Impacts of Hurricane Iniki on Koa Forests

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Abstract

On 11 September 1992, Hurricane Iniki struck koa forests we had studied along an elevation gradient (500 to 1300 m) on western Kaua'i. The hurricane decreased canopy leaf area by 29 to 80 percent, and damage was proportional to pre-hurricane leaf area and canopy height. At some sites, phyllodes were stripped from intact branches, leaving the canopy otherwise intact. At other sites, many large branches and a few entire trees were broken off, thereby removing most of the overstory canopy. 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 six months following the hurricane, tree growth rates decreased in proportion to leaf area lost. Thereafter, growth rates increased, generally following the pattern of leaf area recovery. Survival of severely damaged koa trees (losing more than 75 percent of their crowns) ranged from zero to 80 percent, and was higher at wetter sites. Koa seedling densities were highest at mid-elevation sites as a result of both high emergence and high survival. Seedling densities were lower at sites with greater amounts of hurricane-induced litter. The alien species guava (*Psidium guajava*) generally had higher survival than the native 'a'ali'i (*Dodonea viscosa*), both as adults and as seedlings, but there was relatively little invasion of alien species following the hurricane. 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 two years.

Introduction

Hurricanes are a major force affecting the structure and function of tropical forests. The passage of Hurricane Iniki (11 September 1992) over the island of Kaua'i provided an opportunity to assess mechanisms controlling the patterns of damage and recovery of Hawaiian forests. Prior to the hurricane, we had found that canopy leaf area, canopy height, and woody biomass increment of koa (*Acacia koa* Gray) stands increased along a gradient of increasing elevation and rainfall (Harrington et al. 1995). Taller stands or those with greater amounts of leaf area may be more susceptible to wind damage than would shorter or sparser canopies, and it is reasonable to expect that more severely damaged stands would recover more slowly and show greater reduction in growth and survival. Differences in patterns of damage and recovery across species 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, canopy leaf area, 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. A more detailed account of this study is presented by Harrington et al. (1997).

Severity of hurricane damage has been related to stand characteristics in other studies. Within a site, taller or larger diameter trees are more damaged than smaller trees (Basnet et al. 1992, Foster 1988, Gresham et al. 1991, Reilly 1991, Walker 1991). An analysis of the distribution of damage from the 1938 hurricane in New England indicates that the proportion of damaged trees increased with increasing stand height (Foster and Boose 1992). Therefore, we hypothesized that hurricane damage would be proportional to koa stand stature and canopy leaf area across the elevational gradient, and that within a stand the largest trees would be the most damaged.

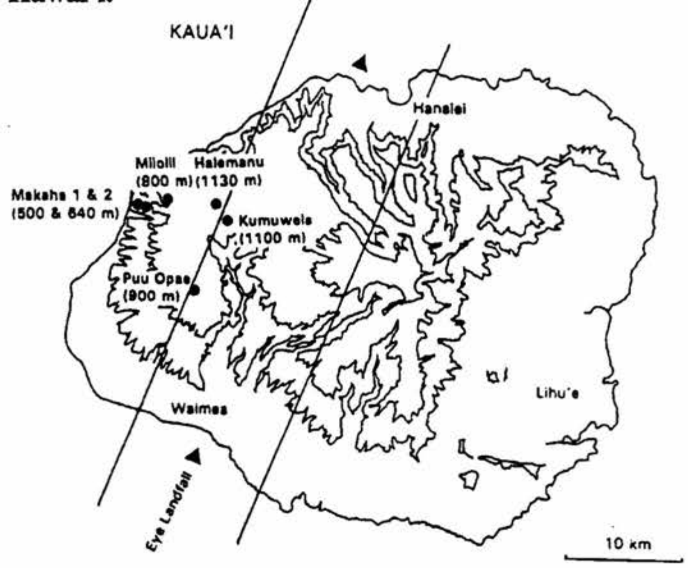
An important impact of hurricanes on forest ecosystems is the large flux of biomass from the canopy to the forest floor. In Puerto Rico, Hurricane Hugo resulted in a loss of 6.0 t ha^{-1} leaves and 13.5 t ha^{-1} branches and boles from aboveground biomass in floodplain forest (Frangi and Lugo 1991) and approximately 10 t ha^{-1} of fine litterfall in subtropical wet and lower montane sites

(Lodge et al. 1991). Leaf litterfall induced by Hurricane Allen ranged from 6.1 to 13.7 t ha^{-1} in lower montane Jamaican forest (Thompson 1983).

