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## Effect of distance, aggregation, and habitat on levels of seed predation for two mammal – dispersed neotropical rain forest tree species

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**Abstract** The effect of seed aggregation and distance from conspecific trees on seed predation was experimentally examined for two neotropical tree species, *Macoubea guianensis* (Apocynaceae) and *Pouteria* sp. (Sapotaceae) in a lowland tropical rain forest in northeastern Peru. Results of these experiments are discussed in the context of the Janzen-Connell model (Janzen 1970; Connell 1971), which predicts decreased seed survival near parent trees due to either density- or distance-responsive mortality, and Howe's model (Howe 1989) which predicts that trees with seeds dispersed in clumps (aggregated) will not suffer density-dependent predation, and will have higher survival of seeds near the parent tree than other trees. We also examined whether predation on seeds of these species was affected by seed placement in or near 30-m-wide strips regenerating after clear-cutting. Both species appeared to be mammal-dispersed but differed in how frugivores handled seeds, seed size, overall fruit crop size, and germination time. Neither of the two species studied appeared to suffer seed predation in a manner predicted by the Janzen-Connell model, and patterns of seed predation for only one of the species was similar to predictions of Howe's model. For neither species did seed predation along the edge of, or in the center of, regenerating clear cuts differ from predation 15 m into the primary forest. For *Pouteria*, seed predation in and near regenerating strips was significantly greater than around forest trees, but the opposite pattern held for *Macoubea*. Overall, seed predation was much greater on *Macoubea*. The difference in seed predation for these

two species was most likely a result of differences in the types of seed predators that attacked these two species.

**Key words** *Macoubea guianensis* · *Pouteria* sp. · Seed predation · Seed dispersal · Forest regeneration

### Introduction

Seed dispersal affects the fitness of parent and offspring plants through its effects on seed density, the distances seeds move from the parent tree, and the habitat where seeds arrive (Jordano 1992; Willson 1992; Schupp 1993). Differences in dispersal may influence early seed and seedling survival by affecting incidence of predation or attack by pathogens (Janzen 1970; Augspurger 1984a, b; Howe 1993), the habitat to which seeds are dispersed (Schupp 1988a, Schupp and Frost 1989), as well as the types of plants with which the developing plant will compete (Howe 1989; Loiselle 1990). Janzen (1970) and Connell (1971) hypothesized that higher seed and/or seedling predation will occur near the parent tree due to predators which search for seeds in either a distance- or density-dependent manner. Support for this hypothesis has been found in studies of a number of different tree species at the seed stage (see review by Clark and Clark 1984; and Schupp and Frost 1989; Forget 1992) and at the seedling stage (Augspurger 1984a; Clark and Clark 1984; De Steven and Putz 1984).

Such distance- and/or density-dependent mortality may have resulted in the selection for characteristics which increased the probability of seeds being dispersed away from the parent plant and sibling seeds. Conversely, plants with seeds not regularly dispersed away from parents or normally dispersed in clumps should be subject to selection for seeds well defended against sources of density – and/or distance-responsive mortality. For example, Howe (1989) suggested that tree species which have fruits primarily consumed by primates or other animals that tend to deposit seeds in large clumps may have evolved seeds and seedlings that are resistant to density-

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dependent mortality, due to secondary chemicals. Consequently, in areas where heavy defaunation has occurred, these species are expected to be at lower risk of population decline (Howe 1989). These species, however, may frequently have seeds occurring in high-density clumps away from the parent trees so that they may be subject to density-dependent seed predation at two scales; the larger scale around the parent tree and a smaller scale of aggregated seeds within a defecation. Separating the effects of distance and this larger-scale density is difficult as most trees have the greatest density (and number) of seeds directly under the parent (Clark and Clark 1984; Willson 1993). Separation of distance versus this smaller scale of aggregated seeds is however possible, and is a focus of this study.

Another way that human activity could influence patterns of seed predation is via habitat alteration. For example, Schupp (1988a, b) and Schupp and Frost (1989) demonstrated differential predation of *Faramaea* seeds and seedlings and *Welfia* seeds in natural treefall gaps when compared to adjacent forest understory. If habitat alterations also effect levels of seed predation, predicting patterns of survival in a more disturbed forest may be difficult.

