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Impact of Hurricane Iniki on native Hawaiian *Acacia koa* forests: damage and two-year recovery

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ABSTRACT: Damage to Hawaiian *Acacia koa* forest by Hurricane Iniki was assessed by comparison with our previous measures of stand structure and leaf area index (LAI) at sites along a precipitation/elevation gradient on western Kauai. Reductions in LAI ranged from 29 to 80% and were correlated with pre-hurricane LAI and canopy height. The canopy damage resulted in a large pulse of litter, ranging from 4 to 19 t ha^{-1} across our study sites. In the first year post-hurricane, LAI recovery and relative increase in stand basal area were negatively correlated with the fraction of canopy LAI lost. The two major overstorey species, *A. koa* and *Metrosiderous polymorpha*, were damaged less than the sub-canopy species, *Dodonaea viscosa* and *Psidium guajava*. Although *D. viscosa* and *P. guajava* were both severely damaged in the hurricane, the alien species *P. guajava* had much higher survival than the native *D. viscosa*, both as adults and as seedlings. However, seedling density of *P. guajava* was limited by low recruitment. At these sites, there was no drastic change in species composition following hurricane disturbance, and forest structure and productivity had recovered to a great degree within 2 y.

KEY WORDS: *Acacia koa*, alien species, canopy, defoliation, *Dodonaea viscosa*, leaf area index, litterfall, *Metrosideros polymorpha*, *Psidium guajava*, seedling recruitment

INTRODUCTION

Hurricanes are a major force affecting structure and function of tropical forests. The passage of Hurricane Iniki (11 September 1992) over the island of Kauai provided an opportunity to assess mechanisms controlling the patterns of damage and recovery of Hawaiian forests. Prior to the hurricane, we had found that leaf area index (LAI), canopy height, and woody biomass increment of *Acacia koa* Gray stands increased along a gradient of increasing elevation and rainfall (Harrington *et al.* 1995). Consideration of aerodynamic drag suggests that taller stands or those with higher LAI would be damaged more than shorter or sparser canopies. This argument can be extended to the demographic structure within a stand, suggesting that the larger size classes of trees would suffer proportionally greater damage than smaller ones. It is reasonable to expect that more severely damaged stands would recover more slowly and show greater reduction in growth and survival: this pattern may have important implications for conservation of native forest if alien species survive better than natives. Also, recruitment of aliens into damaged native forest may cause changes in forest community dynamics and species composition. Our overall objectives were (1) to assess if hurricane-induced damage was related to pre-hurricane stand characteristics along a naturally-occurring gradient of stand height, LAI and productivity, and (2) to assess how species differed in their responses to damage, both as adults and as seedlings, because of the implications for long-term changes in species composition and the impact of alien species on native Hawaiian forest.

Severity of hurricane damage has been related to both site exposure and to stand characteristics (Basnet *et al.* 1992, Bellingham 1991, Foster & Boose 1992, Reilly 1991, Unwin *et al.* 1988). Within a site, taller or larger diameter trees were more damaged than smaller trees (Basnet *et al.* 1992, Foster 1988, Gresham *et al.* 1991, Reilly 1991, Walker 1991), although mortality was not necessarily a function of tree diameter (Bellingham 1991). In some instances, both taller and shorter trees were damaged more than intermediate-sized trees: the taller trees were damaged directly by wind whereas the smaller trees were damaged by falling debris (Frangi & Lugo 1991, Reilly 1991). In north Queensland, closed canopy forests with high tree density were more severely damaged than open canopy forests of similar exposure (Unwin *et al.* 1988). An analysis of the distribution of damage from the 1938 hurricane in New England suggested an interaction between site exposure and stand structure (Foster & Boose 1992). We could not test the effects of landscape position, but we hypothesized that hurricane damage would be proportional to *A. koa* stand stature and LAI across the elevational gradient, and that within a stand, the largest and smallest trees would be the most damaged.

An important impact of hurricanes on forest ecosystems is the large flux of biomass and nutrients from the canopy to the forest floor. Hurricane-induced leaf litterfall has ranged from 6.0 to 13.7 t ha^{-1} and branch and wood litter up to 13 t ha^{-1} (Frangi & Lugo 1991, Lodge *et al.* 1991, Thompson 1983). Such large pulses of debris increase the risk of severe wildfire (Stocker 1981), and transfer significant quantities of nutrients to the forest floor (Frangi & Lugo 1991, Lodge *et al.* 1991, Whigham *et al.* 1991). At our sites, large masses of litter were associated with woody debris, so we hypothesized the severity of damage would overwhelm any potential effects from increased nutrient availability, and thus result in slower recovery at more severely damaged sites.

The presence and amount of litter also has implications for establishment and survival of seedlings. A thick litter layer may impose a physical barrier and thus favour the establishment of plants with larger seeds which have larger reserves (Dalling 1995, Guzman-Grajales & Walker 1991). Litter also reduces the total amount of light reaching the soil surface (Facelli & Pickett 1991, Vazquez-Yanes *et al.* 1990). Germination of *Metrosideros polymorpha* seedlings was inhibited by the presence of a dense litter layer in stands of *Myrica faya* (Walker & Vitousek 1991). Once established, survival of shade-intolerant species was reduced by the presence of litter (Molofsky & Augspurger 1992). Also, a large pulse of litter, such as that induced by a hurricane, could bury seeds and seedlings, thus reducing germination and survival. You & Petty (1991) observed that 60% of the seedling population in *Manilkara bidentata* forests in Puerto Rico died after being buried by litter following Hurricane Hugo. You & Petty (1991) defined ‘recruitment cost’ of seedlings as the number of individuals lost per individual recruited. We hypothesized that this ratio of seedling mortality to recruitment will increase with amount of hurricane induced litterfall as a result of the negative impacts of large pulses of litter on both recruitment and survival.