The presence and amount of litter has implications for establishment and survival of seedlings. A large pulse of litter, such as that induced by a hurricane, could bury seeds and seedlings, thus reducing germination and survival. You and Petty (1991) observed that 60 percent of the seedling population in *Manilkara bidentata* forests in Puerto Rico died after being burried by litter following Hurricane Hugo. However, although a large pulse of litter may have a negative impact on seedling establishment, loss of canopy leaf area results in increased light availability at the forest floor (Brown 1993, Fernandez and Fetcher 1991), and thus accelerated seedling growth rates for the seedlings present (Burton and Mueller-Dombois 1984, Osunkoya et al. 1993, You and Petty 1991). Therefore, it is difficult to predict the potential effects of canopy disturbance on the demography of seedling populations. Another 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 koa forests following Hurricane Iniki.

Differences among species in susceptibility to and recovery from hurricane damage may alter forest species composition. Our study sites were originally chosen for their dominance of koa in the overstory canopy and minimal presence of alien species in the understory (Harrington et al. 1995). However, the exotic species lantana (*Lantana camara*), guava (*Psidium guajava*), and blackberry (*Rubus argutus*), which are believed to threaten the persistence of native Hawaiian forest (Smith 1989, Wagner et al. 1990), were present at some of the sites. Their presence allowed us to assess if alien species exhibited higher rates of recruitment, growth, or survival than native species following disturbance, which could potentially lead to increasing density of these alien plants in native Hawaiian forest.

Figure 1. Path of Hurricane Iniki relative to the location of study sites (•) in *Acacia koa* forests along an elevation/precipitation gradient on west Kaua'i, Hawai'i.



Methods

Study sites. Our study was conducted in koa forests on the northwestern slope of the island of Kaua'i (Figure 1). Sites were located along an elevational gradient ranging from 500 m 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 Pu'u Ka Pele Forest Reserve, Na Pali Kona Forest Reserve, and Koke'e State Park, were established in 1992 to study the effects of rainfall on forest productivity (Harrington et al. 1995). Plots were circular, 20 m in diameter, except for Makaha 1 (500 m asl) and Miloli'i (800 m asl), where 12 m diameter plots was used to allow sufficient gap-free border. Prior to Hurricane Iniki (Table 1), koa stands along the gradient had basal area ranging from 8 to 42 m^2 ha^{-1}, canopy leaf area per unit ground area 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 koa, with some individuals of 'ohi'a (*Metrosideros polymorpha*) present in the canopy and sub-canopy at most sites. The indigenous species, 'a'ali'i (*Dodonaea viscosa*) occurred in the sub-canopy at Makaha 2 (640 m asl), Miloli'i, Pu'u 'Opae (900 m asl), and Halemanu (1130 m asl). Some exotic species were also present at most sites. Lantana was present in the understory at Makaha 1 and Makaha 2; guava was in the sub-canopy at Makaha 2, Puu Opae, and Kumuwela (1100 m asl); and blackberry was present in the understory at the two high-elevation sites, Kumuwela and Halemanu.

Table 1. Site and pre-Hurricane Iniki stand characteristics of six koa (*Acacia koa*) forests growing along an elevation-precipitation gradient on northwestern Kaua'i, Hawai'i.

Site	Elevation (m)	Precipitation (mm y^{-1})	Slope (°)	Aspect (°)	Stem density (ha^{-1})	Mean DBH (cm)	Leaf area (m^2/m^2)
Makaha 1	500	850	10	265	4686	4.0	1.4
Makaha 2	640	1000	25	310	1210	10.8	3.5
Miloli'i	800	1165	12	280	6012	3.7	1.7
Pu'u '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

Hurricane Iniki moved over the island of Kaua'i in a roughly NNE direction, with steady winds of over 230 km hr^{-1} and gusts over 280 km hr^{-1} (National Weather Service 1992). The estimated track of the eye passed closest to Puu Opae and Kumuwela and within a few kilometers of the other sites (Figure 1).

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 Miloli'i. We measured DBH at all six sites during the four days just before Hurricane Iniki struck. 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 percent canopy removed, (2) 25–50 percent canopy removed, (3) 50–75 percent canopy removed, and (4) >75 percent canopy removed. After the hurricane, survival and DBH were measured at six-month intervals for two years.