A management system based on the natural process of gap formation, the strip clear-cut system, has been developed as a potentially sustainable method of timber extraction for tropical rain forests (Hartshorn 1989). In this system, all individual trees regardless of species are harvested from relatively narrow strips, and either sold or used locally (Hartshorn 1989; Gorchov et al. 1993). The sustainability of strip-cut forestry management depends on the natural regeneration of commercially valuable species, many of which are large-seeded (in the Peruvian Amazon this includes trees of the genera *Aspidosperma*, *Brosimum*, *Macoubea*, *Ocotea*, *Parkia*, *Pouteria*, *Swartzia*, and *Virola*; Peters et al. 1989). Studies examining seed survival in gaps suggest that predation may be an important factor affecting the composition and diversity of species that regenerate in logged strips. However, no previous study has investigated seed predation in strips despite its potential importance in recruitment of large-seeded species and hence the sustainability of this forest management system.

This study examined the survival of seeds of two canopy tree species [*Macoubea guianensis* (Apocynaceae) and *Pouteria* sp. (Sapotaceae)] with fruits primarily consumed and seeds likely dispersed by primates. The study consisted of two experiments designed to test the effect of different potential dispersal patterns on seed survival. The first experiment tested the effects of (1) seed aggregation (i.e., in clumps or scattered) and (2) distance from conspecific trees, on seed mortality. The second part of this study examined the effect of differences in habitat on seed predation by examining seed mortality in relation to seed proximity to logged strips.

## Methods

### Study site

This study was conducted between 8 June and 15 August 1992 at the Centro de Investigaciones de Jenaro Herrera, a field station along the Ucayali River 140 km south of Iquitos in the Departamento de Loreto, Peru (73°45'W, 4°55'S). Mean annual rainfall is 2521 mm with June through September generally drier than other months (Spichiger et al. 1989). The study area was approximately 4 km from the Ucayali in an area of non-flooded lowland tropical rain forest, bordered on the west by small agricultural clearings. Many of the larger mammals, including primates, were locally rare due to hunting.

### Study species

Two species of canopy trees, *Macoubea guianensis* (Apocynaceae) and *Pouteria* sp. (Sapotaceae) (hereafter referred to as *Macoubea* and *Pouteria*) were chosen for three reasons;

1. Primates consume fruits and probably are important seed dispersers of both tree species (Notman 1994).
2. These species represent two different fruit/seed types with potentially different dispersal strategies (see below).
3. Both species possessed characteristics suitable for experimental work (i.e., relatively large seeds which were available in sufficient quantities from several adult trees).

*Macoubea* had approximately 20–40 fruits per tree, fruits were approximately 10 cm in diameter and contained approximately 100–3002×0.5 cm seeds. In contrast, *Pouteria* had more fruits per tree (approximately 2000–3000), smaller fruits (approximately 2×4 cm), and each contained only one large (approximately 1×3 cm) seed. At this site *Macoubea* seeds appeared to be dispersed only by two species of tamarins (*Saguinus mystax* and *S. fuscicollis*); *Pouteria* trees were visited by a number of primates but seeds were only infrequently carried away from the parent tree (Notman 1994). Both species appeared to have similar spatial distribution of adults; adult plants were relatively common and scattered over the study area [approximately 1–2 trees/ha, personal observations; also 2 *Macoubea* trees >5 cm diameter at breast height (dbh) were found in 0.9 ha inventoried prior to cutting]. Young saplings (height: >50 cm) of each species were sparse even near adults. Seedlings and saplings were censused within a 20° arc extending 30 m from the base of one parent tree of each species. The survey of *Macoubea* found no saplings, and the survey of *Pouteria* found three saplings (but these may have included other *Pouteria* spp., as saplings are extremely difficult to identify to species). A total of three *Macoubea* saplings were found within the study area; all growing in small light gaps. Van Roosmalen (1985) also found *Macoubea* trees to be most abundant in the high light areas along creeks in the Guianas.

Information on fruit and seed abundance below parent trees was collected while preparing for seed predation experiments. For each of four trees per species, seeds and fruits were counted on six 2×2 m plots, two located 1 m from the base of the tree, two 10 m from the tree, and two 20 m away. The placement of each plot was chosen using a random compass direction from the base of the tree. If plots overlapped, a new direction was randomly selected for the second plot.

### Seed predation experiments

All experiments were done in a similar fashion for both tree species. The *Pouteria* experiment was initiated while the trees were at their peak of fruiting and were frequently being visited by animals. *Macoubea* trees were past their fruiting peak when the experiment began but a number of fruits still remained and occasional animal visits were observed.

Seeds for both aggregation/distance experiments and strip experiments (see below) were collected from around the study trees

from within the 2×2 m plots described above. Almost all *Pouteria* seeds had already been stripped of most of their pulp by primates, remaining pulp was removed using water and a plastic dish scrubber. *Macoubea* seeds were collected from fallen, unopened fruits; seeds were thoroughly rinsed to remove the surrounding sticky pulp. Despite this washing, seeds remained slightly sweet and sticky. Seeds were discarded if they showed visible signs of deformity or infestation or floated in water. Seeds of *Pouteria* were marked with a small "x" using an indelible ink pen. Seeds of *Macoubea* were marked with a small dot of white enamel model paint.

