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Tropical Rain Forest Recovery from Cyclone Damage and Fire in Samoa[1]

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ABSTRACT

In 1990 and 1991, Samoa was struck by two cyclones, Ofa and Val. In the Tafua Rain Forest Preserve on the island of Savai'i, one part of the forest also burned after the first cyclone. Here we report on patterns of regeneration and changes in tree species composition in the Tafua lowland rain forest after five years of recovery from cyclone and fire disturbance. In the unburned area, tree canopy cover increased from 27 percent after the last cyclone to 58 percent, and in the burned area from below 12 to 49 percent. Nine of the ten most common tree species decreased in relative abundance in the entire forest after the last cyclone. One fast growing pioneer species, *Macaranga harveyana,* now makes up 42 percent of the total number of trees (>5 cm DBH) in the unburned area and 86 percent in the burned area. Large interspecific differences occur in size distribution and there are at least four distinguishable regeneration patterns, which may be related to shade tolerance. Mean number of species per plot was generally higher in the unburned area than in the burned area, while the Shannon evenness index was higher in the unburned than in the burned area only for trees above 1 cm DBH. Species with fruits known to be fed upon by birds and/or bats generally made up a larger proportion of all trees in the burned than in the unburned area. In contrast to other studies of post-cyclone regeneration, in which recovery is often rapid due to resprouting of trees, recovery in the Tafua forest was a slow process with regeneration more dependent on vertebrate seed dispersal than on resprouting.

Key words: *cyclones; disturbance; fire; pioneer species; recovery; Samoa; tropical rain forest; vertebrate seed dispersal.*

The effects of tropical cyclones on forest structure, tree recruitment, and community dynamics have received much recent attention (Tanner *et al.* 1991, Everham & Brokaw 1996). Large-scale infrequent disturbances, such as cyclones, are thought to influence local and regional patterns of biodiversity through processes of extinction and colonization (Whittaker 1995). Most studies of cyclone effects have been done in the Neotropics and most attention has been paid to the immediate effects of disturbance (Lugo *et al.* 1983, Brokaw & Grear 1991), or the very first stage of recovery (Frangi & Lugo 1991, Walker 1991, Whigham *et al.* 1991). Long-term studies, however, suggest that successional changes in tree species composition continue for a long time after disturbance (Crow 1980, Weaver 1989, Whitmore 1989a). To increase our understanding of the role that large-scale disturbance plays in rain forest dynamics and the maintenance of biodiversity, it is therefore necessary to study the regeneration process and secondary succession following such events over longer periods of time and at various tropical locations.

This study was performed in the Tafua Rain Forest Preserve on the island of Savai'i, Samoa, which was struck by two cyclones in the early 1990s. The direct effects of these disturbances were investigated by Elmqvist *et al.* (1994), whose work enabled us in this study to distinguish between immediate effects of the cyclones on forest structure and tree species composition, and changes occurring during the first years of recovery. We compared the relative abundance of all common species five years after the cyclones with their relative abundance before and immediately after the cyclones. We also compared two rain forest areas that were subject to disturbance of a different type and intensity: one area subjected to extensive cyclone damage and one subjected also to a forest fire (Elmqvist *et al.* 1994). The effects of forest fires on diversity in the humid tropics is as yet poorly understood, but is receiving increasing attention due to the present high fre-

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quency of fires throughout the tropics (Uhl 1998). A key to the maintenance of species diversity is regeneration in response to disturbance.

Tree recruitment after treefall disturbance in tropical rain forests largely takes place by releasing of seedlings already present in a seedling bank when a canopy gap is formed (advanced regeneration; Uhl *et al.* 1988). Few studies, however, have dealt with the factors that determine the species composition of this seedling bank. It is proposed that the more disturbed a patch has been, the higher the proportion of colonizers from seeds originating outside, as opposed to within the patch (Martínez-Ramos & Soto-Castro 1993). The main seed vectors in tropical rain forest are vertebrate frugivores (Howe & Smallwood 1982, Fujita & Tuttle 1991), and birds and flying foxes are important seed dispersers for many Samoan tree species (Cox *et al.* 1991; P. W. Trail, pers. comm.). As many of these seed dispersers are threatened by habitat loss, it is important to evaluate their role in forest regeneration and recovery after catastrophic destruction. Disturbed areas are also sensitive to invasions by exotic colonizers that threaten indigenous species (Cronk & Fuller 1995). This study in the Tafua Rain Forest Preserve focused on the following questions: (1) are there significant changes in tree species composition over the first five years of recovery following large-scale disturbance?; (2) how do severity and type of disturbance affect tree species diversity?; (3) how important are different regeneration strategies for the recovery process?; (4) how important are seed dispersal vectors such as birds and flying foxes for the recovery process?; and (5) does the severity of disturbance affect the risk for invasions by exotic species?