Canopy leaf area. Pre- and post-hurricane canopy leaf area were estimated at each site using an LAI-2000 plant canopy analyzer (LI-COR Inc., Lincoln, NE). Post-hurricane leaf area was compared with pre-hurricane values to determine leaf area removal. Recovery of leaf area was monitored monthly for the first year and every three months during the second year following Hurricane Iniki.

Light availability. For a given time interval, light availability beneath the forest canopy (Q_t, moles m^{-2}) was estimated as a function of the average canopy leaf area (L) over the interval with the following equation: $Q_t = Q_0 e^{-kL}$, where Q_0 (moles m^{-2}) is the total incident photosynthetically active radiation (PAR) over the time interval and k is the radiation extinction coefficient. PAR (moles m^{-2}) was measured using LI190SB quantum sensors located in clearings at 500, 800, and 1100 m elevation along the gradient (Figure 1). A k value of 0.45 was used 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 one to four days before Hurricane Iniki. Litter traps were not installed at Makaha 2 and Pu'u 'Opae before the hurricane. Hurricane-induced litter was collected 10–18 days after the hurricane. The collections from each site were composited in the field and subsequently separated into leaf, twig (<1 cm diameter), and wood (>1 cm diameter) components, and dried at 70°C.

Seedling recruitment and survival. In July 1993 (ten months following Hurricane Iniki), four permanent quadrats were established at each of the six study sites. No other major disturbances occurred following the hurricance prior to the set up of the quadrats. The quadrats ran out from the center of the pre-existing plots in north, south, east and west directions. Quadrat size was 1 x 8m for a total of 32 m^2 sampling area at all sites except Makaha 1 (500 m) and Miloli'i (800 m). At Makaha 1 and Miloli'i, quadrat size was 1 x 5m 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 tagged and identified by species. In February 1994 and July 1994 new seedlings were identified, tagged, and recorded as recruitment, and growth and mortality of old seedlings 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.

Results

Stand level damage. Types of damage differed across sites along the gradient. Makaha 1 experienced mostly loss of senesced phyllodes and dead twigs, although a few individuals lost major structural branches. At Makaha 2 large gaps were formed in the canopy primarily due to removal of both large and small branches, rather than the stripping of senesced phyllodes from intact branches; one dominant koa tree partly tipped over. At Miloli'i the damage observed was primarily the removal of senesced phyllodes, leaving the canopy otherwise intact. Pu'u 'Opae was the most severely damaged site, with many large branches and a few entire trees broken off, thereby removing most of the overstory canopy. Damage observed at Kumuwela included the breakage of major structural branches, many of which remained suspended in the canopy. Although Halemanu was located close to Kumuwela, damage was limited primarily to the stripping of green foliage from twigs in the canopy, so although much leaf area was removed, the major canopy branch structure remained intact, as with Miloli'i.

Immediate losses in canopy leaf area ranged from 18 to 58 percent, but became greater over time ranging from 29 to 80 percent (Figure 2) because of structural damage to major branches (e.g., Kumuwela and Pu'u 'Opae). Total loss of leaf area was positively correlated with pre-hurricane leaf area and canopy height, as hypothesized (Figure 3a, b).

Removal of foliage and twigs from the canopy resulted in a large flux of biomass to the forest floor. The flux at the high-elevation sites, Kumuwela and Halemanu, was greater than at low-(Makaha 1) and middle-elevations (Miloli'i; Table 2). Total litterfall mass ranged from 3.9 t ha^{-1} at Miloli'i to 18.6 t ha^{-1} at Kumuwela, and fine (leaf and twig) litterfall mass ranged from 3.3 t ha^{-1} at Miloli'i to 14.2 t ha^{-1} at Kumuwela. The proportion of litter composed of wood and twig debris was relatively constant, ranging from 71 percent at Halemanu to 80 percent at Kumuwela.

Table 2. Dry weights of leaf, twig (<1 cm diameter), and wood (>1 cm diameter) litter blown down by Hurricane Iniki and collected eight to ten days after the storm at four study sites along an elevation/ precipitation gradient on northwestern Kaua'i, Hawai'i.

