BIOTROPICA 26(4): 384–391 1994

Effects of Tropical Cyclones Ofa and Val on the Structure of a Samoan Lowland Rain Forest[1]

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ABSTRACT

In February 1990, tropical cyclone Ofa struck Western Samoa with very strong winds (in excess of 200 km/hr). In December 1991, less than 22 months later, tropical cyclone Val struck the same area with similar intensity. In the moist lowland forest of the Tafua Rain Forest Reserve, Savai'i, Western Samoa, we examined the effects of the two cyclones on forest structure, tree mortality, and interspecific differences in damage. Average mortality of trees was high after both cyclones (28% and 33%, respectively). In one forest area, subject to a fire after the first storm, mortality was more than 90 percent.

The frequency of uprooted trees was 31 percent after Ofa, but only 16 percent after Val. Uprooting was significantly more frequent among species lacking buttresses or stilt roots. As a combined effect of the two cyclones, the lowland forest of Tafua suffered a 53 percent tree mortality, with remaining standing trees being severely damaged (topped and with a substantial reduction of main branches). Average tree density dropped from an estimated 476 trees/ha (>5 cm DBH), before Ofa to 225 trees/ha after Val. Existent gap sizes are reflected by the changes in mean canopy cover which decreased from nearly 100 percent before Ofa to 27 percent after Val.

Post-cyclone recovery is often observed to be very rapid, but the very large gaps created in the Tafua forest and the simultaneous loss of the whole guild of vertebrate seed dispersers (flying foxes and fruit pigeons) suggests it will be a long time before the upper canopy is once again closed.

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Sa lavea Samoa e le afa o Ofa i Fepuari 1990 ma matagi malosi e sili atu ona saosaoa i le 200 km/itula. Ae le'i atoa le 22 masina, sa toe lavea Samoa e le afa o Val i Tesema, 1991. Sa matou su'esu'e i le tulaga sa o'o ai le vao matua o Tafua, ae maise i tulaga o le fa'amateina o la'au 'ese'ese. E tele la'au sa mate ai ona o na afa e lua, e tusa ma le 28% i le afa muamua ma le 33% i le afa lona lua. I se tasi itu o le vao o Tafua sa mu, sa mate ai le 90% o la'au. Sa pa'u ai 31% o la'au mai Ofa, ae na'o le 16% mai Val. O le tele o ia la'au sa pa'u, sa leai ni a'a lagolago po'o a'a mai luga, ae na'o a'a i lalo le palapala. Ona o na afa e lua sa mate ai 53% o la'au i Tafua, ma sa leaga ai le tele o isi la'au o totoe. Sa pa'u le numera o la'au ae le'i agi ai na afa mai le 476 la'au/hectare (>5 cm le mafia) i le 225 la'au/hectare ina ua mavae Val. E i ai va i le 27% o le vao ina ua mavae Val. O nisi taimi e vave ona toe tupu ai le vao mai afa fa'apea, ae aua nei va tele i le vao atoa ma le fa'mateaina o manu e feavea'i fatu (pe'a ma lupe), atonu olea umi se taimi se'ia toe lelei ai le vao matua o Samoa.

Key words: *disturbance; forest structure; gap size; lowland rain forest; Samoa; tropical cyclones.*

THE EFFECTS OF TROPICAL CYCLONES on forest structure, recruitment, and community dynamics have recently received considerable attention (*e.g.*, Walker 1991, Brokaw and Grear 1991, Guzman-Grajales and Walker 1991). These studies, based entirely on neotropical forests, particularly in the Caribbean, have suggested some general effects of intense storms on forest structure. For example, tree mortality was often surprisingly low, ranging from three percent in Puerto Rico, following hurricane Hugo (Fangi & Lugo 1991), to 13 percent in Mexico, following hurricane Gilbert (Whigham *et al.* 1991). Tall trees appeared more likely to be defoliated than small trees (Walker 1991). Tall, large-diameter trees had a greater tendency to be up-

[1] Received 22 January 1993; revision accepted 22 December 1993.