METHODS

STUDY SITES.—This study was performed in the Tafua Rain Forest Preserve on the Tafua peninsula, Savai'i, Samoa (13°50′S, 172°20′W) from February to April 1996 and in April 1997. The Tafua rain forest (*ca* 5000 ha) is the largest remaining block of continuous lowland rain forest in Samoa. The rainfall in this area is *ca* 2500 mm/yr with a precipitation peak during October–March. The mean monthly temperature is 26°C and varies less than 1°C. Most of the area is a low relief lava plain below 30 m elevation; there are also two volcanic cones and the highest peak is 108 m. Two severe cyclones, Ofa and Val, struck Samoa in February 1990 and December 1991, respectively, their combined effect resulting in tree mortality greater than 50 percent in the study area (Elmqvist *et al.* 1994). An area of *ca* 750 ha was also subject to a forest fire one month after the first cyclone. Prior to the cyclones the forest was dominated by *Pometia pinnata* (Sapindaceae; Elmqvist *et al.* 1994). Other important species included *Dysoxylum maota* (Meliaceae), *Garuga floribunda* (Burseraceae), *Planchonella torricellensis* (Sapotaceae), and *Syzygium inophylloides* (Myrtaceae). The forest was originally surveyed in May and October 1990 and in August 1992 (Elmqvist *et al.* 1994).

To investigate tree regeneration patterns after the cyclones and the fire we established 19 20 × 20 m plots in February 1996. Five of the plots were situated on the slope and crater ridge of a volcanic cone. The remaining 14 were placed on the lava plain, 5 of which were in the burned area. The larger number of plots in the unburned compared to the burned area was required because of anticipated higher variance between the unburned plots. Plot locations were chosen to be as close to the plots surveyed in Elmqvist *et al.* (1994) as possible. In each plot, two 2 × 20 m transects were placed in a cross (76 m^2). All tree and shrub individuals in the transects were identified to species. We define a tree as a woody plant with a single trunk and lacking branches near the base, and a shrub as any woody, non-climbing plant with multiple trunks and/or branches near the base. Height was measured for all individuals up to 300 cm, and diameter at 130 cm (DBH [diameter at breast height]) was measured for all individuals over 150 cm height. The percentage of tree canopy cover was visually estimated at nine locations within each plot and an average for each plot was calculated. In order to increase the sample size of large trees, we established ten additional 20 × 20 m plots in April 1997, in which all trees over 5 cm DBH were inventoried. Four of these plots were situated on the slope and crater ridge of the volcano. Of the six plots on the lava plain, four were in the burned area. These plots were located as close as possible to plots used in 1996 (within 30 m distance) since we were unable to relocate the exact positions of the 1996 plots. Voucher specimens were collected for all species found and were deposited at the herbarium of the Umeå University. Data on frugivory from P. W. Trail (pers. obs.) were used when evaluating the importance of animal dispersal vectors in recovery.

DATA ANALYSIS.—Individual trees were grouped into three DBH classes (<1 cm, 1–5 cm, and >5 cm). Trees < 1 cm DBH were further divided by height at 100 cm. The largest size class was chosen

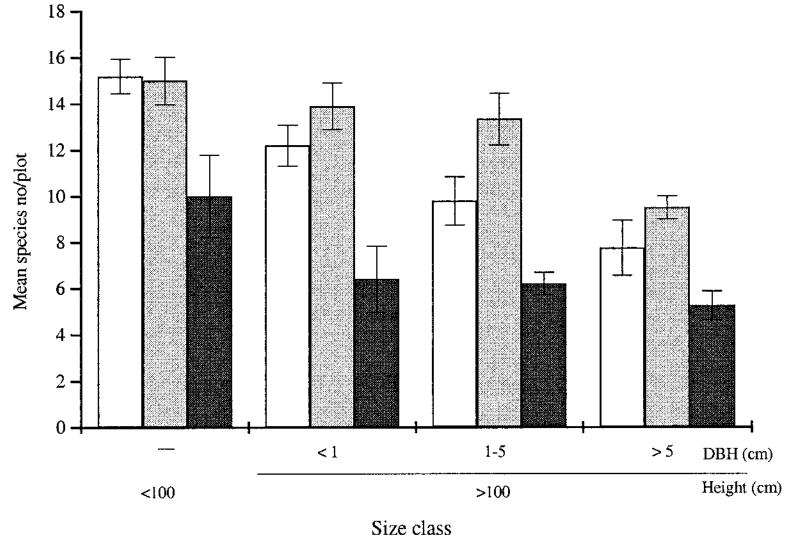

FIGURE 1. Mean number of species ($\bar{x} \pm 1$ SE) encountered in the unburned crater plots (white), the unburned plots on the lava plain (light gray), and the burned plots on the lava plain (dark gray), in the Tafua forest in four size classes: one class (a) <100 cm height; and three classes >100 cm height, divided into (b) <1 cm DBH, (c) 1–5 cm DBH, and (d) >5 cm DBH.

to match the DBH range sampled by Elmqvist *et al.* (1994) in 1991 and 1992. Data from the 1996 plots were used in the analysis of the three smallest size classes. For the analysis of the largest size class, we used the data from the 1997 plots. The evenness index *J,* derived from the Shannon diversity index (Begon *et al.* 1990), was calculated for each size class in the burned plots on the lava plain, the unburned plots on the lava plain, and the unburned crater plots, respectively, as: $J = (-\Sigma_{i=1}^{s} P_i \ln P_i)/\ln S$, where P_i is the proportion of individuals made up by the *i*th species and *S* is the number of species in the sample. Similarly, we also calculated the Berger-Parker dominance index *D,* which is the relative abundance of the most common species, for each size class in each set of plots. For each species we also calculated a weighted average, *W* (Whittaker 1967) of the relative abundance of that species in the four size classes as: $W = (a_1 + 2 \times a_2 + 3 \times a_3 + 4 \times a_4)/(a_1 + a_2 + a_3)$, where a_1 is the relative abundance of the species in the smallest size category, a_2 the relative abundance in the second smallest, and so on. This value ranges from 1 to 4, and a perfectly even distribution of relative abundance over size would yield a value of 2.5.

