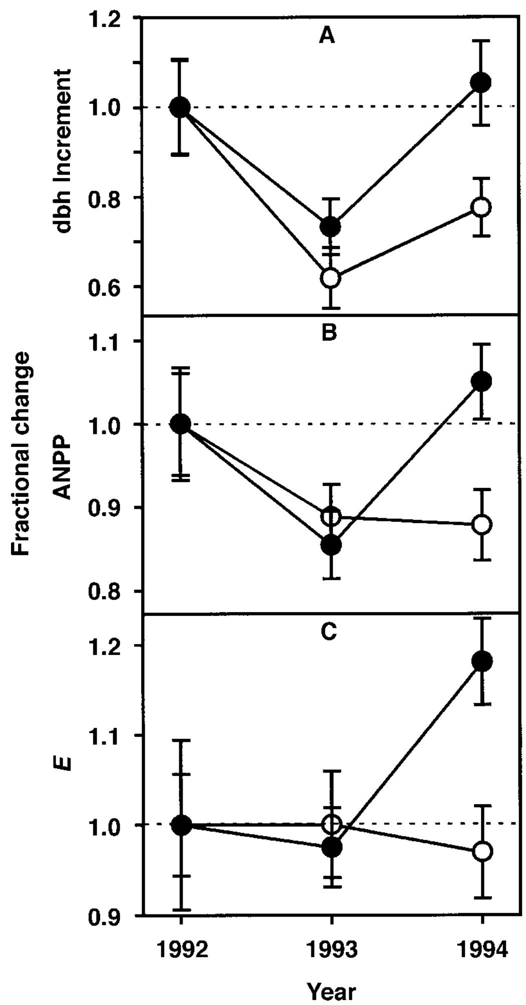


FIG. 7. Fractional change in three forest properties during the 2-yr period including passage of Hurricana Iniki over Kauai, Hawaii: (A) stem diameter (dbh) increment, (B) ANPP, and (C) *E* (ANPP/leaf area). Values are means ± 1 SE. Symbols: ●, +P treatments; ○, −P treatments.

would have a minor impact on *M. polymorpha* forests in nonexposed topographic positions, unless they have predisposing conditions such as decreased vigor associated with older even-aged stands (Mueller-Dombois 1987). Elsewhere, mortality has been observed to continue beyond five years following a hurricane and has had notably larger impacts on demography (Fu et al. 1996, Lugo and Scatena 1996).

Mass of fine litter deposited in control plots during Iniki was 1.4 times greater than annual deposition, which is comparable to that measured in several sites after Hurricane Hugo (Frangi and Lugo 1991, Lodge et al. 1991). Elevated litterfall in the following months was probably caused by a suspended fraction of hurricane-caused litter. In El Verde, Puerto Rico, as much as 46% of hurricane-caused litter was suspended on broken crowns, where it remained for as long as 1 yr after Hurricane Hugo (Lodge et al. 1991).

Nutrient transfer from canopy to forest floor in hurricane-caused litter approximated annual inputs. Lodge et al. (1991) suggested that litterfall caused by Hurricane Hugo would initially increase plant-available nutrients, but that loss of fine roots would limit uptake and rates of nutrient export would increase. The prediction was supported by the measured increase in N trace gas flux and exchangeable cations (Steudler et al. 1991, Silver et al. 1996). Later, immobilization in litter decreased N availability and ANPP by 40% relative to litter removal plots, an effect predicted to continue for >10 yr (Zimmerman et al. 1995; see also Sanford et al. 1991). Another study reports a return to prehurricane levels of available soil nutrients within 9 mo (Silver et al. 1996).

In Kokee, leaching of N and P from litter initially increased available pools but it is unlikely that substantial quantities of N and P were lost from the system because fine roots were relatively intact. This possibility was supported by the absence of measurable change in N trace gas flux in control plots (R. Riley, *personal communication*). Because there was no substantial net immobilization of N and P, it is unlikely that availability and uptake by vegetation further limited ANPP in the 2 yr following Iniki. The different results from forests in Puerto Rico and Kokee may be due in part to large contrasts in nutrient availability, which in Kokee is a much more limiting factor to ANPP.

*M. polymorpha* stem diameter growth decreased in the year following Iniki, unlike some observations elsewhere (Whigham et al. 1991, Merrens and Peart 1992, Harrington et al. 1997), and increases by the second year did not exceed prehurricane values. This was likely the result of the combined factors of reduced photosynthetic area and fine roots, and a low fraction of tree mortality. Decreased stem growth may reflect increased resource allocation to production of new leaves and roots during early stages of recovery while competition for available resources remained relatively high.

*Resistance and resilience*

Structural resistance, measured relative to the amount of mechanical damage to tree crowns, fine roots and leaf area, was greatest for trees in plots where nutrient availability, P in particular, was highly limiting. Plants in nutrient limited systems typically invest more carbon per unit nutrient acquired into structurally robust components (Chapin 1980). This is a growth strategy which imparts structural resistance and longevity to components while effectively increasing residence time of limiting elements and decreasing long-term costs of acquisition (Bloom et al. 1985), and has been particularly well documented in leaves (Chapin 1980, Reich et al. 1991). Although structurally more resistant, nutrient limited trees were functionally no more resistant than nutrient sufficient trees, both having similar relative declines in stem diameter increment and ANPP. In contrast, trees in unfertilized plots were functionally less resilient than those receiving nutrient amendments, especially P, in that stem increment and ANPP recovered slowly or minimally. The increase in functional resilience in plots receiving the limiting element was related to an increase in net photosynthesis per unit leaf area, *E*, to levels well above those before the hurricane.

Our results support the hypothesis that ecosystem resistance and resilience are inversely related, although the structural and functional components of resistance and resilience must be distinguished. Damage to the *M. polymorpha* forest from Hurricane Iniki was intensified by earlier P additions, apparently as a result of an increased susceptibility to wind damage that was related to the effects of increased leaf area and possibly compounded by the effects of decreased LMA (Bellingham et al. 1996). Increased P availability elevated production per unit leaf area and produced an increased recovery rate of stem diameter increment and ANPP.

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