### Experiment 1

The first experiment compared the effect of two levels of aggregation and three distances on levels of seed predation resulting in a total of six different "dispersal" treatments. Each treatment was placed within one of the six 2×2 m plots described above. The two aggregation levels were: (1) clumped, in which a set of seeds were placed together in the center of the plot, and (2) scattered, in which the same number of seeds were scattered in a uniform pattern in a 1-m<sup>2</sup> area within the plot. *Pouteria* seeds were placed in clumps of five seeds whereas the smaller *Macoubea* seeds were placed in clumps of ten; clump size differed for the two species in order to approximate the number of seeds which might reasonably be deposited in a single fecal clump by the larger primates. At each spot where an individual seed or clump of seeds was placed, a small area of leaf litter was also cleared. The three distances used were 1 m, 10 m, and 20 m. For all trees, the 1 m locations were always under the canopy of the adult and the 20 m locations were always outside of the canopy. The majority of sites at 10 m were outside of the canopy of the adult trees, but several were at the edge or under the canopy.

*Pouteria* seeds were placed on 19 July 1992 and checked after 2, 6, 12, 15, 21, and 23 days. *Macoubea* seeds were placed on 21 July 1992 and checked after 2, 4, 6, 9, 13, 17, and 21 days. On each check the number of seeds missing or damaged were recorded. We carefully searched for seeds within approximately 2 m of their original location, any seeds that had moved (due to falling debris, rain or passing animals) were replaced to their original site. The cause of damage was determined whenever possible. Seeds that began to rot during the experiment were replaced with fresh seeds. At the termination of the experiment all remaining seeds were checked to determine if they had begun to germinate and then cut open to check for insects or rotting.

For the purpose of this study, seeds recorded as missing were assumed to be dead. It is possible that some missing seeds may have actually been either removed by scatter-hoarding animals or overlooked.

### Experiment 2

The second experiment tested the effect of habitat on seed predation, specifically position relative to logged strips. Two 30×150 m strips cut within mature forest were used for this experiment; strips were separated by 140 m of forest. The first strip had been cleared 3 years prior and the second strip had been cleared approximately 2 years prior to this experiment. Both strips had been allowed to regenerate naturally after trees >5 cm dbh had been cut and removed (Gorchov et al. 1993).

Seeds of both species were placed along three different transects running parallel to the length of each strip. One transect ran along the center of the strip, one along the edge, and one 15 m outside the strip in mature forest. Along each transect five replicate seed stations were established at 10-m intervals. Each station consisted of two clumps of five seeds (one clump of each species), separated by approximately 3.5 m, and marked with a flagged stake. Seeds were placed on 25 June 1992 and checked after 4, 10, 14, and 18 days. Fates of seeds were determined as in experiment 1.

### Data analysis

To determine the effect of aggregation and distance on seed predation, we used a non-parametric two-factor analysis of variance test which is an extension of the Kruskal-Wallis test and allows testing the significance of the interaction between the two factors (Zar 1985). The dependent variable was number of seeds presumed dead at the end of the experimental period, the independent variables (or main effects) were aggregation and distance.

Temporal patterns of seed removal over time were compared separately for both aggregation and distance effects using a non-parametric log-rank test for equality of survival curves, using the SAS Lifetest procedure (SAS 1989; also see Pyke and Thompson 1986; Schupp 1988a). This test uses ranked data to compare the shape of curves of seed survival over time among treatments, without assuming a specific survival distribution model. We graph the cumulative numbers of seeds presumed dead, equivalent to 1-survival. This test also allows for type I, or right, censoring of the data in order to account for seeds still remaining at the end of the experimental period (Pyke and Thompson 1986). Where the curves of the three distance treatments differed significantly, we tested for differences between pairs of treatments using a Bonferroni adjustment ( $\alpha=0.017$ ).

To compare *Pouteria* and *Macoubea* in the proportion of total seeds presumed dead, a single-factor Kruskal-Wallis test was used.

To test the effect of experimental forestry strips on seed predation, a two factor Kruskal-Wallis test was again used. Number of seeds removed was the dependent variable, whereas main effects were (1) position with respect to the experimental forestry strip (i.e., strip center, edge, or adjacent forest) and (2) forestry strip number (1 or 2). Differences in seed removal between the two plant species were analyzed using a single-factor Kruskal-Wallis test.