Site	Component	Litter (t ha^{-1})
Makaha 1	Leaf	1.3
	Twig	3.6
	Wood	1.2
Miloli'i	Leaf	0.9
	Twig	2.4
	Wood	0.6
Kumuwela	Leaf	3.6
	Twig	10.6
	Wood	4.4
Halemanu	Leaf	3.1
	Twig	6.3
	Wood	1.3

Recovery. Recovery from canopy damage varied over the six sites. Leaf area had returned to pre-hurricane values within one year at Miloli'i and Halemanu (Figure 2). The immediate increase and subsequent slight decline in leaf area at Makaha 1 was the result of flushing and dieback of the alien lantana, which exceeded 2 m in height at the site. Canopy recovery at Pu'u 'Opae took two years, while the canopies at Makaha 2 and Kumuwela still had not fully recovered by that time (Figure 2) due to extensive structural damage.

Tree growth rate generally paralleled the decrease and subsequent recovery of leaf area over time at each site. The percent increase in basal area over the first year following the hurricane was negatively correlated with canopy loss (Figure 4). During the two years following Hurricane Iniki, tree growth rates were positively correlated with leaf area in all sites except Makaha 1 (Figure 5). Diameter increment had recovered to pre-hurricane values at five of the six sites within two years after the hurricane, and exceeded pre-hurricane values at Pu'u 'Opae and Kumuwela.

The two main sub-canopy species, aalii and guava, were both severely damaged in the hurricane, but their

Figure 2. Canopy leaf area at six koa (*Acacia koa*) forest stands on west Kaua'i from spring 1992 (pre-hurricane (m)) to September 1994. Error bars denote standard errors (n=9).

