Journal of Ecology (1991), **79**, 447–457

THE IMPACT OF PHYSICAL DAMAGE ON CANOPY TREE REGENERATION IN TROPICAL RAIN FOREST

DAVID B. CLARK AND DEBORAH A. CLARK
La Selva Biological Station, Organization for Tropical Studies, Apartado 676,
2050 San Pedro, Costa Rica

SUMMARY

(1) This study assesses the frequency, rates of occurrence, and consequences of physical damage to individuals of nine canopy tree species in primary tropical rain forest at the La Selva Biological Station, Costa Rica.

(2) For all species combined, frequency of damage varied from 9 to 27% among five size classes. Frequency of damage was negatively correlated with diameter growth rates for stems 1–30 cm in diameter.

(3) Rates of damage due to falling litter ranged from 1 to 7% year^{-1} for trees up to 30 cm in diameter. Calculated half-lives until death or damage due to falling litter increased from 10 years for stems ≤ 1 cm in diameter to 63 years for stems 10–30 cm in diameter.

(4) Rates of mortality were higher in damaged individuals than in undamaged plants for stems up to 10 cm in diameter. Absolute rates of mortality decreased with increasing stem diameter, but the relative contribution of physical damage as an agent of mortality increased with stem diameter. Litterfall caused at least 20% of the mortality of stems ≤ 1 cm in diameter, and accounted for 41% of the deaths of stems 1–30 cm in diameter.

(5) Damage and death due to falling litter are important factors affecting plant regeneration throughout the humid neotropics. Future studies are likely to show that the same is true for temperate-zone closed-canopy forests.

INTRODUCTION

Canopy trees face a variety of potentially lethal assaults throughout their lives. At every stage, from the understorey to the canopy, individuals can be killed by biological or physical agents. Evolutionary biologists assume that patterns of growth, carbon and nutrient allocation, and architecture have evolved which reduce the effects of different agents of mortality. To examine this assumption analytically, one must first know what actually kills trees at different stages in their ontogeny.

One cause of tree mortality is physical damage due to tree, branch and litter fall. Several studies of particular size classes and species of trees have demonstrated relatively high frequencies of such damage (cf. Hartshorn 1972; Vandermeer 1977; Uhl 1982; Harcombe & Marks 1983; Clark & Clark 1987b; Aide 1987), but it seems that there has been no attempt to look at the role of physical damage through all the juvenile stages of a tree species, or to assess the relative importance of physical damage as a source of mortality through ontogeny. There is also little information on the consequences, other than immediate death, of physical damage to juvenile trees.

This paper examines the effects of physical damage on tree regeneration in a neotropical rain forest. The data come from a long-term study of nine species of canopy and emergent trees (Clark & Clark 1987a,b). The frequency of major stem damage to juveniles and adults, the rates at which this damage occurs, and its impact on short- and medium-term survival are described. The importance of physical damage as a factor affecting tropical tree regeneration is evaluated, and tropical data are compared with the existing information from temperate forests. It is now clear that physical damage is a significant agent of juvenile tree mortality in many neotropical rain forests. It is suggested that physical damage may be just as important in temperate forests, and that future studies should look for these effects.

METHODS

Study site

The study was carried out at the La Selva Biological Station of the Organization for Tropical Studies (OTS). La Selva, a 1500-ha reserve, is located in the Atlantic lowlands of Costa Rica (10°26′N, 84°00′W). The primary forest is classified in the Holdridge life-zone system as tropical wet forest (Hartshorn 1983). Temperature averages *c.* 26 °C (Fetcher, Oberbauer & Strain 1985). The mean annual rainfall is 3841 mm (unpublished OTS data), with an average of at least 100 mm of rain in every month. The study area for this research includes primary-forest watersheds of several first- and higher-order streams, and spans a marked fertility gradient in soil types (entisols, inceptisols and ultisols; Sánchez & Mata 1987). A complete site description is presented in McDade *et al.* (1991).

Study methods

The trees in this study are part of a long-term landscape-scale demographic study of nine species of canopy or emergent trees in the La Selva primary forest (Clark & Clark 1987a). Six of the species have been studied since 1983; three other light-demanding species were added in 1988 (Table 1). All nine species are included in the analyses of frequency of damage. Analyses of the rates and consequences of damage refer only to the six initial species.