As a final analysis, the effect of forest disturbance on seed predation at a larger scale was examined by comparing, for each species, seed removal in intact forest (experiment 1) to seed removal in forest disturbed by strip clearing (experiment 2) using a Kruskal-Wallis test. Number of seeds presumed dead was the dependent variable and the independent variable was forest disturbance; all treatments (i.e., aggregation or distance and position relative to strip) were pooled. The final census period for *Pouteria* seed removal from under intact forest was not included in this analysis, so that all seeds in intact forest were exposed to predation for 21 days and those in disturbed forest for 18 days.

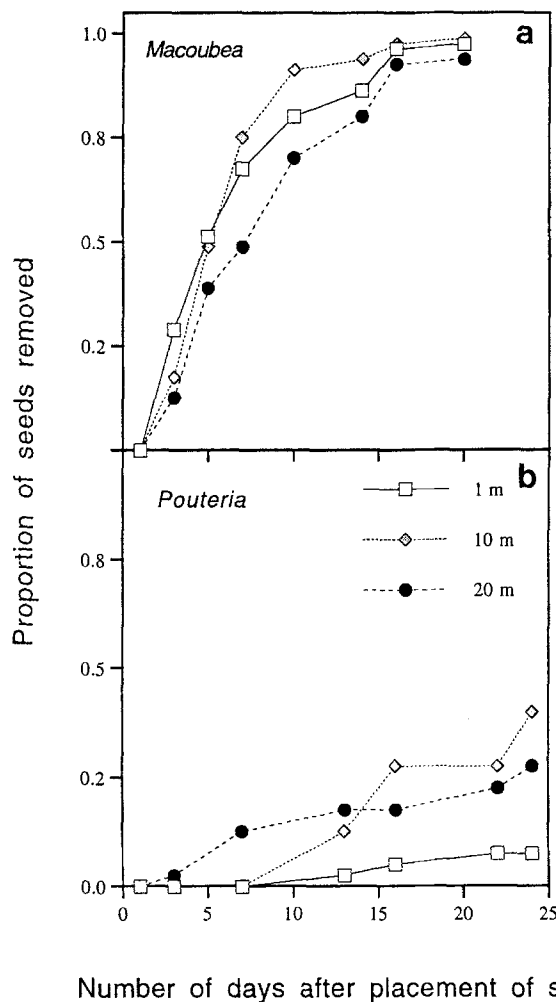
## Results

### Seed densities

The mean number of *Pouteria* seeds, including those in fruits, per 2×2 m plot, was 89.3 ( $\pm 52.2$  SD) at 1 m from a conspecific adult, 4.25 ( $\pm 4.7$  SD) 10 m away, and 0 at 20 m. For *Macoubea*, six of the eight plots at 1 m had 0–2 seeds; the other plots had 80 and 220 seeds; the two plots with high seed numbers included whole fruits that had landed within the plot. No seeds were found in any plots 10 or 20 m from conspecific adults.

### Aggregation/distance experiments

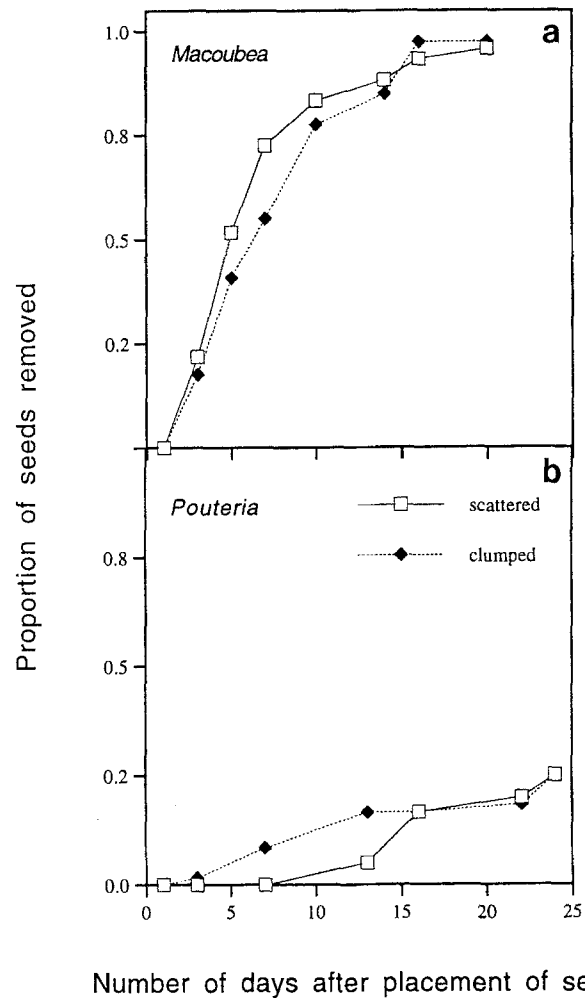
The number of *Macoubea* seeds damaged or missing at the conclusion of the experiment was not significantly different between aggregation treatments ( $K-W=0.70$ ,  $P>0.25$ ,  $df=1$ ) nor between distances ( $K-W=1.73$ ,  $P>0.1$ ,  $df=2$ ), nor was there a significant interaction between