RESULTS

Species diversity.—In total, 56 tree and shrub species were found in this study. Fifty-two species were found in 14 plots in the unburned area, 41 species were found in the 5 plots on the volcanic cone, and 44 species were found in the 9 plots on the lava plain. Twenty-six species were found in 5 plots in the burned area. The mean number of species per plot (trees and shrubs) differed significantly between areas (one-way ANOVA: $P = 0.001$). There was a significantly higher total mean number of species per plot in the crater plots (22.0) and in the unburned plots on the lava plain (22.8) than in the burned plots on the lava plain (14.0) (Sheffe's test: $P = 0.006$, $P = 0.001$, respectively). A similar pattern was shown for all size classes (Fig. 1).

The rank-log abundance diagrams for each size class, the Berger-Parker dominance index, and the evenness index *J* (Fig. 2) all showed that the abundances of all species were more evenly distributed in the unburned than in the burned area in the two largest size classes but not in the two smallest size classes.

Changes in forest structure.—Tree density (>5 cm DBH) decreased from 476 to 225 trees/ha as a direct effect of the cyclones (Elmqvist *et al.* 1994) but has increased to 967 trees/ha in the unburned and 2294 trees/ha in the burned area during recovery. In the two smallest size classes, tree density was higher in the unburned than in the burned plots (Fig. 3). In contrast, tree density was higher in the burned than in the unburned plots in the

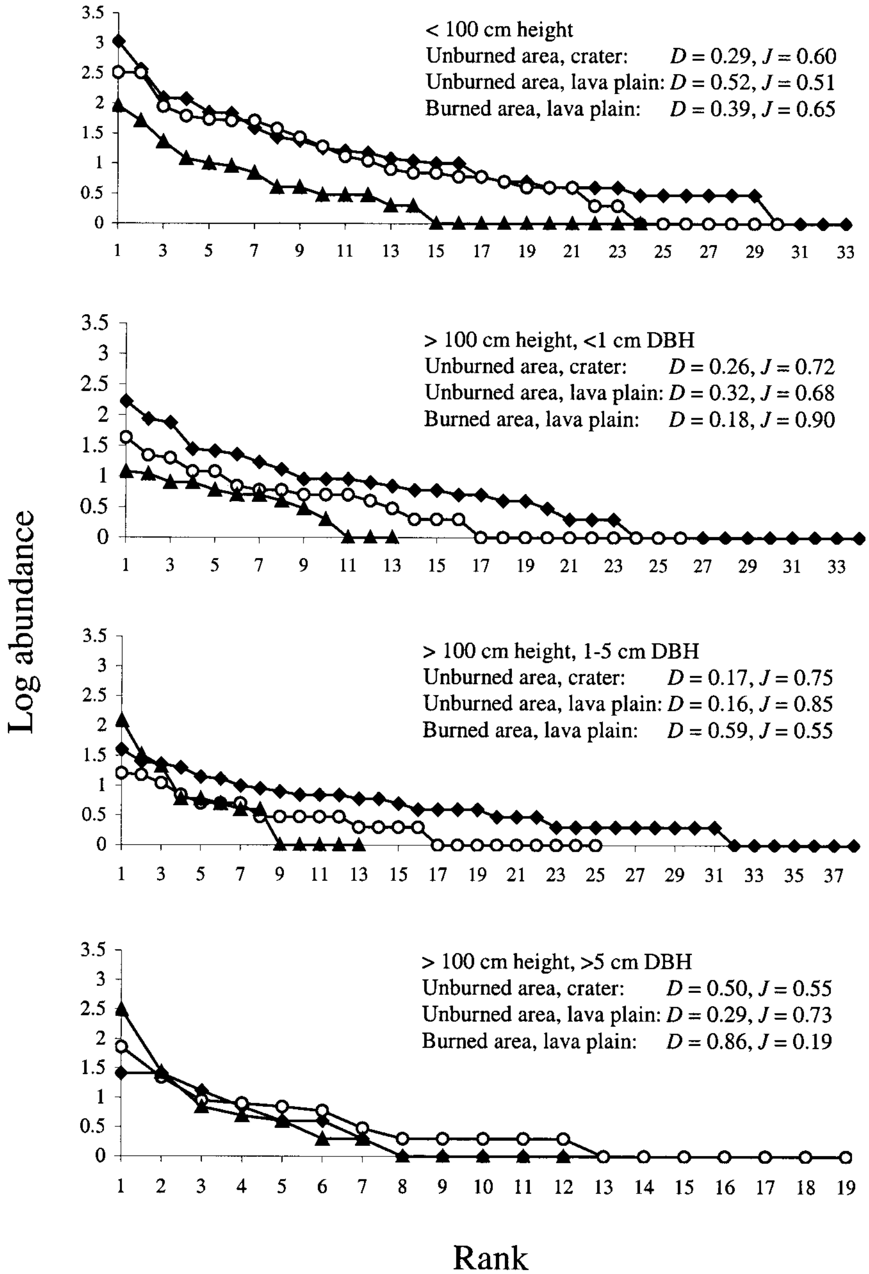

FIGURE 2. Rank-abundance diagrams for tree and shrub species in the unburned crater plots (squares), the unburned plots on the lava plain (circles), and the burned plots on the lava plain (triangles) in the Tafua forest in four size classes. Included are the Berger-Parker dominance index (*D*) and the Shannon evenness index (*J*). Note the different scales.

two largest size classes. Since the last study in 1992, canopy cover has increased from 27 (Elmqvist *et al.* 1994) to 58 percent in the unburned area and from below 12 to 49 percent in the burned area.