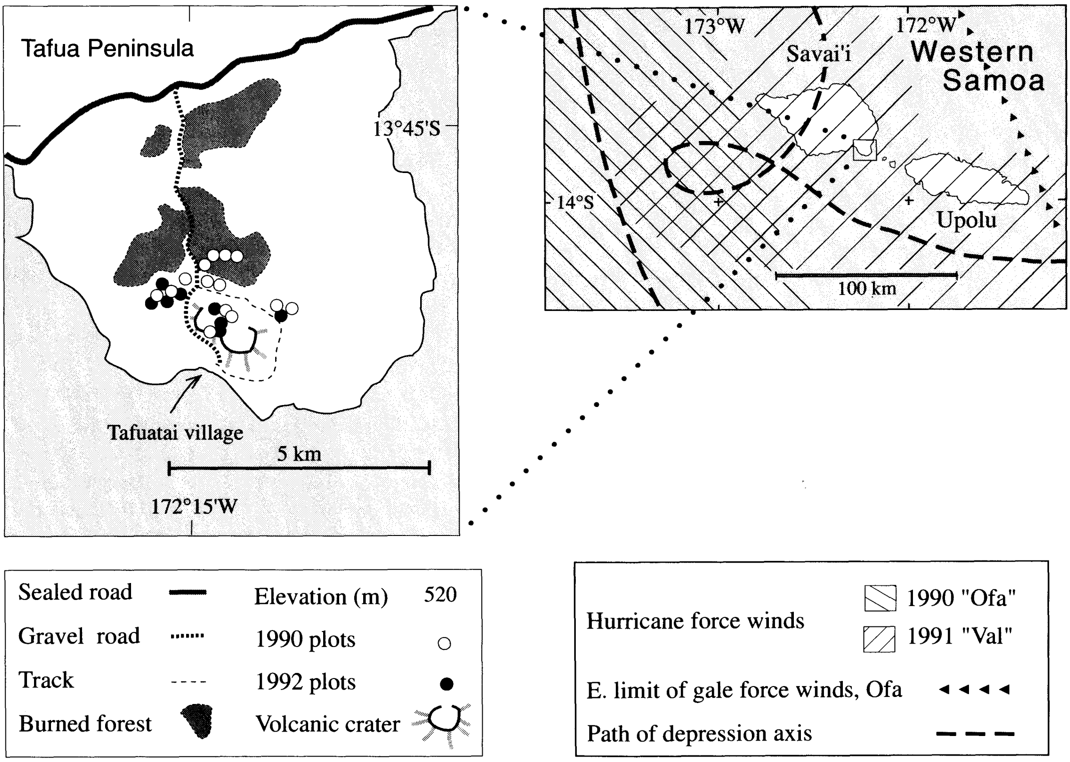

FIGURE 1. Map of the Tafua Rain Forest Preserve, Savai'i, Western Samoa, showing the locations of 14 plots (open dots) surveyed in May and October 1990 (4 and 8 mo after cyclone Ofa respectively) and eight plots (closed dots) surveyed in August 1992 (8 mo after cyclone Val).

rooted; understory trees were more prone to be snapped (Brokaw & Walker 1991, Tanner *et al.* 1991). In all these studies there were large interspecific differences in susceptibility, but no clear pattern based on tree morphology emerged (Brokaw & Walker 1991, Tanner *et al.* 1991).

To date, almost no information has been available on the effects of cyclones on Paleotropical forests. Given that many Pacific oceanic islands lie within a cyclone belt, and have a very different flora, it seemed important to explore whether the generalizations emerging from the Caribbean apply to cyclone damaged forests in the Paleotropics as well. Two recent cyclones on the Pacific islands of Samoa have allowed us to compare storm effects with the recent reports from the Caribbean. In addition, we were able to assess the cumulative impacts of sequential storms.