**Fig. 1a,b** Average proportion of seeds removed over time as a function of distance from conspecific adult trees (**a** *Macoubea guianensis*, **b** *Pouteria* sp.). For each species, rates of removal among treatments are significantly different ( $P < 0.01$ )

main effects ( $K-W=0.35$ ,  $P > 0.5$ ,  $df=2$ ). For *Pouteria*, there was no effect of aggregation on seed predation ( $K-W=0.0$ ,  $P > 0.99$ ,  $df=1$ ). There was, however, a significant effect of distance ( $K-W=6.06$ ,  $P < 0.05$ ,  $df=2$ ); the interaction term was not significant ( $K-W=0.13$ ,  $P > 0.5$ ,  $df=2$ ). A non-parametric equivalent of a Tukey multiple comparison test (Zar 1985) was used to compare distance effects. Seeds at 1 m were preyed upon significantly less than seeds at either 10 ( $q=8.87$ ,  $P < 0.001$ ) or 20 m ( $q=6.31$ ,  $P < 0.001$ ); there was no difference, however, between seeds at 10 and 20 m ( $q=2.56$ ,  $P > 0.1$ ).

Temporal patterns of predation differed significantly between distance treatments (*Macoubea*  $c^2=10.30$ ,  $P < 0.01$ ; *Pouteria*  $c^2=9.45$ ,  $P < 0.01$ ; Fig. 1) but not between aggregation treatments (*Macoubea*  $c^2=1.95$ ,  $P > 0.10$ , *Pouteria*  $c^2=0.11$ ,  $P > 0.6$ ; Fig. 2). Tests comparing each pair of distances showed that for *Macoubea*, seeds located 20 m from a conspecific adult were removed at a significantly slower rate than seeds at either 1 or 10 m, which did not significantly differ from each other (Fig. 1). In contrast, *Pouteria* seed predation was sig-

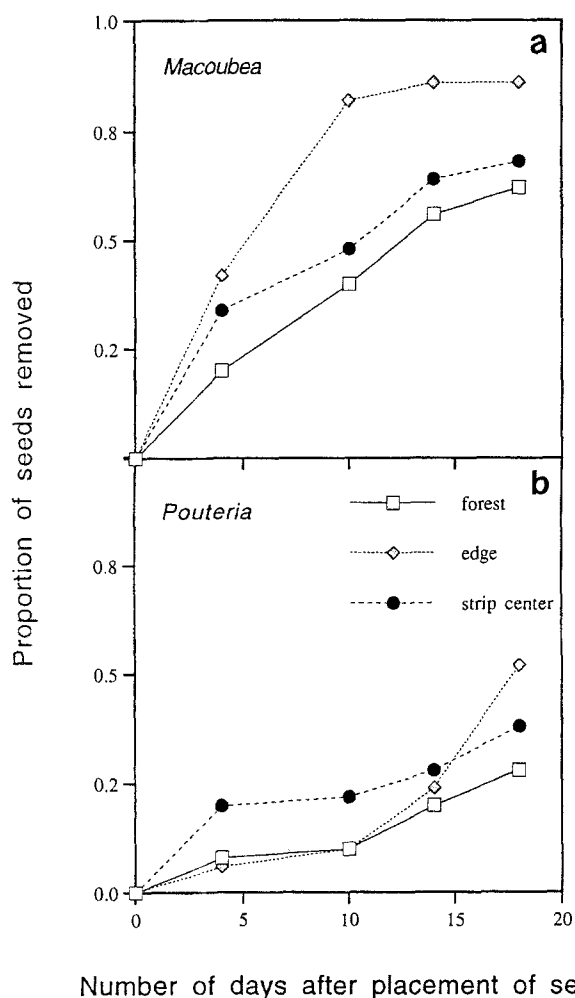


**Fig. 2a,b** Average proportion of seeds removed over time as a function of seed aggregation (**a** *M. guianensis*, **b** *Pouteria* sp.) Rate of removal is not significantly different between treatments (**a**  $P > 0.1$ , **b**  $P > 0.6$ )

nificantly slower 1 m from a conspecific adult than at either 10 or 20 m; seed predation rates at these more distant locations were not significantly different from each other (Fig. 1).