CHANGES IN SPECIES COMPOSITION.—We observed dramatic changes in tree species relative abundance (the percentage of the total number of individuals) both over the five years of recovery and compared

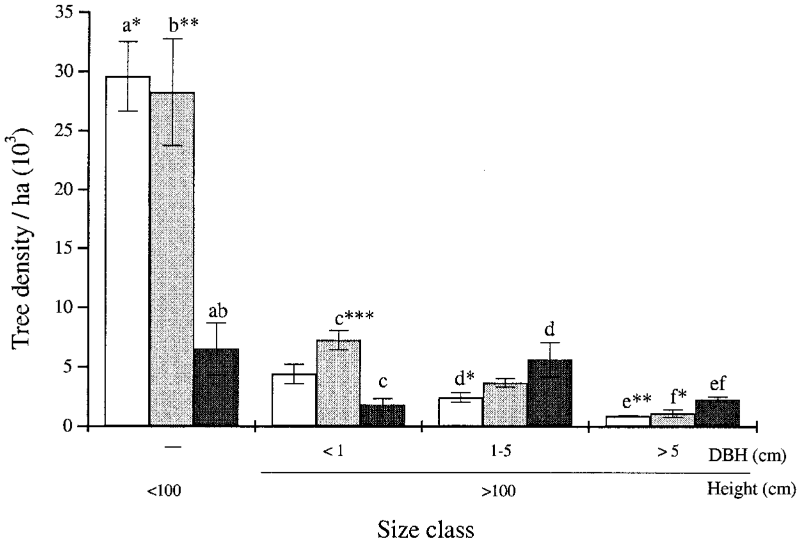

FIGURE 3. Tree density ($\bar{x} \pm 1$ SE) in four size classes in the unburned crater plots (white), the unburned plots on the lava plain (light gray), and the burned plots on the lava plain (dark gray), in the Tafua forest five years after the cyclones. When there is a significant difference between two areas, the same letter has been assigned to them. The significance level is indicated as: $*P \leq 0.05$, $**P \leq 0.01$, and $***P \leq 0.001$.

to pre-cyclone conditions (Table 1). The dominant species prior to disturbance, *P. pinnata,* initially increased in relative abundance as a direct result of the cyclones (Elmqvist *et al.* 1994) but later declined. Several other species also showed a substantial decrease in relative abundance. One common species, *Cananga odorata* (Annonaceae), suffered high mortality due to the cyclones but later increased strongly. The most dramatic change, however, was the strong increase of *Macaranga harveyana* (Euphorbiaceae). The introduced species *Funtumia elastica* (Rubiaceae) also increased in the burned area, where it was represented mainly by saplings (Table 2).

INTERSPECIFIC DIFFERENCES IN REGENERATION PATTERNS.—In Table 2, the relative abundance in the four size classes is shown for all tree species that had a relative abundance greater than one percent in any size class. Notable is the dominance of *M. harveyana* in the two larger size classes in the burned area, as well as in the largest size class in the unburned area. Further, there was a significant difference in relative abundance of *M. harveyana* between the unburned area and the even more disturbed burned area (one-way ANOVA with arcsine transformation, $P < 0.001$), where it formed an almost monospecific canopy layer. Notable also is the dominance of *Aidia cochinchinensis* (Rubiaceae) in the two smaller size classes in the unburned area and the dominance of *Diospyros samoensis* (Ebenaceae) seedlings in the smallest size class in the burned area. A "weighted average" (Whittaker 1967) was calculated on the relative abundance of each species in the four size classes (Table 2). Early establishing species have positively skewed distributions of relative abundance over size and high weighted average values, while late establishing species have negatively skewed distributions and low weighted average values. Species that have a weighted average close to 2.5 are of two types: evenly distributed, showing no obvious regenerative response, or with mound-shaped distributions, showing a pulse of regeneration at some intermediate stage of succession. These four size distribution patterns are exemplified by four species in Figure 4. Most other species in our study can be assigned a certain position on the continuum within these four distribution patterns. The species attaining the highest "weighted average" values were *M. harveyana, Kleinhovia hospita* (Sterculiaceae), *C. odorata,* and *Antirrhoea inconspicua* (Rubiaceae). There was a significant difference in the pooled relative abundance of these four species between areas (two-way ANOVA with arcsine transformation: $P < 0.001$), with significantly higher relative abundance in the burned than in the unburned plots on the lava

TABLE 1. *Relative abundance (stems ≥5 cm DBH) of the most common tree species before the cyclones, immediately after the cyclones, and after five years of recovery in unburned and burned areas.*