On February 2–3 1990, tropical cyclone Ofa, the most severe storm in over 160 years, struck the islands of Samoa, with the eye passing *ca* 80 km west of the island of Savai'i, Western Samoa (Fig. 1). High winds (in excess of 200 km/hr) (Ulafala 1990) caused severe forest damage. A SPOT-SAT satellite false colour image, taken 2 weeks after the storm, showed that only small patches, comprising less than 1 percent of the primary forest on the eastern third of Savai'i Is., Western Samoa, retained normal foliage. This area includes the Tafua peninsula—the largest remaining block of continuous lowland rain forest in Western Samoa—which was established as a rain forest preserve under indigenous control (Cox & Elmqvist 1991, 1993) immediately prior to the cyclone. Twenty-two months later, on December 7–8, 1991, tropical cyclone Val of comparable duration and wind speed (up to 240 km/hr), struck the island. Again forest damage was extensive, with more than 90 percent of the primary forest being completely defoliated. The damage on Savai'i was severe since Val, at its peak intensity, passed straight over the island where it moved at less than 10 km/hr, and made a clockwise loop just south of the island before continuing to the east (Fig. 1) (Pandaram 1992).

In this study, we examined the effects of the two cyclones on forest structure in the Tafua lowland forest, including mortality, interspecific differences in type of damage, and whether tree morphology influenced the probability of uprooting or snapping.

STUDY SITES AND METHODS

Data were collected in the Tafua Rain Forest Preserve (*ca* 5000 ha) on the Tafua peninsula, Savai'i (13°50'S, 172°20'W) in May and October 1990 and August 1992. In this area the pattern of rainfall is moderately seasonal (approx. 2500 mm/year) with a peak in precipitation during October–March. Southeast tradewinds prevail. The mean monthly temperature is 26°C and varies less than 1°C. The highest point on the Tafua peninsula is 108 m above sea level (two small volcanic cones, see Fig. 1), but most of the area is a low relief lava plain below 30 m. The forest is dominated by *Pometia pinnata* Forster (Sapindaceae), a species that occurs on rocky soils below 450 m elevation (Whistler 1992a). Other important canopy species include *Syzygium inophylloides* (Myrtaceae), *Planchonella torricellensis* (Sapotaceae), *Garuga floribunda* (Burseraceae), and *Dyxosylum samoense* (Meliaceae).

To determine the impact of the cyclonic storms we established 14 20 m × 20 m plots after Ofa and 8 20 m × 20 m plots after Val. In all plots, all trees over 5 cm diameter at breast height (DBH) were inventoried. Plot locations were arbitrarily chosen to sample the range of topographic diversity in the area (Fig. 1). No pre-storm information was available from these plots.

After Ofa in 1990, three plots were investigated in May and the remaining eleven in October. A forest fire one month after Ofa damaged approximately 15 percent (estimated from a 4 July 1990 SPOT-SAT image) of the total area of the peninsula, or approximately 750 ha. Four of the October plots were placed in the burned area. After Val, the forest was extremely difficult to penetrate, and we were unable to relocate exactly the 1990 plots (all markers lost). Site descriptions from 1990 were sufficiently detailed to enable us to place eight new plots within 50 m distance of the ten non-burned 1990 plots (Fig. 1).

Within each plot, the following data were recorded or calculated: number of trees of each species standing and uprooted; estimated standing height (m) of trees; number of trees living and dead (a dead tree = bark absent, trunk xylem dry, absence of shoots or leaves); DBH (cm); presence or absence of buttresses or stilt roots; basal area; canopy cover using a convex spherical crown densimeter (Lemmon 1957) and recorded as percent ground area covered, estimated in October 1990 and August 1992 survey only, when all living trees had refoliated; and ground cover of weeds and presence of saplings (1992 survey only). In 1992, it was possible to make a clear distinction between trees uprooted and dead after Ofa and Val, respectively, because decomposition of trees dead after Ofa was very advanced (*e.g.*, no bark left, outer part of the trunk xylem very soft).

Since we were unable to exactly resurvey the 1990 plots and needed to account for spatial variation in storm damage, comparisons on mortality, uprooting, *etc.* were calculated on a per plot basis rather than from the total number of censused trees. Comparisons of differences between species (Table 2) were calculated from the 1990 survey data only because after Val the numbers of trees present per plot of most species were very low. Voucher specimens of collected plants were deposited at the Herbarium of University of Umeå.