Although a large pulse of litter may have a negative impact on seedling establishment, loss of overstorey canopy results in increased light availability at the forest floor (Brown 1993, Fernandez & Fetcher 1991, Turton 1992), and thus accelerated seedling growth rates for the surviving seedlings (Burton & Mueller-Dombois 1984, Osunkoya *et al.* 1993, You & Petty 1991). However, removal of the overstorey canopy on dry sites could result in water stress of seedlings, thus increasing mortality (Brown 1993, Canham & Marks 1985, Stocker 1981). Therefore, it is difficult to predict the potential effects of canopy disturbance on the demography of seedling populations. A goal of this study was to assess how seedling recruitment, survival and growth rates of native and alien species were related to light availability and hurricane-induced litterfall in *A. koa* forests following Hurricane Iniki.

Differences among species in susceptibility to and recovery from hurricane damage may alter species composition. In other studies, hurricanes damaged introduced species more than native species (Basnet *et al.* 1992, Thompson 1983), and conifers more than hardwoods (Foster & Boose 1992). Hurricane Hugo reduced species diversity of South Carolina sloughs, favouring species which were better adapted to these poorly drained sites (Putz & Sharitz 1991). However, there was no reduction in species richness in Nicaraguan rainforest following Hurricane Joan (Yih *et al.* 1991). For some species, resprouting following disturbance is an important mechanism of recovery (Glitzenstein & Harcombe 1988, Harcombe & Marks 1983, Putz & Brokaw 1989, Putz *et al.* 1983, Walker 1991, Yih *et al.* 1991). This recovery, or resilience, may be more important than resistance to damage: Hurricane Joan damaged pine trees less than rainforest trees, but none of the damaged pines resprouted, while almost all damaged rainforest trees resprouted (Boucher 1990). Following Hurricane Hugo in Puerto Rico, *Casearia arborea* lost a higher percentage of foliage than other species, yet it recovered foliage most rapidly (Walker 1991).

Our study sites were originally chosen for their dominance of *A. koa* in the overstorey canopy and minimal presence of alien species in the understorey (Harrington *et al.* 1995). However, the exotic species *Psidium guajava* L. and *Rubus argutus* Link, which are believed to threaten the persistence of native

Hawaiian forest (Smith 1989, Wagner *et al.* 1990), were present at some of the sites. We included these species in our inventories to assess if their rates of recruitment, growth or survival following disturbance were higher than those of native species, which could potentially lead to increasing density of these two exotics in native Hawaiian forest. Because of the dominance of *A. koa* at these sites, we would expect disturbance to favour the non-native invading species only at sites where both extensive canopy damage occurred and where pre-hurricane densities of exotics could not be dismissed as negligible. In our study areas, *R. argutus* reproduces vegetatively from below-ground runners rather than by seed production, but we monitored the survival and growth of these new shoots because they were in direct competition with seedlings on the forest floor.

METHODS

Study sites

Our study sites were dominated by *A. koa*, an endemic, phyllode-forming hardwood species. Sites were chosen on the northwestern slope of the island of Kauai (Figure 1), along an elevational gradient ranging from 500 to 1130 m, with rainfall ranging from 850 to 1800 mm from low to high elevation (Giambelluca *et al.* 1986). Six study sites, in the Puu Ka Pele Forest Reserve, Na Pali Kona Forest Reserve, and Kokee State Park, were established in 1992 to study the effects of rainfall on *A. koa* forest productivity and resource-use efficiency (Harrington *et al.* 1995). A single circular plot, 20 m in diameter, was established at each site along the gradient, except for Makaha 1 (500 m asl) and Milolii (800 m asl), where 12-m diameter plots were used to allow sufficient gap-free border. Prior to Hurricane Iniki (Table 1), stands along the gradient had basal area ranging from 8 to 42 $m^2\ ha^{-1}$, LAI ranging from 1.5 to 5.4, canopy height ranging from 2.6 to 11.3 m and annual wood production ranging from 0.7 to 7.1 $t\ ha^{-1}\ y^{-1}$, all generally increasing with elevation and rainfall (Harrington *et al.* 1995).

The major canopy species at all sites was *A. koa*, with some individuals of *Metrosideros polymorpha* Gaud. present in the canopy and sub-canopy at most sites. The indigenous species *Dodonaea viscosa* Jacq. occurred in the sub-canopy at Makaha 2 (640 m asl), Milolii, Puu Opae (900 m asl) and Halemanu (1130 m asl). Some exotic species were also present at most sites. *Lantana camara* L. was present in the understorey at Makaha 1 and Makaha 2, *Psidium guajava* L. was in the sub-canopy at Makaha 2, Puu Opae, and Kumuwela (1100 m asl), and *Rubus argutus* Link was present in the understorey at the two high elevation sites, Kumuwela and Halemanu.

On 11 September 1992, Hurricane Iniki moved over the island of Kauai at an estimated 32 to 40 km h^{-1} in a roughly NNE direction, with steady winds of over 230 km h^{-1} and gusts over 280 km h^{-1} (National Weather Service 1992).

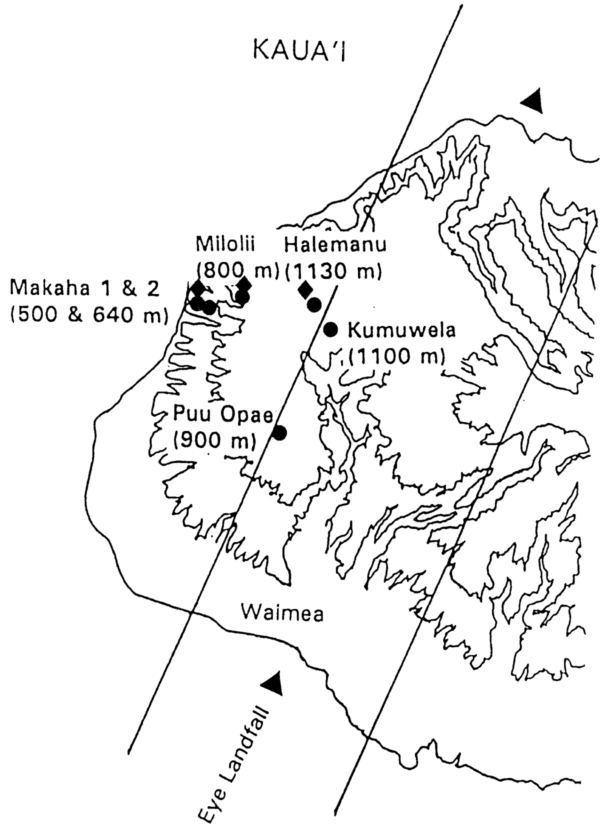

Figure 1. Path of Hurricane Iniki relative to the location of study sites (●) and weather stations (◆) in *Acacia koa* forests along an elevation/precipitation gradient on west Kauai, Hawaii.