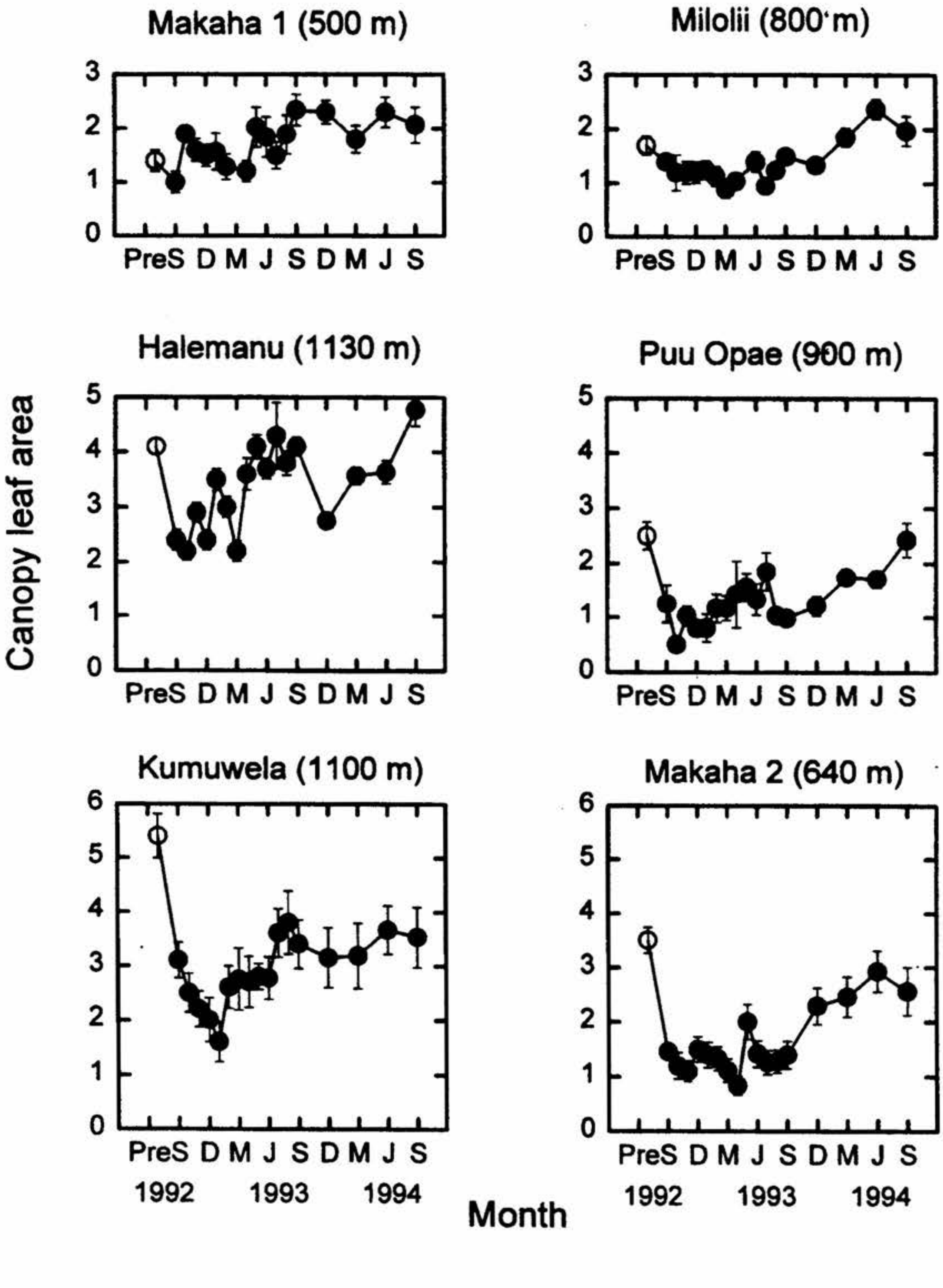


Figure 3. The relationship between amount of canopy leaf area removed and (a)pre-hurricane canopy leaf area, and (b) canopy height in koa (*Acacia koa*) forest stands on western Kaua'i. The six study sites were Makaha 1 at 500 m (●), Makaha 2 at 640 m (○), Miloli'i at 800 m (■), Pu'u 'Opae at 900 m (□), Kumuwela at 1100 m (▲), Halemanu at 1130 m (△).

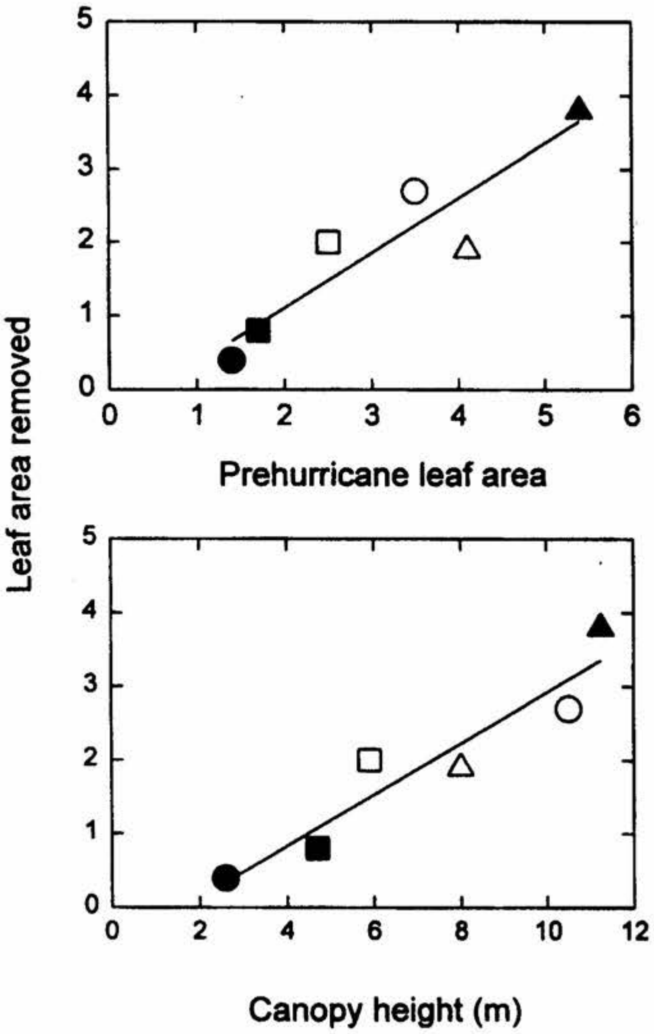
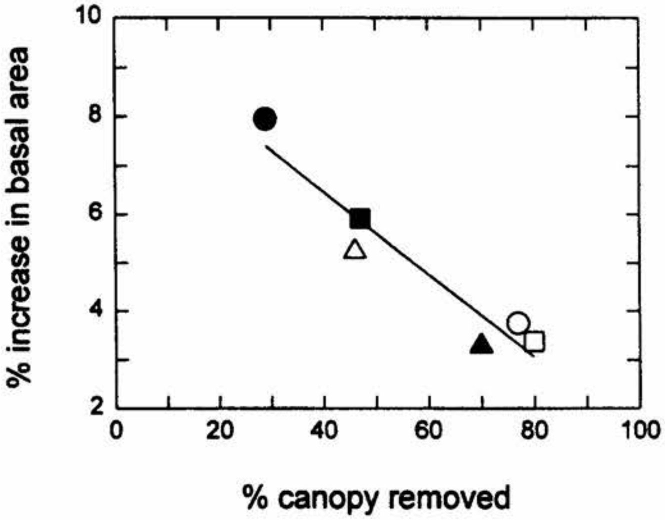