The samples for each species were initially obtained by systematic searches of approximately 150 ha of primary forest. For each species all individuals > 50 cm tall that were encountered in 1982–83 were tagged and mapped. In subsequent years, the sample for some poorly represented size classes was increased using the same sampling methods. Once an individual was added to the study it was censused in every subsequent year. The three light-demanding, shorter-lived species first sampled in 1988 were added using the same methods. In all cases, every individual of the target size or species classes sighted during sampling was included, so as not to bias the sample with respect to the vigour, form or microhabitat of individuals. The samples are not appropriate for calculating intraspecific size-class distributions, because the probability of being (initially) sighted increased with size. However, none of the arguments developed here is based on the relative distribution of individuals among size classes.

TABLE 1. The nine focal species in the long-term study of tree regeneration in primary tropical wet forest at the La Selva Biological Station, Costa Rica. The first six species in the table were censused annually from 1983 to 1989. The last three species were added to the study in 1988.

Species	Family	Adult canopy position	Relative lifespan
Dipteryx panamensis (Pitt.) Record & Mell	Papilionoideae	Emergent	Long
Hyeronima alchorneoides Allemão	Euphorbiaceae	Emergent	Long
Hymenolobium mesoamericanum Lima	Papilionoideae	Emergent	Long
Lecythis ampla Miers	Lecythidaceae	Emergent	Long
Pithecellobium elegans Ducke	Mimosoideae	Emergent	Long
Minquartia guianensis Aubl.	Olacaceae	Canopy	Long
Simarouba amara Aubl.	Simaroubaceae	Canopy	Intermediate
Cecropia insignis Liebm.	Cecropiaceae	Canopy	Short
Cecropia obtusifolia Bertol.	Cecropiaceae	Canopy/Subcanopy	Very short

Each year from 1983 to 1989, all individuals present in the sample were censused during the period January–June. To maintain as close to yearly intervals as possible between measurements, trees were sampled in the same sequence each year. In each census all individuals were evaluated for survival, growth and microsite. Diameter was measured above buttresses or basal stem deformities at a fixed point. Diameters < 4 cm were measured with calipers at a point painted on the stem; for stems $\geqslant 4$ cm in diameter a diameter tape was used at 10 cm below a marker nail. Height (up to 16 m) was measured with a telescoping measuring pole. Beginning in 1984 stem condition for each individual was assessed annually. The categories were: (i) *stem erect but damaged*, i.e. with an abrupt diameter discontinuity $\geqslant 25\%$ of the stem diameter immediately below the point of damage (Fig. 1). This includes individuals which had lost their entire crown (Fig. 1b); (ii) *stem parallel to the ground* (Fig. 1c); (iii) *undamaged*, with neither of the above conditions. Field notes were taken of any obvious causes for new stem damage.

RESULTS

The results for stem condition at first encounter (Table 2) show the prevalence of damage for all post-seedling size classes of the nine species. For the six original long-lived species the percentage of damaged individuals ranged from 10 to 43% for the juvenile size classes ($\leqslant 30$ cm in diameter). In all juvenile and adult size classes, one of the *Cecropia* spp. had the lowest frequency of damage. *Simarouba* was usually intermediate between the *Cecropia* spp. and the other species. Interestingly, the nine species did not differ significantly in frequency of damage at the smallest, intermediate and largest size classes. Within a species, the percentage of damaged stems varied considerably among size classes. Overall, trees between 1 cm and 10 cm in diameter were more likely to be damaged than larger or smaller individuals.

The criterion of 'erect but damaged', i.e. a stem with an abrupt discontinuity $\geqslant 25\%$ of the stem diameter below the damage, was arbitrary. This level of damage was chosen because it was feasible to apply to individuals of greatly differing size. Many of the 'undamaged' individuals had clearly suffered major stem trauma which had partially healed with time. Table 2 therefore presents a conservative picture of the extent of stem damage in these species.

FIG. 1. Tree saplings at La Selva Biological Station, Costa Rica. Photographs by Gerardo Vega. (a) Tree sapling showing an abrupt discontinuity in stem diameter ≥25% of the diameter of the undamaged stem. Such stems were classified as 'damaged'. (b) Tree sapling that had its crown snapped off by a falling tree and subsequently resprouted. (c) Juvenile *Dipteryx panamensis* flattened by a falling branch, but still alive. Individuals in this condition may eventually resprout or right themselves, but many simply die.

TABLE 2. The frequency of damaged stems (percentages, with *n* in parentheses) for juveniles and adults of nine tree species in primary tropical wet forest at the La Selva Biological Station, Costa Rica. Figures are the percentage of stems in each size class that at first encounter were either erect but with a stem discontinuity ⩾25% of the undamaged stem diameter, or alive but horizontal. The smallest diameter class includes only plants which were ⩾50 cm tall at first encounter. The probability values are the probabilities of a difference in frequency of damage among the species (χ^2 or Fisher's exact tests); the two species or size classes with less than ten individuals are omitted from these analyses.

	Diameter class (cm)				
	⩽1	>1–4	>4–10	>10–30	>30
Dipteryx panamensis	10·2 (127)	18·2 (22)	20·0 (10)	10·0 (10)	11·1 (72)
Hyeronima alchorneoides	— (3)	17·6 (17)	28·0 (25)	21·1 (38)	9·3 (43)
Hymenolobium mesoamericanum	33·3 (15)	43·5 (23)	30·4 (23)	20·6 (34)	6·7 (15)
Lecythis ampla	15·8 (76)	43·1 (65)	35·9 (39)	35·3 (34)	7·1 (42)
Pithecellobium elegans	10·4 (48)	25·0 (40)	23·1 (39)	15·9 (44)	6·7 (164)
Minquartia guianensis	19·0 (63)	36·7 (79)	23·7 (76)	10·6 (94)	13·8 (109)
Simarouba amara	11·9 (84)	9·4 (64)	9·1 (33)	5·0 (60)	6·1 (33)
Cecropia insignis	10·0 (20)	17·6 (17)	15·8 (19)	7·1 (56)	0·0 (15)
Cecropia obtusifolia	14·3 (14)	5·9 (17)	5·9 (17)	1·1 (89)	— (1)
Mean (total)	13·6 (450)	27·3 (344)	22·8 (281)	11·5 (459)	8·9 (494)
Probability of difference among species	0·26	<0·001	0·16	<0·001	0·47

For all nine species, there was a significant ($P < 0{\cdot}05$ or 0·01) negative Spearman's correlation between frequency of damage and both median and maximum 1988–89 diameter growth for the three largest juvenile size classes. In all three size classes damage frequency was more strongly negatively correlated with the maximum observed growth rate than with the median rate. For the ⩽1-cm-diameter class, only six species had more than ten individuals for the 1988–89 period; there was no significant correlation between the percentage of damaged individuals and median or maximum diameter growth for these species.

It is relatively easy to assess the prevalence of damage in a sample of individuals at a given time, but this variable is potentially affected by several different phenomena. Faster-growing trees will remain in a given size class for shorter periods than slower-growing individuals. Lower accumulated damage could simply be due to shorter periods of exposure. Rates of damage repair, as well as the inherent propensity to be damaged in the first place, may vary interspecifically.

In order to understand the factors underlying the observed levels of damage, the rates at which damage occurred to previously undamaged individuals were evaluated. This analysis only included individuals for which there was clear evidence in field notes that the damage was caused by falling debris. Field evidence may disappear with time, and some instances may have gone unnoticed. The rates of physical damage due to litterfall shown in Table 3 are therefore conservative: actual rates may be considerably higher. Stems are also damaged by a variety of agents in addition to falling litter, including lightning, arthropods, mammals and strangulation by lianas. Rates of these types of damage were not measured.

Rates of major stem damage due to falling litter were quite high for small

TABLE 3. Annual rates of physical damage caused by litter to previously undamaged stems for different juvenile size classes of the first six species in Table 1 combined. Only individuals with clear evidence that the damage or death was due to falling litter are included. All undamaged individuals are included every year; thus, an individual may appear in up to five year-to-year calculations if its stem condition was classified as 'undamaged' at each census. Exponential rates of mortality or damage are calculated as $m = 100(\ln(n_0) - \ln(n_1))/t(\text{years})$; half-life in years until death or damage is calculated as $t(0{\cdot}5) = \ln(0{\cdot}5)/0{\cdot}01\,m$ (both from Swaine & Lieberman 1987).