Table 1. Site and pre-Hurricane Iniki stand characteristics of six *Acacia koa* forests growing along an elevation/precipitation gradient on northwestern Kauai, Hawaii

Site	Elevation (m)	Precipitation (mm y^{-1})	Slope (°)	Aspect (°)	Stem density (ha^{-1})	Mean DBH (cm)	LAI
Makaha 1	500	850	10	265	4686	4.0	1.4
Makaha 2	640	1000	25	310	1210	10.8	3.5
Milolii	800	1165	12	280	6012	3.7	1.7
Puu Opae	900	1270	10	20	1878	9.4	2.5
Kumuwela	1100	1750	17	210	2992	10.0	5.4
Halemanu	1130	1800	10	170	8244	5.0	4.1

The estimated track of the eye passed closest to Puu Opae and Kumuwela and within a few kilometers of the other sites (Figure 1). Iniki, classified as a category 5 storm (on the Saffir-Simpsom scale), was the most powerful storm experienced in the Hawaiian Islands in at least 90 y, although the island of Kauai was struck by Hurricane Iwa just 10 y prior, in 1982.

Damage assessment and growth response

Background data collected prior to the storm included stem diameter at 1.3 m (DBH) for all trees (>2.0 cm) in our measurement plots in spring 1992 at all sites except Milolii. We measured DBH at all six sites during the 4 d just before Hurricane Iniki struck. After the hurricane, survival and DBH were measured at 6-mo intervals for 2 y.

We assessed initial damage to our field sites from 10 to 18 d following Hurricane Iniki. Damage classes, ranging from 1 to 4, were based on visual estimates of percent of canopy removed: (1) <25% canopy removed, including trees with no visible damage, (2) 25–50% canopy removed, (3) 50–75% canopy removed, and (4) >75% canopy removed. Trees were grouped into DBH classes of 5 cm intervals for the purpose of chi-squared tests of whether damage class was independent of species and diameter class (Statistix 4.0, 1992). Separate tests were carried out for each site.

Leaf area index

Pre- and post-hurricane LAI was estimated at each site using an LAI-2000 plant canopy analyzer (LI-COR Inc., Lincoln, NE). In previous work, LAI measurements from harvest of the phyllodinous *Acacia auriculiformis* and other tropical hardwoods agreed well with optical LAI estimates (Harrington & Fownes 1995). Mean LAI was determined from nine readings taken 1 m above each litter trap; time of day and sensor orientation were held constant for each stand during the study. Post-hurricane LAI values were compared with pre-hurricane values to determine leaf area removal. Recovery of LAI was monitored monthly for the first year and every 3 mo during the second year following Hurricane Iniki.

Transmitted radiation

For a given time interval, transmitted radiation (Q_t, moles m^{-2}) was estimated as a function of the average LAI over the interval with the following equation:

$$Q_t = Q_o e^{-kLAI}$$

where Q_o (moles m^{-2}) is the incident photosynthetically active radiation (PAR) totalled over the time interval and k is the radiation extinction coefficient (Russell *et al.* 1989). A k value of 0.45 was used for the *A. koa* stands in this study (Meinzer *et al.* 1996).

Litterfall

Litterfall induced by the hurricane was estimated from nine litter traps (each 0.19 m^2) per site which had been put in place from 1–4 d before Hurricane Iniki. Litter traps were not installed at Makaha 2 and Puu Opae before the hurricane. Hurricane-induced litter was collected 10–18 d after the hurricane. The nine samples collected from each site were separated into leaf, twig (<1 cm diameter) and wood (>1 cm diameter) components. Litter was dried (70 °C), weighed, and leaf and twig components were then composited by site and analyzed for nutrient contents by the University of Hawaii Agricultural Diagnostic Service Center.

Seedling growth and demography

In July 1993 (10 mo following Hurricane Iniki) four permanent quadrats were established at each of the six study sites. No major disturbances, aside from typical winter storms, occurred following the hurricane prior to the set up of the quadrats. The quadrats ran out from the centre of the pre-existing plots in north, south, east and west directions. Quadrat size was 1 m × 8 m for a total of 32 m^2 sampling area at all sites except Makaha 1 (500 m) and Milolii (800 m). At Makaha 1 and Milolii, quadrat size was 1 m × 5 m for a total of 20 m^2 sampling area, to accommodate the smaller size of the pre-existing measurement plots (see *Study sites* above). In July 1993, all seedlings within these quadrats were labelled with small plastic stakes, identified by species, and seedling height was measured. In February and July 1994 new seedlings were identified, labelled and measured, old seedlings were remeasured; and recruitment, survival and growth rate were calculated. We defined a recruit as a seedling which was not present at the previous inventory but had since germinated and had survived until the following inventory. Our inventory method did not account for seedlings which became established and subsequently died between two measurement times. Relative growth rate (RGR, cm cm^{-1} mo^{-1}) was calculated as:

$$RGR = (\ln(H_{t+1}) - \ln(H_t))/\Delta t$$

where H is seedling height (cm) and Δt is the measurement interval (mo).

Weather data

Weather stations (Campbell Scientific, Inc., Logan UT) were located in clearings at 500, 800 and 1100 m elevation along the gradient (Figure 1). PAR (moles m^{-2}) was measured using a LI190SB quantum sensor, and rainfall (mm) was measured using a TE525 tipping bucket raingage. Measurements were made at 15-s intervals, and daily PAR and rainfall totals were stored in a datalogger (model CR10).