RESULTS

CYCLONE EFFECTS: PATTERNS OF MORTALITY AND TREE DAMAGE.—Forest damage was extensive after both storms. Average tree density dropped from 476 trees/ha (>5 cm DBH) before Ofa to 225 trees/ha after Val. Uprooted trees showed a 90 percent mortality after Ofa and a 98 percent mortality after Val. Overall tree mortality was high—28 percent after Ofa and 31 percent after Val, and as a result of both storms the cumulative mortality was greater than 50 percent.

A significantly higher proportion of trees were uprooted after Ofa (31%) compared to after Val (16%) (Table 1). When analysed across species, uprooted trees resulting from Ofa were smaller in diameter than living trees still standing (*t*-test (unequal variance), $t = 2.15$, $P < 0.03$, df = 260). After Val the difference in DBH between fallen and standing living trees was not significant ($P > 0.05$).

There were relatively few dead trees among those that remained standing 6 to 8 months after Ofa (5.6%). By contrast, after Val, a rather high proportion of the remaining standing trees were dead (22.5%). The proportion of snapped trees increased from 47 percent after Ofa to 67 percent after Val, and the average height of standing living trees decreased from 12.8 m to 10.2 m (Table 1).

As a result of the two storms, large gaps were present in the forest. Gap size is reflected by changes in mean canopy cover which decreased from nearly

TABLE 1. *Patterns of tree mortality, uprooting, and damage in the Tafua rain forest preserve recorded 6–8 mo after cyclones Ofa (January 1990) and Val (December 1991).* N = *number of plots (data from the four plots in the burned area only included in percent snapped trees), or number of trees. Means ± 1 SE are given.*

	"OFA"	*N*	"VAL"	*N*
Mortality (%)[a]	28.2 ± 6.1	10	32.5 ± 5.0	8
Uprooted trees (%)[b]	31.1 ± 0.7	10	16.3 ± 0.6	8
DBH fallen trees (cm)[a,c]	20.9 ± 1.6d	83	21.1 ± 3.4d	42
DBH standing living trees (cm)[a,c]	28.5 ± 3.9e	168	29.8 ± 3.4d	196
DBH standing dead trees (cm)[c]	—		12.3 ± 1.6e	24
Percent dead, standing trees[b]	5.6 ± 3.9	10	20.5 ± 0.04	8
Percent snapped trees[b]	47.3 ± 0.1	14	67.2 ± 3.6	8
Height of snapped trees (m)[b]	10.8 ± 1.1	184	7.2 ± 0.6	159
Tree height (m) (>5 cm DBH) all living trees[b]	12.8 ± 0.8	85	10.2 ± 0.5	102
Canopy cover (%)[b]	69.1 ± 8.0	10	26.7 ± 3.9	8
Basal area (m^2/ha)[b]	23.2 ± 1.6	10	16.5 ± 1.2	8

[a] Not significant.
[b] $P < 0.05$ (Mann-Whitney *U*-test).
[c] Different letters indicate significant difference at vertical variable comparisons using unequal variance *t*-tests.

100 percent to 69 percent after Ofa and to 27 percent after Val.

EFFECTS OF THE FIRE.—The storm Ofa in combination with the fire was very destructive, with average mortality estimated to be 91 percent in the burned area (Table 2). No large difference in vulnerability to fire among the six most abundant species was detected. Canopy cover was close to 100 percent before the cyclone (January 1990) but decreased to 12 ± 1% ($N = 4$) in the burned area (October 1990). As a consequence of the high mortality in the burned area, estimates of basal area were also low—6.3 ± 1.3 m^2/ha (± 1 SE) compared with 23.2 ± 1.6 in the non-burned area.