	Relative abundance (%)			
Species	Before Ofa and Val[a]	After Ofa and Val[a]	After 5 years Unburned area	After 5 years Burned area
Pometia pinnata (Sapindaceae)	25.0	34.2	12.4	1.1
Cananga odorata (Annonaceae)	22.1	4.6	15.0	1.9
Aglaia samoensis (Meliaceae)	12.3	5.2	<1.0	<1.0
Syzygium inophylloides (Myrtaceae)	10.8	8.5	1.7	<1.0
Mammea glauca (Clusiaceae)	10.0	5.8	1.7	<1.0
Dysoxylum maota (Meliaceae)	7.1	15.1	2.1	<1.0
Planchonella torricellensis (Sapotaceae)	5.8	11.2	<1.0	<1.0
Macaranga harveyana (Euphorbiaceae)	<1.0	<1.0	42.1	85.8
Antirrhoea inconspiqua (Rubiaceae)	<1.0	<1.0	6.9	<1.0
Inocarpus fagifer (Fabaceae)	2.0	4.8	3.4	<1.0
Kleinhovia hospita (Sterculiaceae)	<1.0	<1.0	2.6	1.4
Diospyros samoensis (Ebenaceae)	1.0	2.3	1.3	<1.0
Myristica fatua (Myristicaceae)	<1.0	<1.0	3.0	<1.0
Rhus taitensis (Anacardiaceae)	<1.0	<1.0	<1.0	7.4

[a] Data from Elmqvist *et al.* 1994.

plain in the 1–5 cm DBH size class (Sheffe's test: $P < 0.001$; Table 2).

VECTORS AND SEED DISPERSAL.—We found a marked difference between the burned and the unburned areas in the relative abundance of animal dispersed species versus species with fruits that are not known to be fed upon by potential seed dispersers (Fig. 5). Chi-square analysis, using the Haber correction for continuity, showed that encountered frequencies differed significantly from expected in all size classes ($\nu = 1$, $\alpha = 0.05$). In the burned area, species with fruits fed upon by birds and/or bats made up a significantly larger proportion of the tree community in all size classes than species that are not known to be so. In the unburned area, however, the proportion of species not known to be bird and/or bat dispersed in the smallest size class was larger, while the two categories were about equal in the second smallest size class. For the two larger size classes, there was a larger proportion of bird and/or bat dispersed species, although not as marked a difference as in the burned area.

DISCUSSION

The combined effect of the two cyclones, each with a severe impact of its own, resulted in large immediate changes in structure and species composition of the Tafua forest (Elmqvist *et al.* 1994). The area subjected to a forest fire was even more adversely affected, with a tree mortality of more than 90 percent (Elmqvist *et al.* 1994). In this second survey of the forest nearly five years after the second cyclone, distinct patterns of regeneration start to emerge. Despite heterogeneity in the effect of the cyclones, strong differences are exhibited between the burned and the unburned parts of the forest.

SPECIES DIVERSITY.—Two community properties, species number and equitability or evenness, are often considered the main aspects of species diversity (Begon *et al.* 1990). Mean number of species per plot was significantly higher in the unburned than in the burned area, indicating a higher species richness in the unburned area. Evenness was also greater among tree species in the unburned than in the burned area in the two largest size classes. In the two smallest size classes, however, greater evenness was found in the burned than in the unburned area. This pattern may be explained by the complete dominance of a small number of pioneer species in the largest size classes in the burned area. These species are now less abundant among smaller plants.

REGENERATION STRATEGIES AND SPECIES COMPOSITION.—The density of seedlings and small saplings (<1 cm DBH) was much lower in the burned than in the unburned area. This, in combination with a low proportion of canopy tree species, indicates that

TABLE 2. *Relative abundance in four size classes of all tree species contributing more than 1 percent in any size class after five years of recovery in (a) the unburned area and (b) the burned area. A weighted average, calculated on the relative abundance of each species in the four size classes, is also given (Whittaker 1967).*