Figure 4. The relationship between the percentage increase in stand basal area one year after the hurricane and the percentage of the pre-hurricane canopy leaf area that was removed by the hurricane.



recovery from severe damage was quite different. At one of the two sites where it occurred, all severely damaged guava trees survived, and on the other site, two thirds of the severely damaged trees survived (Table 3). In contrast, the native 'a'ali'i generally had less capacity to recover: none of severely damaged trees survived at one of the three study sites where it occurred, and 50 and 86 percent of severely damaged individuals survived at the other two sites (Table 3).

Seedling density, recruitment, and survival. Total seedling densities varied by an order of magnitude across sites, and generally increased with increasing light availability at the forest floor (Figure 6), but were not correlated with hurricane induced litterfall. Koa had the highest density and annual recruitment of seedlings at the intermediate sites (Miloli'i (800m) and Pu'u 'Opae (900m)) along the rainfall gradient (Table 4). 'A'ali'i, however, experienced the highest seedling density and recruitment at the driest, low elevation site, Makaha 1 (500 m). Densities and recruitment of guava seedlings and blackberry shoots were relatively low at the sites where they were found, even though blackberry was the predominant understory species at the two wet sites, Kumuwela (1100m) and Halemanu (1130m). Seedling growth and survival were not correlated with light, precipitation, or litterfall for any of the four species. However, the ratio of annual mortality/emergence of koa increased linearly with amount of hurricane-induced litterfall (Figure 7), resulting in lower seedling densities at sites with higher amounts of hurricane litterfall.

Figure 5. The relationship between tree diameter increment and stand canopy leaf area in koa (*Acacia koa*) forest stands on western Kaua'i for the first two years following the hurricane. Each point represents a single six-month interval.