INTERSPECIFIC DIFFERENCES.—The most abundant tree species *Pometia pinnata* (Sapindaceae) is a large (maximum height of 30 m), buttressed, slow-growing, native canopy tree. This species showed relatively high resistance to strong winds during Ofa and the estimated mortality (13%) was the lowest observed among the six most abundant species (Table 2). After Val mortality for *Pometia* was estimated as 25 percent. By contrast, the second most abundant species in our plots, the fast-growing, medium-sized, subcanopy tree *Cananga odorata* (Annonaceae) was the most vulnerable. After Ofa, an estimated 67 percent of the trees were uprooted, 50 percent of the remaining standing trees were snapped, and overall mortality was estimated to be 46 percent. After Val, mortality for *Cananga* was close to 60 percent. These differences were clearly reflected in the change of relative abundances of the two species following Ofa and Val (Table 3).

No significant within-species differences were

TABLE 2. *Effects of cyclone Ofa on the six most abundant tree species in a lowland forest on Savai'i, Western Samoa. Measurements were made in May and October 1990. Means ± 1 SE are given. Mortality values for the burned area given within parentheses.*

	Uprooted (%)	Mortality (%)	DBH uprooted (cm)	DBH standing (cm)	Proportion snapped (%)	Height of snapped (m)	*N*
Canopy trees							
Pometia pinnata	19	13 (90)	37.8 ± 6.7	44.4 ± 7.7	31	13.2 ± 2.9	49
Syzygium inophylloides	16	20 (75)	—		38	10.2 ± 3.4	19
Planchonella torricellensis	29	33 (100)	26.2 ± 8.2	17.9 ± 2.2	24	12.5 ± 0.9	17
Understory trees							
Cananga odorata	67	46 (99)	15.1 ± 1.4	17.1 ± 2.0	50	4.4 ± 0.6	44
Mammea glauca	22	21 (88)	20.8 ± 5.7	13.1 ± 1.8	36	4.5 ± 1.1	22
Aglaia samoensis	36	39 (100)	9.8 ± 0.9	8.2 ± 0.7	27	6.9 ± 0.9	23

TABLE 3. *Relative abundance of trees (standing, living with DBH > 5 cm) of different species in the Tafua lowland forest before and after the cyclones Ofa and Val. Based on samples from 10 and 8 (20 m × 20 m) plots in the unburned area, respectively. C = potential canopy tree, U = understory tree (based on Christophersen 1935). * = rare species at <0.5 tree per plot, + = no living specimen left.*

Species	Relative abundance %				Buttresses
	Before "Ofa"	After "Ofa"	After "Val"		
Pometia pinnata (Sapindaceae)	25.0	31.1	34.2	C	Yes
Cananga odorata (Annonaceae)	22.1	10.9	4.6	U	No
Aglaia samoensis (Meliaceae)	12.3	10.3	5.2	U	No
Syzygium inophylloides (Myrtaceae)	10.8	10.9	8.5	C	Yes
Mammea glauca (Guttiferae)	10.0	9.8	5.8	U	No
Planchonella torricellensis (Sapotaceae)	5.8	8.8	11.2	C	Yes
Dysoxylum samoense (Meliaceae)	7.1	8.1	15.1	C	Yes
Garuga floribunda (Burseraceae)	2.9	4.1	4.6	C	Yes
Inocarpus fagifer (Leguminosae)	2.0	3.0	4.8	C	Yes
Diospyros samoensis (Ebenaceae)	1.0	2.1	2.3	U	Yes
Myristica fatua (Myristicaceae)	*	*	*	U	Stilt
Rhus taitensis (Anacardiaceae)	*	*	*	C	Yes
Terminalia catappa (Combretaceae)	*	*	*	C	Yes
Kleinhovia hospita (Sterculiaceae)	*	*	*	C	Yes
Guettarda speciosa (Rubiaceae)	*	*	*	U	No
Alphitonia ziziphoides (Rhamnaceae)	*	+	+	U	No
Canthium merrillii (Rubiaceae)	*	*	*	U	No
Flacourtia rukam (Flacourtiaceae)	*	*	*	U	No
Canarium vitiense (Burseraceae)	*	*	*	C	Yes
Ervatamia obtusiuscula (Apocynaceae)	*	*	*	U	No

found when comparisons of DBH of standing and uprooted trees were made (Table 2).