Species	Relative abundance (%)				Weighted average
		>100 cm height			
	<100 cm height	<1 cm DBH	1–5 cm DBH	>5 cm DBH	
(a) Unburned area					
Aglaia samoensis (Meliaceae)	1.4	1.1	1.4	<1.0	2.37
Aidia cochinchinensis (Rubiaceae)	45.0	31.6	14.8	<1.0	1.68
Antirrhoea inconspicua (Rubiaceae)	<1.0	1.2	1.2	6.9	3.50
Cananga odorata (Annonaceae)	<1.0	<1.0	7.8	15.0	3.61
Canarium harveyi (Burseraceae)	1.8	2.3	2.0	<1.0	2.17
Citronella samoensis (Icacinaceae)	<1.0	<1.0	1.2	<1.0	2.84
Cryptocarya elegans (Lauraceae)	1.5	1.5	1.2	<1.0	1.92
Diospyros samoensis (Ebenaceae)	14.8	16.1	7.5	1.3	1.88
Dysoxylum maota (Meliaceae)	5.6	1.5	2.3	2.1	2.08
Elatostachys falcata (Sapindaceae)	<1.0	<1.0	1.2	<1.0	2.47
Erythrospermum aquminatissimum (Flacourtiaceae)	<1.0	1.2	1.2	<1.0	2.31
Ficus godeffroyi (Moraceae)	<1.0	2.1	4.9	<1.0	2.63
F. scabra (Moraceae)	<1.0	<1.0	1.4	<1.0	2.98
Funtumia elastica (Rubiaceae)	<1.0	1.2	1.2	<1.0	2.41
Inocarpus fagifer (Fabaceae)	<1.0	<1.0	1.2	3.4	3.34
Kleinhovia hospita (Sterculiaceae)	<1.0	<1.0	<1.0	2.6	3.82
Macaranga harveyana (Euphorbiaceae)	<1.0	<1.0	7.2	42.1	3.83
Mammea glauca (Clusiaceae)	3.5	4.4	2.9	1.7	2.23
Morinda citrifolia (Rubiaceae)	<1.0	<1.0	3.5	<1.0	2.65
Myristica fatua (Myristicaceae)	2.3	2.6	3.5	3.0	2.64
Planchonella garberi (Sapotaceae)	2.4	12.0	5.2	<1.0	2.14
P. torricellensis (Sapotaceae)	<1.0	3.0	2.9	<1.0	2.28
Pometia pinnata (Sapindaceae)	10.8	5.9	11.6	12.4	2.63
Rhus taitensis (Anacardiaceae)	<1.0	<1.0	1.7	<1.0	3.05
Syzygium inophylloides (Myrtaceae)	2.8	4.8	2.3	1.7	2.26
(b) Burned area					
Aidia cochinchinensis (Rubiaceae)	4.8	1.4	<1.0	<1.0	1.23
Antirrhoea inconspicua (Rubiaceae)	1.6	1.4	<1.0	<1.0	1.47
Cananga odorata (Annonaceae)	4.0	15.7	9.8	1.9	2.30
Diospyros samoensis (Ebenaceae)	36.7	11.4	<1.0	<1.0	1.25
Dysoxylum maota (Meliaceae)	<1.0	2.9	<1.0	<1.0	2.32
Elatostachys falcata (Sapindaceae)	9.3	<1.0	<1.0	<1.0	1.00
Ficus scabra (Moraceae)	1.2	1.4	<1.0	<1.0	1.76
Funtumia elastica (Rubiaceae)	<1.0	7.1	1.9	<1.0	2.11
Garuga floribunda (Burseraceae)	1.2	11.4	2.8	<1.0	2.14
Kleinhovia hospita (Sterculiaceae)	<1.0	<1.0	<1.0	1.4	4.00
Macaranga harveyana (Euphorbiaceae)	3.6	8.6	57.5	85.8	3.45
Mammea glauca (Clusiaceae)	1.2	5.7	<1.0	<1.0	1.90
Morinda citrifolia (Rubiaceae)	20.6	7.1	2.3	<1.0	1.42
Planchonella garberi (Sapotaceae)	2.8	17.1	1.9	<1.0	1.96
Pometia pinnata (Sapindaceae)	<1.0	<1.0	2.8	1.1	3.07
Rhus taitensis (Anacardiaceae)	1.6	4.3	15.4	7.4	2.99

recovery is a much slower process in the burned than in the unburned area. On the other hand, the densities of larger saplings and pole-sized trees (>1 cm DBH) of early successional species were higher in the burned area. In this part of the forest, a more or less continuous canopy has been built up almost exclusively by *M. harveyana,* a fast growing pioneer species that is common in secondary forest (Arvidsson 1996). This canopy, however, is at a much lower level (8–10 m) than the one present before the cyclones, and only scattered remnant trees rise high above it. The presence of a low but very dense can-