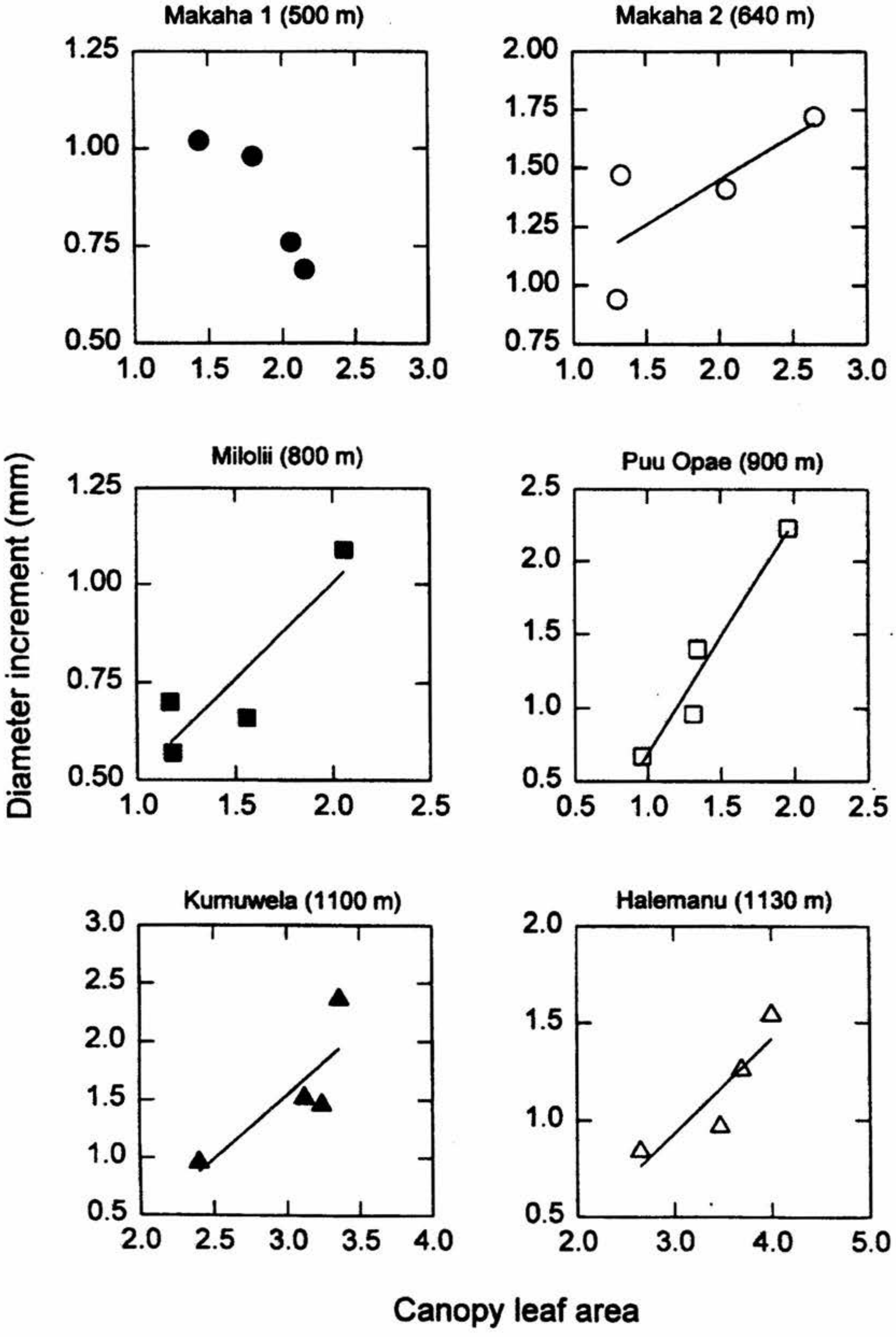


Table 3. The total number of individuals (N) of koa (*Acacia koa*), aalii (*Dodonaea viscosa*), ohia (*Metrosideros polymorpha*), and guava (*Psidium guajava*)at six study sites on northwestern Kauai; with the percentage of the individuals in each damage class immediately following Hurricane Iniki and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

			Damage class				% survival of class 4
Site	Species	N	1	2	3	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
Miloli'i	*A. koa*	68	91	5	2	2	0
	D. viscosa	21	38	10	19	33	86
Pu'u '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

Discussion

Damage. The strongest pattern of damage among sites was the correlation of leaf area loss with pre-hurricane leaf area and canopy height. Our results agree with data from nearby 'ohi'a forest, where differences in pre-hurricane canopy leaf area among plots had been created by fertilization in a randomized block design (Herbert and Fownes 1995). In these plots, leaf area loss was also correlated with pre-hurricane leaf area (Herbert 1995). However, very severe localized damage, greater than that observed in our studies, occurred in other forests on Kaua'i. This severe damage 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).

The magnitude of hurricane-induced litterfall observed across our sites was within the range of hurricane-induced litterfall observed in other tropical forests (Frangi and 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 koa forests on the island of Hawai'i ranged from 6.3 to 12.2 t ha^{-1} y^{-1}, with foliar litter comprising approximately 70 percent 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 koa forests, although the wood-to-leaf ratios were approximately reversed.

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 Pu'u '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 percent of total leaf area. This interpretation is supported by the large masses of woody litter at these sites (Table 2). The parallel trends in leaf area recovery and diameter increment agree with our pre-hurricane

Figure 6. The relationship between total seedling density and light availability in koa (*Acacia koa*) forest stands on western Kaua'i following Hurricane Iniki.

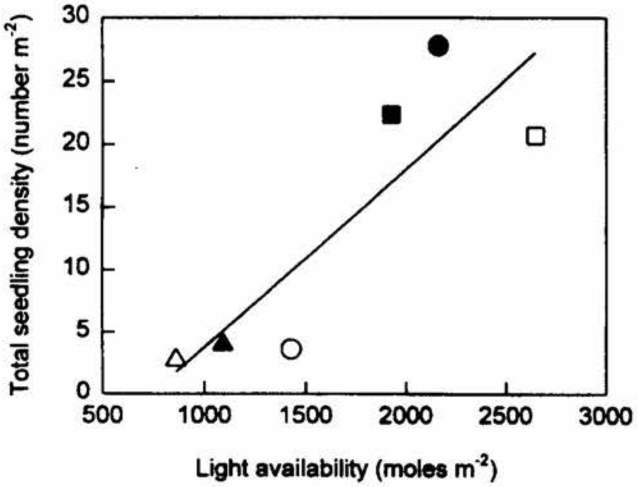


Figure 7. The ratio of seedling mortality to seedling emergence for koa (*Acacia koa*) as a function of the amount of Hurricane-induced litterfall.