RESULTS

Stand level damage

The severity of damage differed among the sites (Figure 2), and was related to the types of damage incurred. Makaha 1 primarily lost senesced phyllodes

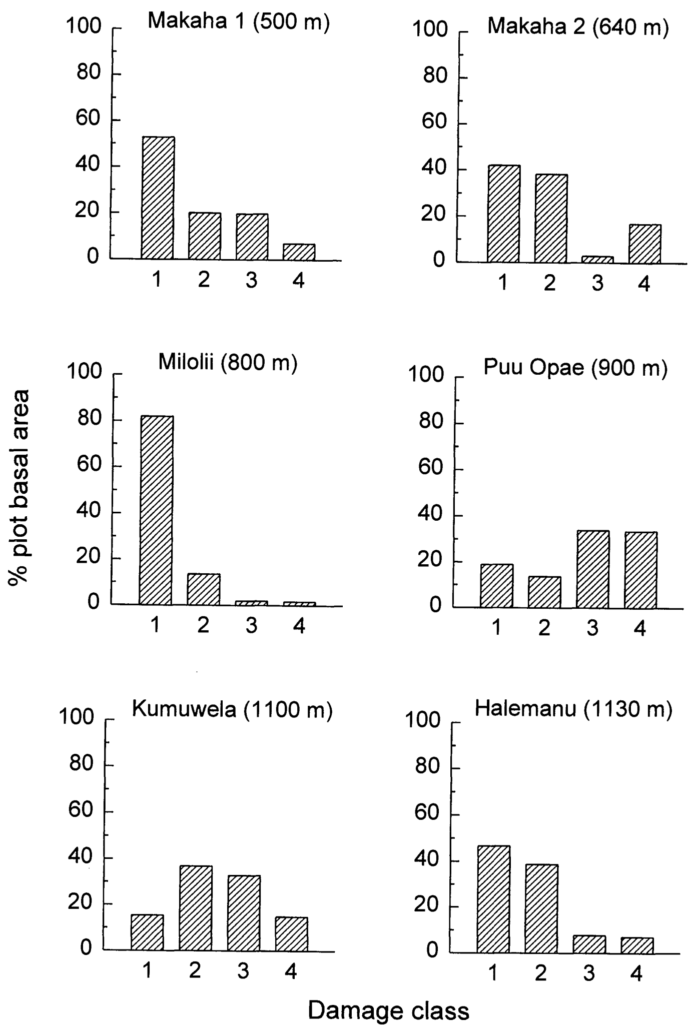

Figure 2. Percentages of the total plot basal area (including all species) of the six *Acacia koa* forest stands that were in each damage class immediately following Hurricane Iniki. Damage classes as percentage of the canopy removed: (1) <25%, (2) 25–50%, (3) 50–75%, and (4) >75%.

and dead twigs, although a few trees lost major structural branches. At Makaha 2 large gaps were formed in the canopy primarily by branch breakage, rather than by phyllode stripping. At Milolii the damage was primarily the removal of senesced phyllodes, leaving the canopy otherwise intact. Puu Opae was the most severely damaged site, with many large branches and a few entire trees broken off. Damage at Kumuwela included the breakage of major structural branches, many of which remained suspended in the canopy. Although Halemanu is located close to Kumuwela, damage was limited primarily to the stripping of green foliage from twigs in the canopy (Figure 2).

Immediate losses in stand LAI ranged from 18 to 58%, but became greater over time ranging from 29 to 80% (Figure 3) because of structural damage to

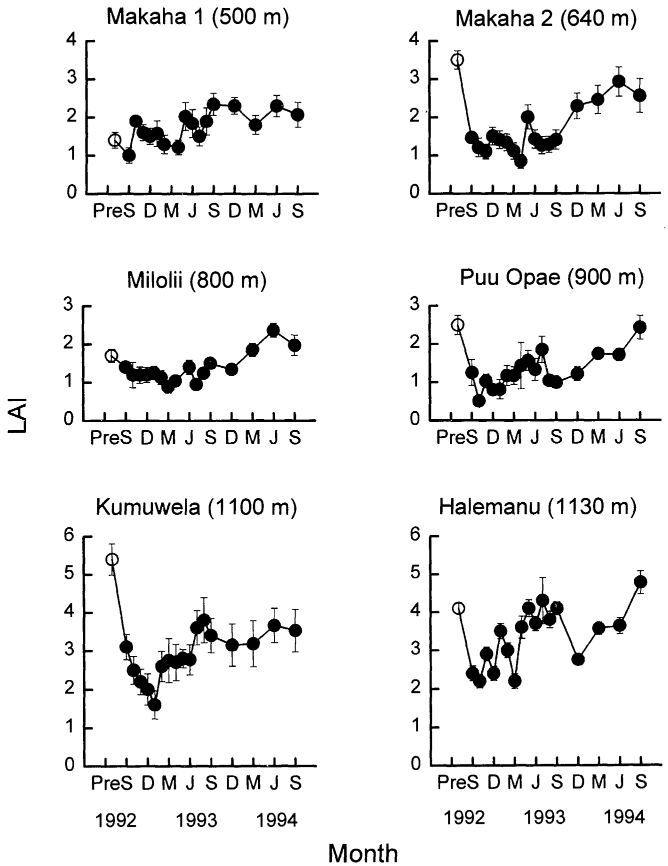

Figure 3. Stand leaf area index (LAI) from spring 1992 (pre-hurricane, (○)) to September 1994. Error bars denote standard errors (n = 9).

major branches (e.g. Kumuwela and Puu Opae), or wrenching of roots on steep slopes (e. g. Makaha 2). The total loss of LAI was positively correlated with pre-hurricane LAI and canopy height, as hypothesized (Figure 4a, b).

Removal of foliage and twigs from the canopy resulted in a large flux of biomass and nutrients to the forest floor. The flux at the high elevation, high LAI sites, Kumuwela and Halemanu, was greater than at low (Makaha 1) and middle elevations (Milolii; Table 2). Total litterfall mass ranged from 3.9 t ha^{-1} at Milolii to 18.6 t ha^{-1} at Kumuwela, and fine (leaf and twig) litterfall mass ranged from 3.3 t ha^{-1} at Milolii to 14.2 t ha^{-1} at Kumuwela. The proportion of litter composed of wood and twig debris was relatively constant, ranging from 71% at Halemanu to 80% at Kumuwela. Total nutrients in leaf plus twig components ranged from 26–169 kg N ha^{-1}, 0.4–4.6 kg P ha^{-1}, and 4.6–24.2 kg K ha^{-1} (Table 2).