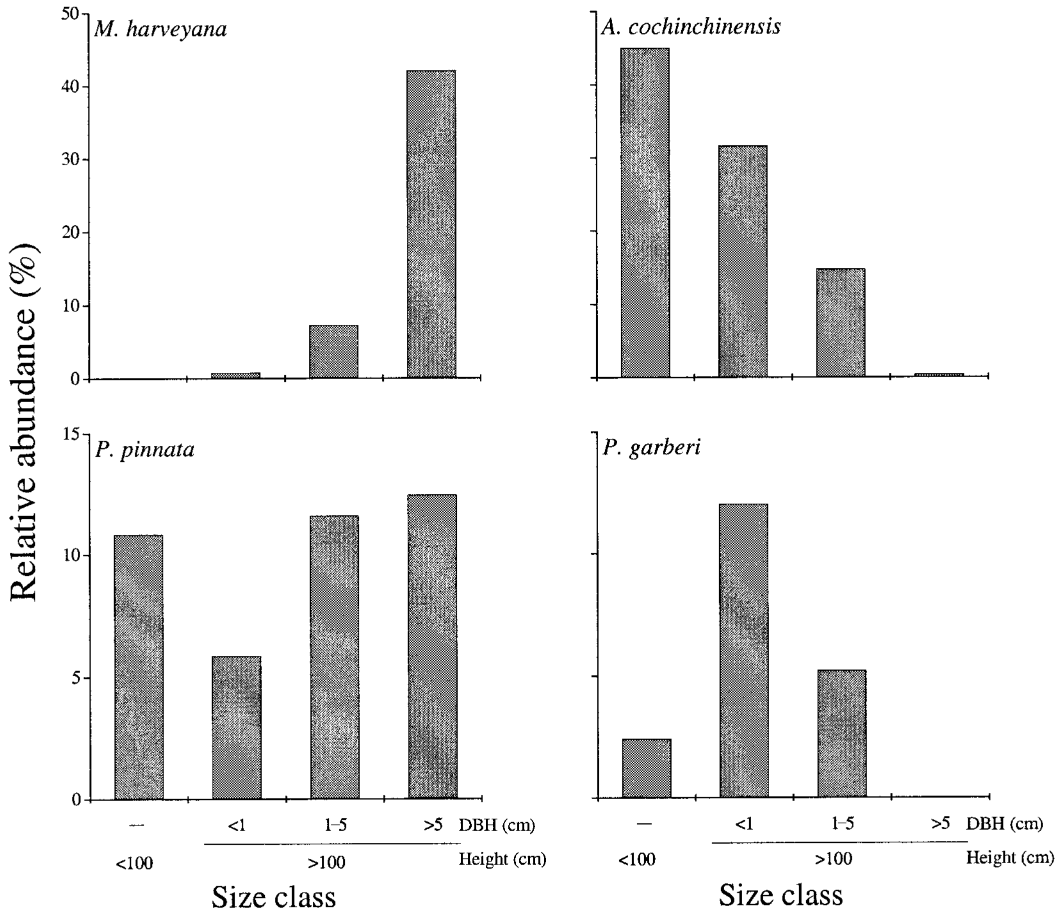

FIGURE 4. The relative abundance of four tree species in four size classes five years after the disturbance, exemplifying four distinct size distribution patterns characteristic of early establishing species (*Macaranga harveyana*), late establishing species (*Aidia cochinchinensis*), intermediate pulse species (*Planchonella garberi*), and species showing no obvious regenerative response to disturbance (*Pometia pinnata*). Note the different scales.

opy in post-cyclone succession has also been reported for a Nicaraguan rain forest (Vandermeer *et al.* 1997). In Nicaragua, however, the canopy consisted primarily of resprouting climax species (Yih *et al.* 1991), a process observed also on Barro Colorado Island, Panama (Putz & Brokaw 1989), and Jamaica (Bellingham *et al.* 1994, Negrelle 1995). In contrast, the burned portion of the Tafua forest is dominated by pioneer species, regenerated from seeds, a pattern observed also in Puerto Rico (Frangi & Lugo 1991, Guzmán-Grajales & Walker 1991). The differences in importance of pioneer species may reflect differences in mean gap sizes among the studies (Brokaw 1985, Putz & Brokaw 1989) and differences in gap-size requirement among pioneer species (Brokaw 1987). The greater dominance of *M. harveyana* in the burned than in the unburned part of the Tafua forest reflects the greater extent to which the canopy was opened in the burned area, a result of the post-burn mortality of canopy trees (Elmqvist *et al.* 1994). Moreover, regeneration from seeds appears to be the most important path of regeneration, in the Tafua forest, even in small gaps.

Interspecific differences in response to disturbance.—In plant communities subject to frequent disturbances, we would expect its component species to exhibit some life history adaptations to the disturbance regime. Two main strategies have been suggested by Clark (1991): (1) most adults are killed as a result of the disturbance and the population recovers by means of recruitment from juveniles (type A response); and (2) most adults survive and recruitment is sparse at each disturbance

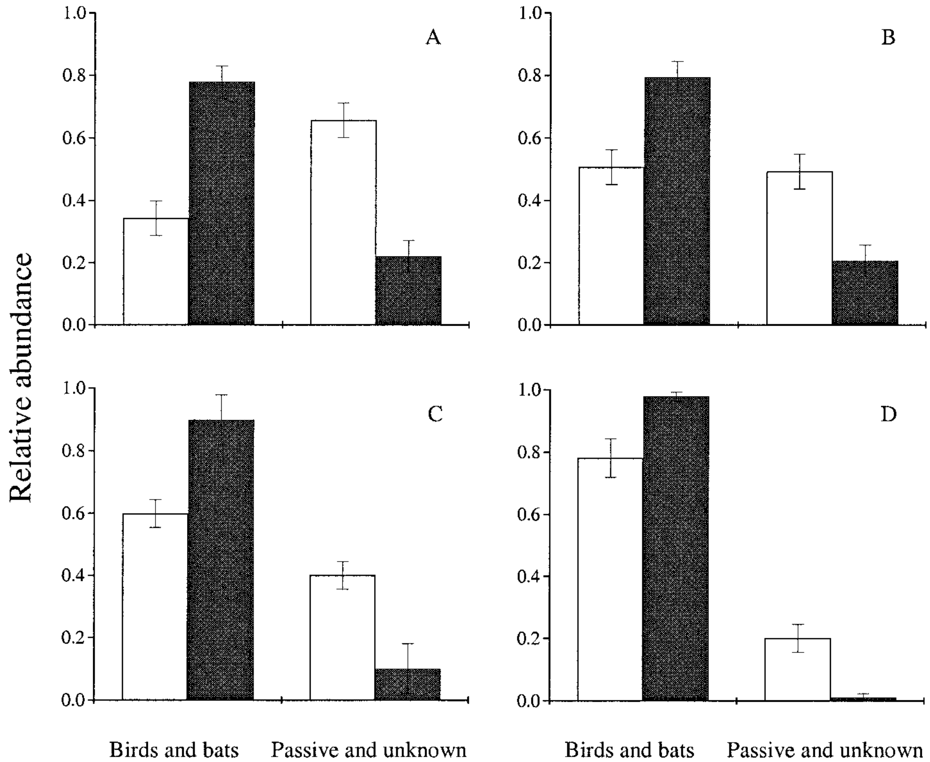

FIGURE 5. Proportion ($\bar{x}$ ± 1 SE) of trees belonging to species with fruits that are thought to be dispersed by birds and/or bats and species with fruits not thought to be dispersed by those animals in the unburned (white) and burned (dark gray) plots on the lava plain divided into four size classes: (a) <100 cm height; and three classes >100 cm height, further divided into (b) <1 cm DBH, (c) 1–5 cm DBH, and (d) >5 cm DBH in the Tafua forest.