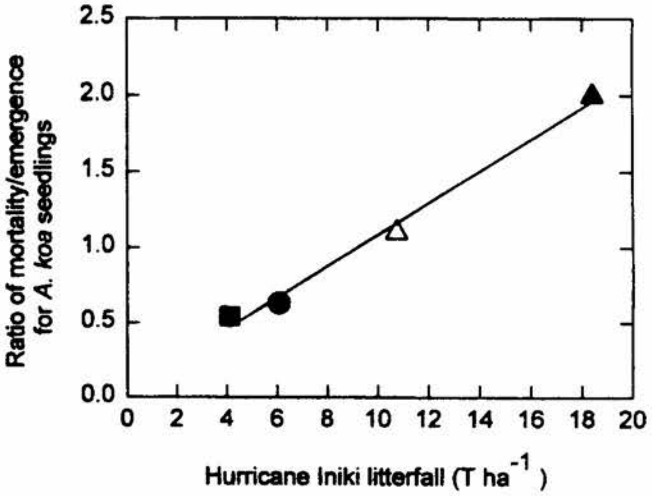


Table 4. Seedling density in July 1993 and July 1994, and annual (July 1993 - July 1994) seedling mortality and emergence, and percent survival, for koa (*Acacia koa*), 'a'ali'i (*Dodonea viscosa*), guava (*Psidium guajava*), and blackberry (*Rubus argutus*) on sites damaged by Hurricane Iniki on western Kaua'i.

		Density (m^{-2})				
Species	Site	July 1993	July 1994	Mortality (m^{-2} y^{-1})	Recruitment (m^{-2} y^{-1})	Survival (%)
A. koa	Makaha 1	0.1	0.4	0.6	0.9	50
	Makaha 2	1.4	3.0	0.8	2.3	61
	Miloli'i	12.6	18.8	7.0	12.9	57
	Pu'u 'Opae	21.3	19.4	7.4	5.7	36
	Kumuwela	1.5	1.0	0.9	0.5	47
	Halemanu	0.4	0.4	0.3	0.3	57
D. viscosa	Makaha 1	2.6	22.1	3.4	22.7	53
	Makaha 2	<0.1	0.5	<0.1	0.5	100
	Milolii	2.5	3.5	1.3	2.1	38
	Pu'u 'Opae	0.5	0.3	0.2	0.1	40
	Halemanu	<0.1	0.1	<0.1	0.1	67
P. guajava	Makaha 1	0.9	1.6	0.2	0.6	67
	Makaha 2	0	<0.1	0.0	<0.1	
	Pu'u 'Opae	1.9	2.3	0.8	0.6	48
R. argutus	Kumuwela	2.5	2.4	1.7	1.6	35
	Halemanu	2.4	2.0	2.7	2.2	9

observation that diameter increment was correlated with canopy leaf area (Harrington et al. 1995).

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 'a'ali'i suggests that the more resilient alien guava will increase its importance in the understory. At Makaha 1, the rapid flushing of lantana leaf area may suppress future recruitment of 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 koa forest was in general not catastrophic and, to a great degree, forest structure and productivity had recovered within two years.

Acknowledgments

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Questions

Q: Your last point seemed fairly important. If the native species don't do as well as the alien species, we're going to have to go back in there again and get more of the guava out. Is that really your conclusion, that in the long run the guava will survive a lot better?

A: My data are only from a single disturbance event. The data showed that guava had much higher survival than the other subcanopy species on the site, the *Dodonea*. So I can't say how guava is going to do versus other native species on other sites with different species compositions. Although we didn't have a big recruitment, with other aliens coming in, I'm saying this is something to watch out for. They have an ability to have some resilience after a disturbance like that.

Q: I went to the island after the hurricane and saw the native plants looking a lot more disturbed than the eucalyptus and stuff.

A: There are two things going on. You've got resistane to disturbance, and also there's an ability to recover from it. A couple of the slides showed the eucalyptus hammered, but it had the ability to come back. It's just a characteristic of that family; they can sprout back after being cut, after being totally defoliated. Guava is the same family as eucalyptus. 'Ohi'a is too. Jim Fownes had a graduate student looking at 'ohi'a in the forest at Koke'e after the hurricane, and he found out that they came back.