Uprooting in relation to morphology.—Uprooting was more frequent among species lacking buttresses or stilt roots. As a result, the proportion of trees having buttresses or stilt roots among all standing trees in the plots increased from 58 ± 4.3 percent (Mean ± SE) to 70 ± 5.2 percent after Ofa (Mann-Whitney *U*-test, $P < 0.05$, $N = 14$) and 73.1 ± 4.4% ($N = 8$) after Val.

Out of the 20 species found in the plots, eleven species had buttresses, and one *Myristica fatua* had stilt roots. When comparing the 10 most common tree species (>0.5 trees per plot), only three species lacked buttresses (Table 3).

DISCUSSION

Cyclones represent relatively frequent, large-scale disturbance factors in many parts of the island South Pacific. Excluding Ofa and Val, there have been two very severe storms in Samoa in the past 50 years (Skowron 1987). However, the combined effect of the two recent cyclones, occurring within an unusually short interval (22 months), was very destructive. The Tafua lowland forest was completely defoliated twice during this period and suffered a 53 percent tree mortality, and the remaining living trees were severely damaged, *i.e.*, snapped and with a substantial reduction of main branches. Average mortality after Ofa and Val was relatively high (28% vs 31%) and very high (90% vs 98%) for uprooted trees. These values are much higher than what has been reported in most other studies of cyclone-damaged wet or moist tropical forests (Brokaw & Walker 1991, Tanner *et al.* 1991, Bellingham *et al.* 1992), where mortality has varied between 2–17 percent measured within one month up to 3 years after the cyclones.

The high mortality observed in the Tafua preserve after Ofa might have been aggravated following the cyclone by an unusually long period of 6 weeks with no precipitation which caused a potentially severe water stress during the period of refoliation. The fire that occurred during this drought period caused extremely high tree mortality (>90%) within the burned portions of the forest. While extensive fires are usually perceived as rare in wet, lowland, tropical forests, cyclones generate enormous amounts of vegetative litter. This litter, if combined with an interval of low rainfall, creates unusual conditions for fire propagation (*cf.* Whigham *et al.* 1991). Although droughts may be common in the lowlands of Samoa (*e.g.*, Curry 1955), the frequency of fires in the Tafua area is unknown, but probably low. One large fire occurred in September 1983 at the end of dry season in the northwestern part of Savai'i (Skowron 1987), an area which is considerably drier than the Tafua area. Val struck the islands in the beginning of the rainy season (December 1991) and this storm was reported to be followed by a period of heavy precipitation ('Ulu Taufa'asisina, pers. comm.).

After Val, the relatively high overall tree mortality was not primarily caused by uprooting, as was mainly the case after Ofa. Instead, a significant portion was due to high mortality among small standing trees. Complete defoliation and extensive damage to branches occurring twice within a 22 month period is likely to be particularly severe for trees in small size classes. However, in all size classes standing trees which were leafing out had large wounds offering portals for attack by insects and microorganisms. This suggests that mortality indirectly caused by the storms will continue to increase for several years.

There were some distinct differences between the two storms in their effects on the forest. While Ofa caused an uprooting of 31 percent of the trees, this frequency was significantly lower after Val. It is likely that the most wind sensitive trees were already downed by Ofa. Additionally, the trees which remained standing after Ofa typically had no, or few, lateral branches remaining. These trees were left with a structure significantly less susceptible to windthrow even though the wind speed in this area during Val was perceived by locals as higher than during Ofa.

Uprooting was more frequent among species lacking buttresses or stilt roots. As buttresses and stilt roots are found in tree species from a large number of distantly related families (Richards 1952), these structures are presumed to have evolved independently. The adaptive significance of buttresses and the high frequency of tree species with buttresses or stilt roots in lowland tropical forests, in contrast to their rarity in temperate and boreal forests, have been the focus of extensive speculation (Richards 1952; Smith 1972, 1979; Black & Harper 1979). Hartshorn (1983) grouped the hypotheses dealing with buttress formation into categories: adaptive responses to wind or gravity stresses; negative geotropism; and conduction shortcut. The first hypothesis has historically been the one most often proposed as an explanation for the presence of buttresses (Richards 1952, Baker 1973, Henwood 1973, Ennos 1993), and the results of our study support the wind-resistance hypothesis. However, in studies following hurricane Hugo in Puerto Rico, no clear difference in wind resistance between trees with different morphology, *e.g.*, buttressed or non-buttressed, was found (Walker 1991, see also Putz *et al.* 1983), and many factors other than morphology, such as soil type, aspect, slope, *etc.*, are likely to influence the pattern of windfall.