event (type B response). The first strategy maximizes the chance of successful reproduction at the next recruitment opportunity while the second strategy maximizes the number of recruitment opportunities during the reproductive life of each individual plant. In this study, the response of the two most common species prior to the cyclones, *C.odorata* and *P. pinnata,* exemplifies these two distinct strategies. The understory species *C. odorata,* exemplifying the first strategy, suffered a very high mortality in the cyclones and consequently decreased dramatically in relative abundance. This species, however, regenerated abundantly from seeds during recovery and regained its position as the second most frequent tree species in the Tafua forest. *Pometia pinnata,* exemplifying the second strategy, showed a much lower mortality than most species due to the cyclones and so initially increased in relative abundance as a direct result of the disturbance. Furthermore, recruitment of this species was not particularly high during recovery. These two types of responses have also been referred to in terms of resistance and resilience (Boucher *et al.* 1994, Bellingham *et al.* 1995). *M. harveyana* represents a third group of species. It was largely absent from the primary forest prior to the cyclones (Elmqvist *et al.* 1994) but was abundant along roadsides and in plantations. After the disturbances it increased in abundance through colonization from areas outside the original primary forest.

We found large interspecific differences in distribution of relative abundance over size. When a weighted average was calculated, four species attained clearly higher values than the rest (*M. harveyana, K. hospita, C. odorata,* and *A. inconspicua*). These species therefore can be assumed to have regenerated abundantly from seeds immediately after the cyclones and that regeneration has decreased over time, a pattern typical of pioneer species. *Macaranga*-species are recognized as important pioneers in other parts of the Palaeotropics (Whitmore 1989b). *K. hospita* and *C. odorata* are commonly found in areas of human activity, indicating that they possess some secondary traits, and *A. incon-*

spicua, like *M. harveyana,* was uncommon in the forest before the cyclones. These four species together were more common in the burned than in the unburned area in all size classes, indicating the importance of the severity and type of disturbance for the relative abundance of pioneer and climax species.

Several species experienced drastic declines in relative abundance during the five-year period, among them *P. pinnata,* a canopy species that was the most common tree before the cyclones. Much of the decline in relative abundance of these species was due to the strong increase of *M. harveyana.* It is also possible that some species suffered an extended period of increased mortality, as was observed in a Mexican forest after Hurricane Gilbert (Whigham *et al.* 1991). The persistence of this change will depend on the rate at which different climax species will replace the currently dominating short-lived pioneers. Long-lived pioneers (*e.g., Rhus taitensis*) will remain a characteristic feature for a long time, at least in the burned part of the forest.

Importance of vertebrate seed disperser.—The lower local species richness in the burned compared to the unburned area suggests that seed immigration from the surrounding unburned forest is important for the recovery of species diversity in this area. We found species with fruits consumed by birds and/or flying foxes to have higher relative abundance than species not known to be so in all size classes in the burned area. This was not the case in the unburned area where species not known to be bird and/or bat dispersed made up a larger proportion in the smallest size class and the two categories were about equal in the second smallest size class. The greater dominance by bird-dispersed *M. harveyana* may account for the larger proportion of animal-dispersed species in the burned than in the unburned area for the two largest size classes, but not for the difference in the two smaller size classes in which this species was absent. This suggests that the importance of vertebrate seed dispersers increase with the severity of disturbance. Furthermore, seeds of bat-dispersed species were more effectively dispersed over long distances from intact forest than were seeds of bird-dispersed species in cleared areas of Peru (Gorchov *et al.* 1993). In Samoa, flying foxes are likely to cross large, open areas even more frequently than smaller fruit bats, which further indicates their importance in forest regeneration after catastrophic forest destruction. Animal seed dispersers are in general thought to be of great importance in the recovery process from catastrophic forest destruction. Holling *et al.* (1995) suggested that the period after a destructive event (pest, fire, or storm), which they called the reorganization period, is characterized by processes that reorganize species assemblages. During this phase, succession may be pushed along different pathways, depending on the presence or absence of key factors. Vertebrate frugivores in this perspective may be viewed as key organisms in the reorganization phase in which their absence may have forced succession into a different pathway dominated by wind- and passively dispersed plants, and perhaps also may have resulted in a great risk of invasion by wind-dispersed exotic opportunistic species.

Disturbance and invasive species.—Since cyclones result in large gap formation, reduced canopy cover, and increased edge effects, they may facilitate invasion by exotic species. On oceanic islands with highly endemic floras, such invaders are especially likely to cause displacements and extinction. A well-known example is the invasion of the Tahitian flora by the introduced species *Miconia calvescens* (Melastomataceae; Meyer & Florence 1996). In the Tafua forest, our data show that an exotic tree species, *F. elastica* (Rubiaceae), has increased after the cyclones. This species has been recognized as a serious forest weed in other parts of Samoa (Whistler, pers. comm.). More juveniles of *F. elastica* were found in the burned area where disturbance was more severe than in the unburned area, supporting the hypothesis that severe large-scale disturbance may increase the vulnerability of a plant community to invasions that can severely reduce biodiversity.

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