Species and size class differences

Damage class distributions were not independent of species at Milolii ($\chi^2 = 33.01$, df = 3, P<0.0001), Puu Opae ($\chi^2 = 35.49$, df = 9, P<0.0001), Kumuwela

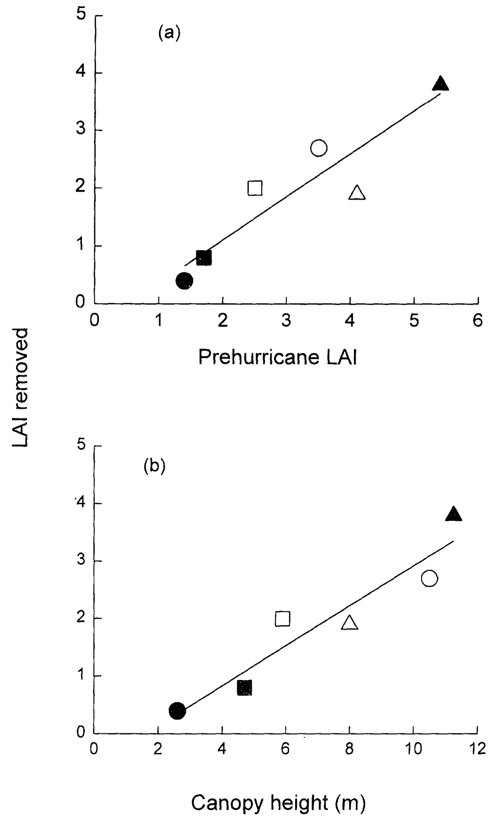

Figure 4. The relationship between amount of reduction in leaf area index (LAI) and (a) pre-hurricane LAI and (b) canopy height. The six study sites were Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Milolii at 800 m (■), Puu Opae at 900 m (□), Kumuwela at 1100 m (▲), and Halemanu at 1130 m (△). Solid lines represent significant ($P<0.05$) regressions (LAI removed = −0.3850 + 0.7479 pre-hurricance LAI, $r^2 = 0.85$, $P = 0.0095$; LAI removed = −0.5602 + 0.3483 Canopy height, $r^2 = 0.90$, $P = 0.0041$).

Table 2. Dry matter and nutrient flux in leaf, twig (<1 cm diameter), and wood (>1 cm diameter) litter blown down by Hurricane Iniki and collected 8–10 d after the storm. Standard errors are shown in parentheses for litter mass

Site	Component	Litter (t ha^{-1})	N (kg ha^{-1})	P (kg ha^{-1})	K (kg ha^{-1})
Makaha 1	Leaf	1.3 (0.36)	20	0.6	5.8
	Twig	3.6 (2.46)	34	0.8	4.3
	Wood	1.2 (2.03)	nd	nd	nd
Milolii	Leaf	0.9 (0.41)	9	0.1	2.0
	Twig	2.4 (1.51)	17	0.3	2.6
	Wood	0.6 (1.62)	nd	nd	nd
Kumuwela	Leaf	3.6 (3.00)	66	1.9	8.0
	Twig	10.6 (4.13)	103	2.7	12.7
	Wood	4.4 (7.57)	nd	nd	nd
Halemanu	Leaf	3.1 (1.07)	53	1.4	14.1
	Twig	6.3 (2.53)	57	1.5	10.1
	Wood	1.3 (1.92)	nd	nd	nd

nd = not determined

Table 3. The total number of individuals (N) of *Acacia koa*, *Dodonaea viscosa*, *Metrosideros polymorpha*, and *Psidium guajava* at six study sites on northwestern Kauai; with the percentage of the individuals in each damage class immediately following Hurricane Iniki and the percent survival of damage class 4 individuals, 6 mo after the hurricane. Damage classes defined in terms of percentage of the canopy removed were: (1) 0–25%, (2) 25–50%, (3) 51–75%, and (4) >75%

Site	Species	N	Damage class 1	2	3	4	% survival of class 4
Makaha 1	*A. koa*	53	51	22	12	15	50
Makaha 2	*A. koa*	36	47	33	5	14	80
	M. polymorpha	37	30	32	0	38	79
Milolii	*A. koa*	68	91	5	2	2	0
	D. viscosa	21	38	10	19	33	86
Puu Opae	*A. koa*	66	27	23	24	26	53
	D. viscosa	9	0	0	0	100	0
	M. polymorpha	16	6	44	25	25	25
	P. guajava	6	0	0	0	100	67
Kumuwela	*A. koa*	87	18	23	24	35	80
Halemanu	*A. koa*	252	44	23	12	21	69
	D. viscosa	96	25	43	3	29	50
	M. polymorpha	39	90	5	0	5	100

($\chi^2 = 53.89$, df = 3, P<0.0001), and Halemanu ($\chi^2 = 100.2$, df = 9, P<0.0001). Overall, the two main overstorey species, *A. koa* and *M. polymorpha* had a greater proportion of individuals in damage class 1 and a lower proportion of individuals in damage class 4 than did the sub-canopy species *D. viscosa* and *P. guajava* (Table 3).

Damage to *A. koa* trees was not independent of diameter class at Makaha 1 ($\chi^2 = 8.54$, df = 3, P = 0.0362), Puu Opae ($\chi^2 = 18.25$, df = 9, P = 0.0324), Kumuwela ($\chi^2 = 29.04$, df = 9, P = 0.0006) and Halemanu ($\chi^2 = 24.97$, df = 9, P = 0.0030), although neither the smallest nor the largest trees were consistently more damaged among the sites. At Makaha 1 and Kumuwela, trees in the smallest diameter classes showed the greatest susceptibility to severe damage (Figure 5). At Puu Opae, severe damage occurred in all diameter classes, but trees in the two largest size classes suffered most, with more than 50% of the individuals classified as damage classes 3 and 4 (Figure 5). At Halemanu, the 0–5 cm and the 10–15 cm size classes were more damaged than the intermediate 5–10 cm size class. Patterns of damage among diameter classes were thus most strongly related to prior stand structure: the hypothesized greater damage to large and small size classes only occurred when there was substantial representation across a wide range in diameter classes before the hurricane.