Over all density and distance treatments the percentage of seeds dying was lower for *Pouteria* ( $25.0 \pm 0.06\%$  SE) than for *Macoubea* ( $95.4 \pm 0.01\%$  SE) ( $F=453.18$ ,  $P < 0.0001$ ,  $df=1$ ).

Although it was usually not possible to determine the cause of mortality or removal, 38 (16%) of the *Macoubea* seeds scored as dead were clearly eaten by very small ants. These ants made a small hole in the seed coat and carried off the endosperm and embryo leaving behind a mostly intact seed coat or large fragments. The remaining seeds reported as dead were either missing or it was not possible to determine the predator (e.g., seeds broken into fragments too small to recognize). Of the eight *Macoubea* seeds still remaining at the end of the experiment, five were found to be rotten inside when broken open, and only three appeared viable, none of which had germinated. Of the 32 *Pouteria* seeds scored



**Fig. 3a, b** Average proportion of seeds removed over time as a function of seed location in relation to logged strips (a *M. guianensis*, b *Pouteria* sp.). Rates of removal among locations were not significantly different for *Pouteria* sp. ( $P < 0.4$ ). Rates of removal among locations were significantly different for *Macoubea guianensis* ( $P < 0.001$ )

as dead, 8 (25%) were attacked by various beetle larvae, 5 (16%) appeared to have been eaten by small rodents (seed fragments found with tooth marks), and 19 (59%), were missing. Of the 88 remaining (i.e., not preyed-on) *Pouteria* seeds, 70 (79%) had begun to germinate by the conclusion of the experiment, 6 (7%) were found to be rotten when cut open, and the remaining 12 (14%) appeared viable but had not begun to germinate.

#### Experiments in logged strips

For both *Macoubea* and *Pouteria*, there were no significant differences in total number of seeds removed between the two strips (*Macoubea*: K-W=1.68,  $P > 0.25$ ,  $df=1$ ; *Pouteria*: K-W=2.11,  $P > 0.1$ ,  $df=1$ ) or among the three locations (strip center, edge, and nearby forest) (*Macoubea*: K-W=3.63,  $P > 0.1$ ,  $df=2$ ; *Pouteria*: K-W=2.56,  $P > 0.25$ ,  $df=2$ ) nor was there any significant interaction between these effects (*Macoubea*: K-W=0.81,

$P > 0.5$ ,  $df=2$ ; *Pouteria*: K-W=1.49,  $P > 0.5$ ,  $df=2$ ). Temporal patterns of seed removal also did not differ between strips for either species (*Macoubea*:  $c^2=3.77$ ,  $P > 0.05$ ; *Pouteria*:  $c^2=2.97$ ,  $P > 0.08$ ), nor among locations for *Pouteria* ( $c^2=0.82$ ,  $P > 0.40$ ) (Fig. 3). The pattern of *Macoubea* seed predation was, however, significantly different between locations ( $c^2=13.63$ ,  $P < 0.001$ ); seed mortality occurred faster at the edge of the forestry strip than within or outside of the strip (Fig. 3).

As in the aggregation/distance experiments, when compared across all treatments significantly fewer ( $F=59.2$ ,  $P < 0.0001$ ,  $df=1$ ) *Pouteria* seeds were removed ( $39.3\% \pm 0.06$  SE) than *Macoubea* seeds ( $72.0 \pm 0.07\%$  SE).

Out of 108 *Macoubea* seeds scored dead in this experiment, cause of death could only be determined for 17 (16%) seeds; 9 were clearly eaten by ants, 5 were attacked by other insects, and 3 were partially eaten by small mammals. None of the surviving seeds had begun to germinate by the end of the experiment; four (10%) of these surviving seeds were found to be rotten when cut open. Out of 59 *Pouteria* seeds scored dead, the type of predator was determined for 17 (28%) of the seeds: 9 were attacked by unidentified insects or insect larva and 8 were partially eaten by small mammals. Most (68%) of surviving seeds had germinated by the end of the experiment, 21% were found to be rotten, and the remaining 11% appeared viable but had not yet begun to germinate. However, these results should be interpreted cautiously as the cause of mortality is unknown for most seeds (*Macoubea* 84% and *Pouteria* 72%), and most likely is due in great part to small mammals removing the entire seeds. Consequently this source of mortality is probably more important to these plant species than indicated here.

#### Comparison of seed predation in strips versus forest understory

For *Pouteria* the total number of seeds removed was significantly higher in the disturbed forest area than in the undisturbed forest understory ( $F=5.43$ ,  $P < 0.02$ ,  $df=1$ ); whereas for *Macoubea* it was significantly lower ( $F=10.38$ ,  $P < 0.002$ ,  $df=1$ ).