Buttress formation is often more common on shallow soils where a thin humus layer overlies rock (Ennos 1993). Our study area is a very young lava formation, with vesicular lava bedrock extensively exposed at the surface on all plots surveyed. The root mass of windthrown canopy trees was typically a dense, nearly flat-bottomed pad of contorted spreading roots up to several meters in radius which entrapped surface blocks of lava rubble; it had remarkably few remnants to suggest anchorage of roots to the underlying bedrock.

While our observations indicate differential survival of buttressed and non-buttressed trees in one cyclone-prone area, careful phylogenetic analysis, particularly of taxonomic groups containing both forms, is necessary to elucidate evolutionary mechanisms.

We found pronounced interspecific differences in susceptibility, with slow-growing hardwood species like *Pometia pinnata* showing low mortality and actually increasing in relative abundance as a result of the storm. On the other hand, fast growing species, such as *Cananga odorata,* showed very high mortality and declined dramatically in abundance. While this reflects differences in resistance to strong winds, we also found indications of strong interspecific differences in resilience (*i.e.,* regeneration capacities). In the 1992 survey, *Pometia pinnata* was by far the most abundant species among the very small size classes (<2 cm DBH), indicating a strong resprouting capacity. Although recovery after cyclones, at least based on studies in the Caribbean (*e.g.,* Brokaw & Walker 1991), appear to be very rapid, regeneration time (upper canopy closure) in the Tafua lowland forest might be very long. We base this prediction primarily upon the extensive mortality recorded and on the existence of extremely large gaps (canopy cover reduced from 100% to 27%).

In addition, there are other factors that might contribute to a slow regeneration. First, in both the October 1990 and August 1992 survey, we found a very high (often 100%) ground cover of weedy vines, predominantly *Mikania micrantha* (Asteraceae). This vine, which is a rather recent introduction, grows very fast and in English it is called "milea-minute" vine, and it is now present everywhere in the forest, where there are sufficiently large gaps, covering seedlings, saplings, and small trees. Whistler (1992b) suggested that this vine in combination with other alien species (*e.g., Passiflora foetida* (Passifloraceae)) already is responsible for the decline of several indigenous weed species. The effects of vines on the recruitment of primary canopy species is often assumed to be strongly negative (*e.g.,* Cameron 1962), however, this has so far not been supported by any experimental evidence (Savage 1992).

Following the two storms, the rate of regeneration in the existing large gaps may be substantially affected by the large reduction of the whole guild of vertebrate seed dispersers including two species of flying foxes *Pteropus samoensis* and *P. tonganus* and several species of fruit pigeons, *e.g., Ducula pacifica, Ptilinopus perousii* (Elmqvist *et al.* 1994). This may have prolonged consequences for the ability of many plant species to recolonize the disturbed habitats (Cox *et al.* 1991, 1992; Elmqvist *et al.* 1992).

We still do not know to what extent large quantitative changes caused by cyclones also results in qualitative changes of species composition. Long term studies of patterns of regeneration after cyclones constitute one important research strategy for constructing predictive models of cyclone influence on the diversity and long term dynamics of tropical moist forests.

ACKNOWLEDGMENTS

We thank 'Ulu Taufa'asisina and family for logistical support, and the Tafua village for its commitment to rain forest conservation. We also want to thank Matauaina Taufa'asisina for invaluable help in the field with identification of species, and Poseta, Sandra Banack, Lisa George, and Emeli Pontén for helpful support with field work. This study was supported by a grant from World Wide Fund for Nature (Sweden). We are grateful for all the help, support and encouragement we received from the conservation society on Savai'i, Fa'asao Savai'i.

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