Recovery

Recovery from canopy damage varied over the six sites. LAI had returned to pre-hurricane values within 1 y at Makaha 1, Milolii and Halemanu (Figure 3). LAI at the Halemanu site decreased as a result of storms in March and December 1993. The March storm resulted in canopy loss comparable to that following Hurricane Iniki, but in each case the canopy recovered within a few

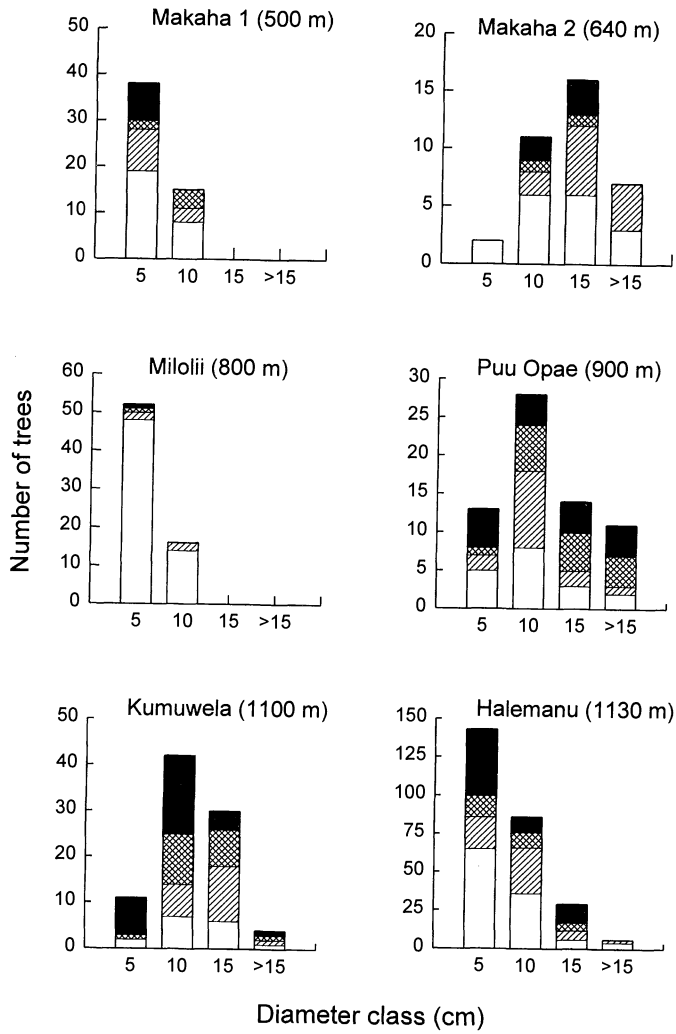

Figure 5. The number of *Acacia koa* trees in damage classes 1 (□), 2 (▨), 3 (▩) and 4 (■), within each stem diameter (dbh) size class (0.1–5.0, 5.1–10, 10.1–15, >15 cm).

months. The immediate increase and subsequent slight decline in LAI at Makaha 1 was the result of flushing and dieback of the exotic species *L. camara*, which exceeded 2 m in height at the site. Canopy recovery at Puu Opae took 2 y, while the canopies at Makaha 2 and Kumuwela still had not fully recovered by that time (Figure 3), due to extensive structural damage to the canopy.

Tree growth rates were controlled by the decrease and subsequent recovery of LAI at each site. In the first year post-hurricane, LAI recovery and relative increase in stand basal area were negatively correlated with fraction of canopy LAI lost (Figure 6). During the first 6-mo interval following the hurricane, diameter increment rates were lower than pre-hurricane rates at all sites except Makaha 1. Diameter increment had recovered to pre-hurricane values

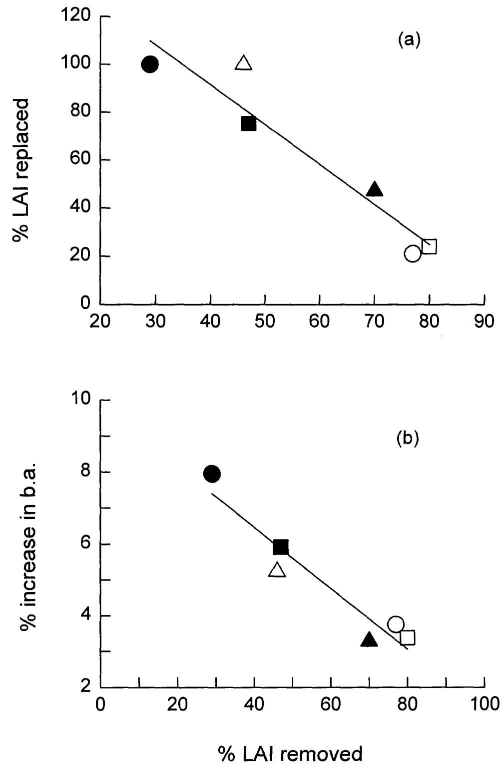

Figure 6. Percentage recovery of (a) the total leaf are index (LAI) lost in Hurricane Iniki, and (b) the percentage increase in plot basal area (b.a.), 1 y after the hurricane, versus percentage of the pre-hurricane LAI that was removed by the hurricane. Symbols for the six study sites as in Figure 4. Lines represent significant ($P<0.05$) regressions (% LAI replaced = 158.25 – 1.6668 % LAI removed, $r^2 = 0.91$, $P = 0.0031$; % increase in b.a. = 9.8747 – 0.0852 % LAI removed, $r^2 = 0.91$, $P = 0.0031$).

at three of the six sites within 2 y after the hurricane, and exceeded pre-hurricane values at Puu Opae and Kumuwela (Table 4).

The two subcanopy species, *D. viscosa* and *P. guajava*, were severely damaged in the hurricane, but the native *D. viscosa* generally had less capacity to recover from severe damage. At Puu Opae, the one site where both species occurred

Table 4. Mean diameter increment rates (mm 6-mo^{-1}) of *Acacia koa* measured pre-hurricane (March–September 1992), immediately post-hurricane (September 1992–March 1993), and 2 y post-hurricane (March–September 1994) at the six study sites. Standard errors are shown in parenthesis.