## Discussion

#### Seed predation models

Neither the Janzen-Connell escape hypothesis (Janzen 1970; Connell 1971), nor the model of Howe (1989) for trees with clumped seed dispersal adequately explain the patterns of seed predation observed for *M. guianensis* and *Pouteria* sp.. Results of experimental manipulation of seed distance failed to support the Janzen-Connell model. Seeds of *Pouteria* actually experienced less predation near the parent tree than did seeds farther away.

This result may be due to density-dependent predation at a smaller scale. Near parent trees predators may have foraged preferentially on the higher density of seeds naturally occurring outside of the 2×2 m experimental plots, whereas at the two greater distances densities were greater in the plots than in their surroundings. The effect of the surrounding seed shadow was not, however, explicitly tested.

The slower rate of removal of *Macoubea* seeds farthest from parent trees suggests that there may be some distance-dependent predation occurring. Although predation was high at all distances, in years of lower predator populations or more seeds, absolute differences in survival may result.

Stronger distance/density effects may also be operating at later life history stages (Wright 1983; Augspurger and Kitajima 1992). It is likely that *Pouteria* seedlings experience much higher levels of mortality than do the seeds. I observed extremely high numbers of young seedlings, yet sapling densities were low. In addition, because of high variability in these systems it is possible that greater replication may have revealed effects of distance or aggregation.

The model of Howe (1989) for trees whose seeds are primarily dispersed in fecal clumps offers one possible explanation for why some trees may not fit the Janzen-Connell model. A rejection of the Janzen-Connell model should not, however, necessarily result in acceptance of Howe's model. Given the extremely high rates of seed predation for *Macoubea*, the lack of distance-dependent predation is unlikely due to chemical defenses. On the other hand, the low levels of seed predation on *Pouteria* and the lack of an effect of seed aggregation suggest seeds may be chemically defended. Although chemical defenses were not examined in this study, extremely high rates of seed predation were observed at this site on other species of Sapotaceae with morphologically similar fruits and seeds, suggesting that predators ignored seeds of this species.

We hypothesize that differences in survival patterns for *Macoubea* and *Pouteria* are due, in large part, to differences in predators. For *Macoubea*, predation by ants may have played an important role in the high rates of predation regardless of density or distance from conspecific trees. High densities of ant colonies scattered throughout the forest floor (Levey and Byrne 1993) mean that foraging ants may frequently come across scattered seeds. Therefore seeds subject to ant predation may suffer density-independent predation. In addition, seeds in clumps generally were not removed all at once but rather a few at a time. This pattern suggests that large resources could not be rapidly exploited, and may explain the lack of a significant aggregation effect for total predation as well as mortality rate.

#### Effect of habitat on seed predation

Although seed predation did not vary on a small scale (strips of regenerating forest versus adjacent mature for-

est), at a larger scale seed predation did differ. Seed predation around conspecific trees within the mature forest understory differed significantly from predation within or near the forestry strips for both species. This suggests the influence of the strip due to changes in the vegetation and/or environmental conditions extend beyond 15 m. Other studies of natural forest gaps and human disturbed forest suggest that forest disturbance may exert an effect at larger scales. In Los Tuxtlas, Mexico, the effective area of a gap, defined by vegetation type, is on average 3.4 times larger than the actual canopy opening (Pompa et al. 1988). Elevated temperatures, reduced humidity, and increased light were found up to 40 m from the forest edge at isolated forest reserves in Brazil (Kapos 1989).

Changes in habitats (such as areas of disturbance) are likely to affect the composition and abundance of seed predators such that certain suites of seed predators become more important in certain habitats (Emmons 1982). For tree species attacked by these seed predators recruitment probabilities are also likely to vary among habitats (Sork 1987; Schupp et al. 1989; Terborgh 1992; Schupp 1993, 1995; Leigh et al. 1993). Different tree species are likely to show different patterns of recruitment among habitats, due to their susceptibilities to different suites of seed predators. Higher rates of seed predation within treefall gaps have been observed for a number of species (Schupp 1988a, b; Schupp and Frost 1989; Samper 1992), possibly due to increased rodent predation (Schupp et al. 1989). Our finding of greater mortality of *Pouteria* in and near strips of regenerating forest may have been due to greater predation by rodents in this habitat.