	Number of individuals					
Year 1	with no major damage in year 1	horizontal in year 2	erect with stem damage in year 2	dead due to fallen litter by year 2	Exponential rate of death or damage due to litter	Half-life (years) until death or damage due to litter
≤1 cm diameter, ≥50 cm tall						
1984	121	2	3	3	6·84	
1985	157	8	1	1	6·58	
1986	154	3	1	1	3·30	
1987	151	15	0	3	12·69	
1988	136	5	1	1	5·28	
Total	719	33	6	9	6·91	10·03
>1–4 cm diameter						
1984	75	1	2	0	4·08	
1985	105	3	0	0	2·90	
1986	134	3	1	0	3·03	
1987	121	2	2	0	3·36	
1988	136	3	2	1	4·51	
Total	571	12	7	1	3·57	19·44
>4–10 cm diameter						
1984	72	0	0	0	0·00	
1985	100	0	0	0	0·00	
1986	105	0	4	0	3·88	
1987	107	0	3	1	3·81	
1988	112	0	2	0	1·80	
Total	496	0	9	1	2·04	34·03
>10–30 cm diameter						
1984	79	0	0	0	0·00	
1985	107	0	2	0	1·89	
1986	140	0	0	0	0·00	
1987	157	0	2	1	1·93	
1988	158	0	2	0	1·27	
Total	641	0	6	1	1·10	63·13

individuals (Table 3), and decreased with increasing stem size. The type of damage also varied with stem size. Many small stems that were knocked horizontal survived at least 1 year; larger stems were more likely to be killed outright when knocked horizontal. Larger stems that survived were damaged mainly by having the crowns broken off (Fig. 1b). The individuals < 16 m tall in Table 3 that were damaged but still standing ($n = 25$) lost a median of 38% of their height at the time of trauma.

The short-term consequences of stem damage from all sources differed among size classes (Table 4). One-year mortality in the ≤1-cm-diameter class did not differ significantly between stems classified as damaged and those undamaged. Death rates in general are high in this size class, and many of the undamaged stems are dying from the general effects of suppression (cf. Clark & Clark 1987b). It may be that

TABLE 4. The relationship between mortality during a given year and damage status at the start of that year (percentages, with *n* in parentheses). Data were combined for horizontal and erect damaged stems. Figures are from the 1984–89 annual censuses for the first six species listed in Table 1. As in Table 3, surviving individuals are counted once for each year until death; an individual surviving from 1984–88 would thus appear five times in these calculations. Sample sizes given in parentheses are the total number of instances of each condition for all the census years combined. The probability value refers to the probability of a significant association between stem condition and survival (χ^2 or Fisher's exact test).

	% Dead in year 2		
Stem diameter (cm)	Undamaged in year 1	Damaged in year 1	*P*
≤1	10·0 (719)	13·4 (134)	0·24
>1–4	0·2 (571)	4·9 (246)	<0·001
>4–10	0·4 (496)	2·0 (153)	0·09
>10–30	0·2 (641)	0·0 (131)	N.T.

N.T. = no statistical test possible.

TABLE 5. Annual mortality rates for different juvenile size classes of canopy and emergent trees in a tropical wet forest. Figures are for the first six species in Table 1 combined, with results from the 1983–89 annual censuses combined as in Table 4. All surviving individuals are counted once for each census until death, and thus may appear several times.

		Number killed in year 2 by		
Diameter class (cm)	Number in year 1	unknown causes	litterfall	Total annual mortality (%)
≤1	1048	93	23	11·07
>1–4	927	10	6	1·73
>4–10	730	3	2	0·68
>10–30	850	0	1	0·12

the effects of physical damage are small in relation to the generally unfavourable conditions faced by this size class. In larger size classes, however, where the overall death rate is much lower, trees with damaged stems showed greater mortality than undamaged individuals. For trees 1–4 cm in diameter, mortality of damaged individuals averaged 4·9% year^{-1}, compared to 0·2% year^{-1} for stems with no major damage. Damaged stems also had higher mortality in the 4–10-cm size class, but the difference was not statistically significant. There was insufficient mortality in the 10–30-cm class to test for an effect of stem damage.

With repeated annual censuses it is also possible to assess the longer-term impacts of physical damage on survival. The overall rates of annual mortality for all species combined (Table 5) indicate that in approximately half of the cases where an individual was knocked flat or had its stem broken, the plant was still alive at the first census after the trauma. These plants were listed as litterfall victims if they died in a subsequent census without substantial regrowth taking place. The criteria for attributing death to physical damage were restrictive: they included only cases with obvious physical evidence of falling debris causing the damage. Undoubtedly these rates are conservative.

The data in Table 5 show that litterfall accounts for a significant proportion of the mortality in all size classes. While overall mortality rates dropped sharply with increasing tree size, the proportion of deaths that were due to litterfall increased with stem diameter. For individuals ≤ 1 cm in diameter litterfall accounted for 20% of the deaths, while for 1–30-cm-diameter trees 41% of the mortality was caused by falling debris (Fisher's exact test, $P = 0{\cdot}05$, litterfall vs. other deaths, ≤ 1 cm diameter vs. 1–30 cm).

Of all litterfall mortality in this study, 25% was due to falling palm leaves, 44% to fallen branches, and 31% to fallen trees or mixed causes. The median diameter of individuals killed by palm leaves was 0·8 cm (range 0·4–1·9 cm).

DISCUSSION

Death from above – no way out?

From germination to reaching the canopy, trees at La Selva face a continual onslaught of falling debris. Many individuals will pass several decades or more in the smaller size classes (Lieberman *et al.* 1985; Clark & Clark 1987b; D. B. Clark & D. A. Clark unpublished data). Given the observed rates of physical damage, most stems will face major trauma or death during their passage from the understorey to the canopy.

There are two ways trees can substantially decrease exposure to physical damage. Because much damage is caused by objects falling from overhead, saplings which tend not to grow under the crowns of other trees will have lower rates of physical damage than saplings growing under closed canopies (cf. Putz & Brokaw 1989). For the two *Cecropia* species, a substantial fraction of the subadult population occur in microsites with no canopies above (D. B. Clark & D. A. Clark unpublished data). In the present study the *Cecropia* spp. did in fact show notably lower frequencies of damage. Putz & Brokaw (1989) also found that *Cecropia insignis* was the least damaged of the species they studied on Barro Colorado Island (BCI) in Panama.

The other way to minimize physical damage is to grow fast. This would both increase the rate of damage repair and decrease the amount of time spent as a vulnerable small individual. The three fastest-growing species in Table 2 (the *Cecropia* spp. and *Simarouba*; D. B. Clark & D. A. Clark unpublished data) did in fact have the lowest frequency of damage as larger juveniles. Putz & Brokaw (1989) also noted less damage among light-demanding, fast-growing species on BCI. Clearly, fast growth and avoidance of overhead crowns are linked in the light-limited conditions of tropical rain-forest understorey.

For juveniles ≤ 1 cm in diameter there is apparently no escape from stem damage. In spite of their contrasting life histories, these nine species did not differ in the frequency of damaged individuals in this size class.

A new paradigm for tree mortality in tropical rain forest

The results presented here suggest an ontogenetic shift in the relative importance of different mortality agents for tropical rain-forest trees. Numerous authors have shown that biotic factors such as herbivores and pathogens account for a substantial fraction of the mortality of young seedlings (reviewed in Clark & Clark 1984; see also Augspurger 1984a; De Steven & Putz 1984; Howe, Schupp & Westley 1985; Sork 1987). Based on the present study, it is suggested that for tropical rain-forest trees: (i) the relative importance of biotic factors as mortality agents decreases with increasing sapling size; and (ii) the relative importance of physical damage as an agent of mortality increases with increasing sapling size.

Few data are available to test this hypothesis. In a-posteriori non-experimental studies it will always be difficult to determine what portion of mortality is due to predators, pathogens, competition or physiological causes (Clark & Clark 1984). Nonetheless, Hubbell & Foster (1990) have demonstrated that mortality of 1–4-cm-diameter saplings on BCI is increased by proximity to conspecific adults. These pioneering data suggest that future studies should look for herbivore- or pathogen-based mortality in large juveniles. It is suggested, however, that the fastest progress in assessing the relative importance of mortality agents will come from studies of physical damage. Compared to mortality caused by pathogens, herbivores or physiological factors, mortality from physical damage is relatively easy to detect and document. If the percentage of mortality due to physical factors can be determined, the summed importance of all other agents of mortality is automatically known. Knowledge of the relative importance of mortality due to physical damage is interesting in itself. It may also provide valuable guidance for future research.

Physical damage and tree regeneration in tropical and temperate forests

In any rapidly growing or internally dynamic forest the potential exists for significant impacts of physical damage. Published data suggest that such damage is important in both neotropical and temperate forests. For sixteen species of *Piper* at La Selva, Gartner (1989) found damage frequencies, from all causes, of 12–100%. Six species had a higher proportion of damaged individuals than all the tree species in the present study. This may reflect the fact that *Piper* shrubs and treelets never grow to a size where they can escape a high risk of damage in the understorey. Gartner found lower frequencies of damage in open habitats than in forest, and lower damage rates for species that specialize on openings.

Previous studies of tree seedlings at La Selva have reported litterfall mortality rates of 14–20% over periods of 9–12 months (Hartshorn 1972; Vandermeer 1977; Clark & Clark 1987b, 1989). These rates are considerably higher than the 2·2% annual mortality due to litterfall found for the smallest saplings in this study (Table 5). Because of their greater stature, small saplings should be less vulnerable than seedlings to death from litterfall. In addition, the shorter intercensus intervals used in the previous studies probably increased the chances of detecting evidence of litterfall damage.

The importance of physical damage at La Selva is also dramatically shown by demographic data for two treelet species, *Compsoneura sprucei* (A. DC.) Warb. (Myristicaceae) and *Jacaratia dolichaula* (Donn. Sm.) Woodson (Caricaceae) (S. Bullock, unpublished data). Over a 10-year period *Compsoneura* suffered at least 8% mortality and 11% severely damaged stems due to falling debris ($n = 116$); 21% of the *Jacaratia* were killed and 10% were severely damaged by falling litter ($n = 182$). Given the 10-year interval between censuses, these are likely to be underestimates.

Significant levels of physical damage have also been measured in other neotropical rain forests. At Los Tuxtlas, Mexico, Córdova Casillas (1985) found that 18% of the seedling mortality of the canopy tree *Nectandra ambigens* Blake. (Lauraceae) was due to litterfall. On BCI in Panama, Aide (1987) found that 22–47% of the mortality of erect liana juveniles 30–350 cm tall was due to damage from fallen limbs. In Venezuela, Uhl (1982) showed that 38% of the death of 1–10-cm-diameter trees was due to branch or treefall. All of these rates are similar to those found in the present study (Table 5). Also on BCI, Putz & Brokaw (1989) evaluated the frequency of damage in mixed species plots using the definition of stem damage developed during this study (an abrupt diameter change $\geqslant 25\%$ of stem diameter). The frequency of damage they measured, approximately 30% for stems 10–30 cm in diameter, was higher than for all but one of the species studied at La Selva (Table 2).

These studies demonstrate that physical damage is a major cause of juvenile tree mortality in the humid neotropics. The limited data from temperate forests suggest that physical damage is also important in these ecosystems. Runkle (1985) summarized a variety of temperate forest studies showing gap formation rates of 0·5–2% of forest area annually. This dynamism must be reflected in physical damage to small plants. In addition, many branchfalls that are lethal to small trees fail to produce canopy openings. Harcombe & Marks (1983) found that 12% of the mortality of 5–19-cm-diameter saplings in a Texas hardwood–pine forest was due to breakage by other trees. In Pacific North-west mature Douglas-fir stands it has been estimated that at least 15% of tree mortality is due to branch and treefalls (unpublished data cited by Franklin, Shugart & Harmon 1987).

Temperate forest ecologists have long appreciated the effects of physical damage due to large-scale disturbances (cf. Webb 1989 and references therein). Neotropical continental wet tropical forests, however, are rarely affected by such disturbances (Clark 1990). As a result, forest ecologists in the neotropics may have paid closer attention to the effects of small-scale, frequent disturbances such as tree and branchfalls. We predict that future studies will show that physical damage is also a major cause of juvenile tree mortality in both temperate and Old World tropical closed-canopy forests. If so, life-history analyses of trees in these forests will have to incorporate the effects of physical damage in addition to the more commonly studied biological, physiological and abiotic factors.

ACKNOWLEDGMENTS

We thank the Organization for Tropical Studies for logistic and financial assistance during this work, which was also partially supported by grants from the United States National Science Foundation. Gary Hartshorn encouraged two neophyte tree biologists at the beginning of this study and urged us to include *Pithecellobium elegans,* for which we are lastingly grateful. Pia Paaby and Larry Dyer provided useful comments on the manuscript, and Steve Bullock furnished unpublished data. We are particularly appreciative of Sr Gerardo Vega's unstinting collaboration during 7 years of field work and data management.

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(Received 1 October 1990; revision received 21 February 1991)