Site	Pre-hurricane	September 1992–March 1993	March–September 1994
Makaha 1	0.90 (0.111)	1.02 (0.201)	0.76 (0.140)
Makaha 2	2.42 (0.400)	0.94 (0.190)	1.72 (0.289)
Milolii	nd	0.57 (0.098)	1.09 (0.162)
Puu Opae	1.08 (0.318)	0.67 (0.104)	2.23 (0.219)
Kumuwela	1.95 (0.281)	0.96 (0.128)	2.36 (0.343)
Halemanu	1.55 (0.135)	0.84 (0.071)	1.54 (0.149)

nd = not determined

Table 5. Seedling density in July 1993 and July 1994, and annual (July 1993–July 1994) mortality and recruitment, percent survival and relative height growth rate for *Acacia koa*, *Dodonea viscosa*, *Psidium guajava*, and *Rubus argutus*.

Species	Site	Density (m^{-2}) 1993	Density (m^{-2}) 1994	Mortality (m^{-2} y^{-1})	Recruitment (m^{-2} y^{-1})	Survival (%)	RGR (cm cm^{-1} mo^{-1})
A. koa	Makaha 1	0.1	0.4	0.6	0.9	50	0.005
	Makaha 2	1.4	3.0	0.8	2.3	61	0.024
	Milolii	12.6	18.8	7.0	12.9	57	0.006
	Puu Opae	21.3	19.4	7.4	5.7	36	0.002
	Kumuwela	1.5	1.0	0.9	0.5	47	0.011
	Halemanu	0.4	0.4	0.3	0.3	57	0.020
D. viscosa	Makaha 1	2.6	22.1	3.4	22.7	53	0.053
	Makaha 2	<0.1	0.5	<0.1	0.5	100	0.119
	Milolii	2.5	3.5	1.3	23.1	38	0.025
	Puu Opae	0.5	0.3	0.2	0.1	40	0.009
	Halemanu	<0.1	0.1	<0.1	0.1	67	0.018
P. guajava	Makaha 1	0.9	1.6	0.2	0.6	67	0.022
	Makaha 2	0.0	<0.1	0.0	<0.1	nd	nd
	Puu Opae	1.9	2.3	0.8	0.6	48	0.009
R. argutus	Kumuwela	2.5	2.4	1.7	1.6	35	0.017
	Halemanu	2.4	2.0	2.7	2.2	9	0.025

nd = not determined

together, two thirds of the severely damaged *P. guajava* trees survived, while none of severely damaged *D. viscosa* trees survived (Table 3).

Seedling density and recruitment

Total seedling densities varied by an order of magnitude across sites (Table 5), and generally increased with increasing PAR transmitted to the forest floor (Figure 7). *Acacia koa* had the highest density and annual recruitment of seedlings at the intermediate sites (Milolii and Puu Opae) along the rainfall gradient (Table 5). Recruitment of *A. koa* was approximately equal to seed production at the lower and mid-elevation sites, but was much lower than seed

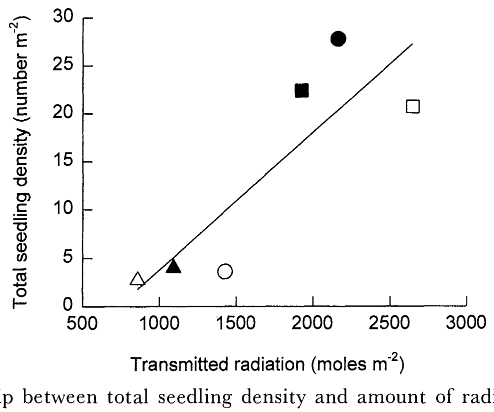

Figure 7. The relationship between total seedling density and amount of radiation transmitted through the forest canopy. Symbols for the six study sites as in Figure 4. Line represents significant ($P<0.05$) regression (total seedling density = −10.5136 + 0.0143 transmitted radiation, $r^2 = 0.73$, $P = 0.0291$).

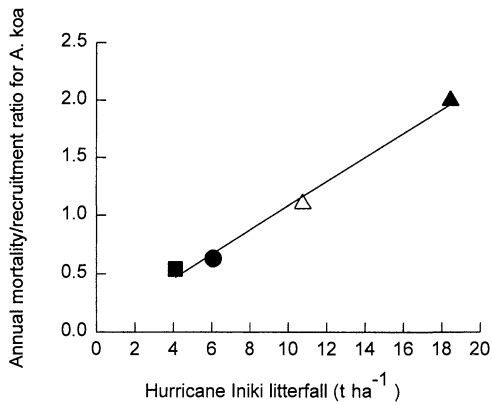

Figure 8. The ratio of annual mortality to recruitment for *Acacia koa* seedlings versus the amount of litterfall resulting from Hurricane Iniki. Symbols for the six study sites as in Figure 4. Line represents significant ($P<0.05$) regression (annual mortality/recruitment ratio = 0.0377 + 0.1046 Hurricane Iniki litterfall, $r^2 = 0.99$, $P = 0.0050$).

production at the two high elevation sites, suggesting that recruitment of *A. koa* seedlings was not limited by seed source at Halemanu and Kumuwela. *D. viscosa* experienced the highest seedling density and recruitment at the driest, low elevation site, Makaha 1. Densities and recruitment of *P. guajava* seedlings and *R. argutus* shoots were relatively low at the sites where they were found, even though *R. argutus* was the predominant understorey species at the two wet sites, Kumuwela and Halemanu (Table 5).

Seedling survival and growth

Neither seedling survival nor growth were correlated with light, precipitation, litterfall, or seedling density for any of the four species. However, the annual mortality/recruitment ratio of *A. koa* increased linearly with amount of hurricane-induced litterfall (Figure 8), resulting in lower seedling densities at sites with higher amounts of hurricane litterfall, as we hypothesized.

Comparing species, the highest growth rates did not necessarily correspond to the highest rates of survival. At sites where *A. koa*, *D. viscosa*, and *P. guajava* were all present, growth was highest for *D. viscosa*, followed by *P. guajava* and then *A. koa*, but survival was highest for *P. guajava*, followed by *D. viscosa* and then *A. koa* (Table 5). At the two sites where *R. argutus* was present, its survival was lower than the other species, and its growth rates were varied. It experienced relatively high growth at one site and a negative growth rate (shoot tip die-back) at the other.

DISCUSSION

Damage

The strongest pattern of damage among sites was the correlation of LAI loss with pre-hurricane LAI and canopy height, suggesting a primary effect of aerodynamic drag. Because our gradient of stand characteristics coincided with distance from the estimated eye track (Figure 1), it could be argued that differences in damage were only coincidentally related to LAI and height. We believe this explanation is unlikely based on data from nearby *M. polymorpha* forest, where differences in pre-hurricane LAI among plots had been created by fertilization in a randomized block design (Herbert & Fownes 1995). In these plots, LAI loss was also correlated with pre-hurricane LAI (Herbert 1995). Furthermore, severe damage to forest occurred throughout Kauai and was not limited to the path of the eye. Very severe localized damage, greater than that observed in our studies, was often associated with violent microbursts which appear to be more or less random in occurrence because they are not related to either topography or stand characteristics (National Weather Service 1992).

At some sites, especially Kumuwela, estimated overstorey LAI continued to decline for several months following the hurricane as a result of gradual dropping of phyllodes from damaged branches suspended in the canopy. Because the optical LAI technique cannot distinguish living from dead foliage, it probably underestimated the immediate loss of LAI and delayed our detection of canopy recovery. A similar pattern of suspended litter was observed after Hurricane Hugo (Lodge *et al.* 1991) and in *M. polymorpha* forest on Kauai (Herbert 1995).

The magnitude of hurricane-induced litterfall observed across our sites was within the range of hurricane-induced litterfall observed in other tropical forests (Frangi & Lugo 1991, Lodge *et al.* 1991, Thompson 1983). We have no measurement of pre-hurricane litterfall at our sites for direct comparison, but litterfall in mature *A. koa* forests on the island of Hawaii ranged from 6.3 to 12.2 t ha^{-1} y^{-1}, with foliar litter comprising approximately 70% of the total fine litterfall (Scowcroft 1986). Therefore, the flux of litter we observed as a result of the hurricane was equal to or greater than total annual litterfall observed in other *A. koa* forests, although the wood to leaf ratios were approximately reversed.

Large nutrient transfers result from large litter mass and higher nutrient concentration in green leaves in hurricane-induced litterfall (Frangi & Lugo 1991, Lodge *et al.* 1991, Whigham *et al.* 1991; Table 2). However, we also observed large transfers of nutrients in the twig component, which had a relatively low nutrient concentration but had a large total mass (Table 2). Although high-nutrient green leaf litter may decompose relatively rapidly, large pools of slowly decomposing twigs and wood could immobilize nutrients, thus reducing availability for plant uptake (Zimmerman *et al.* 1995).

Recovery

The six sites varied in their response to canopy damage, and the differences observed were attributable to the amount and type of damage incurred. The slow recovery of Puu Opae, Makaha 2, and Kumuwela was caused by the loss of major structural branches, resulting in large gaps in the canopy and loss of 69 to 80% of LAI. This interpretation is supported by the large mass of woody litter at Kumuwela (Table 2). The relatively slow-growing *M. polymorpha* forest on Kauai had not fully regained pre-hurricane LAI after 2 y (Herbert 1995). In contrast, rapid recovery of defoliated tropical forest canopies was observed following Hurricane Gilbert (Whigham *et al.* 1991) and Hurricane Hugo (Frangi & Lugo 1991) and a tropical cyclone (Turton 1992).

Our frequent measurements of LAI for the 2 y following Hurricane Iniki allowed us to closely track fluctuations in canopy leaf area. Results from the Halemanu site indicate that significant disturbances are more frequent than hurricanes, and that the impact of winter storms on forest canopies can be almost as severe as that of Iniki. These decreases in LAI corresponded to increases in litterfall over the same time intervals (data not shown) indicating that the decreases were real and did not result from measurement error. The results of our intensive long-term monitoring show that leaf area, a major control of forest productivity, is extremely dynamic and that relatively important perturbations are more frequent than previously believed.

The parallel trends in LAI recovery and diameter increment agree with our pre-hurricane observation that diameter increment was correlated with LAI (Harrington *et al.* 1995). At Puu Opae and Kumuwela, diameter increment was actually greater 2 y post hurricane than it was prior to the hurricane, possibly as a result of greater growth efficiency of the remaining trees which had been released from suppression. A similar increase in diameter increment was observed following Hurricane Gilbert in those species that regenerated well (Whigham *et al.* 1991).

Although sample size for hurricane-induced litterfall is small (four sites), and results should be interpreted with care, our results suggest that hurricane-induced litterfall had an impact on seedling density. Sites that received the most hurricane litterfall experienced reduced germination (as reflected in low recruitment/seedfall ratios), and increased seedling mortality (as reflected in high mortality/recruitment ratios). However, our sites with the greatest amount of hurricane-induced litter also had the highest overstorey canopy LAI at the time of this study. Therefore, we cannot rule out the possibility that low light transmission through the overstorey canopy alone may explain low seedling population densities at these sites.

The differences among species in recovery from damage has implications for future species composition. The comparatively low survival of both adults and seedlings of the native *D. viscosa* suggests that the more resilient alien *P. guajava* will increase its importance in the understorey. However, we have no data on seedling populations prior to 10 mo post-hurricane, so we do not know the importance of seedlings present pre-hurricane, or the recruitment of seedlings within the first 10 mo post-hurricane. At Makaha 1, the rapid flushing of *L. camara* leaf area may suppress future recruitment of *A. koa*. However, there was little entry of new seedlings of alien species in these sites, suggesting that changes would be incremental rather than drastic. Based on our study sites, the impact of Hurricane Iniki on native *A. koa* forest was in general not catastrophic, and to a great degree, forest structure and productivity had recovered within 2 y.

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