In conclusion, this study illustrates how disturbance of natural forests by hunting or logging may affect the interaction between trees and their seed predators. In this study neither tree species appeared to suffer mortality at the seed stage in patterns predicted by the Janzen-Connell model, suggesting that for these species, the presence of dispersers may not be as important for regeneration. This may be particularly true for *Pouteria*, which appeared, at least at the seed stage, to fit the model of Howe (1989) model of a clump-dispersed tree. For this species, however, predation increased in disturbed forest within and near forestry clearings, perhaps making dispersal more important for *Pouteria* in forests where disturbances such as logging takes place. In contrast, predation of *Macoubea* seeds appeared high regardless of whether seeds were clumped or scattered, or near or far from the tree. For this species seed survival was greater in disturbed forest, perhaps because there were fewer of its major seed predators. Therefore, for *Macoubea* and similar species, loss of dispersers may have a much larger impact on seed survival and increased disturbance may actually increase the chance of seed survival. Knowledge of what types of seed predators attack a given tree species may therefore be important to predicting the effect of disturbance on seed survival.

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## References

- Augspurger CK (1984a) Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712
- Augspurger CK (1984b) Pathogen mortality of tropical trees: changes in cohort distance with time. *Oecologia* 61:211–217
- Augspurger CK, Kitajima K (1992) Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73:1270–1284
- Clark DA, Clark DB (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol Monogr* 62:315–344
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Den Bour PJ, Gradwell PR (eds) *Dynamics of populations*. Center for Agricultural Publishing and Documentation Wageningen, pp 298–312
- De Steven D, Putz FE (1984) Impact of mammals on early recruitment of a tropical canopy trees *Dipteryx panamensis*, in Panama. *Oikos* 43:207–216
- Emmons LH (1982) Ecology of *Proechimys* (Rodentia, Echimyidae) in South-eastern Peru. *Trop Eco* 23:280–290
- Forget P-M (1992) Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24:408–414
- Gorchov DL, Cornejo F, Ascorra C, Jaramillo M (1993) The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *Vegetatio* 107/108:339–349
- Hartshorn GS (1989) Application of gap theory to tropical forest management: natural regeneration on strip-cuts in the Peruvian Amazon. *Ecology* 70:567–569
- Howe HF (1989) Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79:417–426
- Howe HF (1993) Aspects of variation in a neotropical seed dispersal system. *Vegetatio* 107/108:149–162
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Jordano P (1992) Fruits and frugivory. In: Fenner M (ed) *Seeds: the ecology of regeneration in plant communities*. CAB International, Wallingford, pp 105–156
- Leigh EG, Wright SJ, Herre EA, Putz FE (1993) The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evol Ecol* 7:76–102
- Levey DJ, Byrne MM (1993) Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology* 74:1802–1812
- Loiselle BA (1990) Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. *Oecologia* 82:494–500
- Notman E (1994) The effect of density, distance, and micro-habitat, on levels of seed predation for two neotropical trees. Masters thesis, University of Missouri, Saint Louis
- Peters CM, Gentry AH, Mendelsohn RO (1989) Valuation of an Amazonian rainforest. *Nature* 339:655–656
- Pompa JF, Bongers F, Martinez-Ramos M, Veneklaas E (1988) Pioneer species distribution in treefall gaps in neotropical rain forest: a gap definition and its consequences. *J Trop Ecol* 4:77–88
- Pyke DA, Thompson JN (1986) Statistical analysis of survival and removal rate experiments. *Ecology* 67:240–245
- SAS (1989) SAS/STAT user's guide, version 6, 4th edn, v1&2. SAS Institute, Cary
- Samper CK (1992) Natural disturbance and plant establishment in an Andean cloud forest. Ph D Thesis, Harvard University, Cambridge
- Schupp EW (1988a) Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76:525–530
- Schupp EW (1988b) Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51:71–78
- Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108:15–29
- Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am J Bot* 82:399–409
- Schupp EW, Frost EW (1989) Differential predation of *Welfia georgii* seeds in treefall gaps and the forest understory. *Biotropica* 21:200–203
- Schupp EW, Howe HF, Augspurger CK, Levey DJ (1989) Arrival and survival in tropical treefall gaps. *Ecology* 70:562–564
- Sork VL (1987) Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68:1341–1350
- Spichiger L, Meroz J, Loizeau PA, de Ortega S (1989) Contribucion a la Flora de la Amazonia Peruana. Los arboles del arboreto Jenero Herrera, vol 1. Conservatoire et Jardin Botaniques de Genève) Switzerland
- Terborgh J (1992) Maintenance of diversity in tropical forests. *Biotropica* 24:283–292
- Roosmalen MGM van (1985) Fruits of the Guianan flora. Institute of Systematic Botany, Utrecht University, Netherlands
- Willson MF (1992) The ecology of seed dispersal. In: Fenner M (ed) *Seeds: the ecology of regeneration in plant communities*. CAB International, Wallingford, pp 61–86
- Willson MF (1993) Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108:261–280
- Wright SJ (1983) The dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds and the effect of distance to the parent palm. *Ecology* 64:1016–1021
- Zar JH (1985) *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs