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Spatial distribution, fruit production and seed removal of a rare, dioecious canopy tree species (*Aglaia* aff. *flavida* Merr. et Perr.) in Papua New Guinea

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ABSTRACT. All mature individuals of *Aglaia* aff. *flavida* (Meliaceae) were mapped in a 260 ha study area at the Crater Mountain Biological Research Station in Papua New Guinea. Sixty-four reproductively mature trees were found in an aggregated distribution with a mean inter-tree distance of 88.9 m. The sample consisted of 35 female and 29 male trees with a mean shortest distance between sexes of 232 m. Seed production and seed removal of 22 female trees was monitored throughout the 1992 fruiting season. Female trees within 200 m of male trees generally produced large seeds crops (> 100 seeds) whereas trees farther than 200 m from the nearest male had small seed crops (< 100 seeds) regardless of female size (DBH). Most seeds (63.2%, n = 3312) produced in a sub-sample of 22 trees came from the five most fecund trees, which also produced 74.1% of the seeds that were removed by vertebrate dispersers. Where a minority of a population of rare tropical trees produce the majority of progeny, sustainable harvest practices would be most effective where highly fecund individuals are identified and conserved.

KEY WORDS: cassowary, conservation, dioecy, Meliaceae, Papua New Guinea, seed dispersal, tropical rainforest.

INTRODUCTION

Rainforest tree communities typically contain many rare species (i.e. species that occur in low densities (Rabinowitz *et al.* 1986)). Ecological studies of such species have been hampered by exiguous data due to small sample sizes often inherent in such studies (Hubbell & Foster 1986). Rarity poses a problem to reproduction in self-incompatible and dioecious tree species (Ashton 1984) which are fairly numerous in tropical rainforests (Bawa 1992, Bawa *et al.* 1985a,b). For such species, seed set could be influenced by distance to the nearest pollen source, especially if pollinators cannot effectively move large distances. Most tropical dioecious trees are pollinated by small, unspecialized insects (Bawa 1980, 1994) that are potentially inefficient as long-distance pollen vectors.

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Rarity poses an additional liability to the reproductive success of many tropical dioecious trees that produce single- or few-seeded ornithochorous diaspores (Bawa 1980). Fruit crop size affects seed removal (Christensen *et al.* 1991, Foster 1990, French *et al.* 1992, Howe & De Steven 1979, Jordano 1982). If pollination success is low, due to long distances of males from females, the resulting small fruit crop might attract few frugivores, lowering seed removal rates and thus depressing reproductive success further. Furthermore, fruit removal may be affected by the surrounding neighbourhood. Proximity to other fruit resources might elevate fruit removal by attracting dispersers if dispersers are not limiting (Sargent 1990). Alternatively, isolated fruit resources might have higher removal by avoiding competition for limited dispersers (Manasse & Howe 1983, Moore & Willson 1982). The spatial distribution of flowering and fruiting trees has important consequences for the fitness components: seed set and seed removal.

The conservation of low-density species poses a problem because it is difficult to ascertain how large a forest reserve must be to maintain populations of such species. Few data exist that can be incorporated into models predicting the impact of selective harvesting schemes for rare tropical taxa (Gomez-Pompa & Burley 1991, Oldeman & van Dijk 1991), yet many selectively logged tropical hardwoods typically have low-density populations. Studies on the ecology of rare, non-timber species have implications for the management of ecologically similar timber species as well as conservation of biodiversity.

This study was undertaken in order to understand better the reproductive consequences of rarity by examining seed production and seed removal of a rare dioecious rainforest canopy in Papua New Guinea. This species produces a large diaspore that is almost exclusively dispersed by a frugivorous bird, the Dwarf Cassowary, *Casuaris bennetti*. The study investigates the following questions: how does the distance between male and female plants affect seed set? How does fruit crop size affect seed removal? How does the distance between fruiting trees (neighbourhood effects) affect seed removal? Potential implications of the results for conservation and the harvest of low-density tropical hardwoods are discussed.

STUDY AREA AND SPECIES

The Crater Mountain Biological Research Station is 10 km east of Haia, Chimbu Province, Papua New Guinea (06° 43.4' S, 145° 05.6' E) in the Crater Mountain Wildlife Management Area on traditional lands of the Pawaiian people. The study area spanned 850 to 1300 m elevation in the valley of the Oo River, in the Pio drainage. The area is entirely forested, mostly primary forest, with some patches of second growth forest from abandoned gardens, landslips and treefall gaps. Vegetation is difficult to classify, because it spans the transition from mixed evergreen hill forest to sub-montane forest (Paijmans 1976). Tree diversity is high with no strongly dominant canopy tree species but with many rare species (D. D. Wright, unpubl. data).

Voucher specimens (deposited at Kew Gardens, and the Academy of Natural Sciences, Philadelphia) of the study species were provisionally determined (C. Pannell, *pers. comm.*; Pannell 1992) as *Aglaiia* aff. *flavida* Merrill et Perry (hereafter called *Aglaiia*). I selected this species because it was rare, easily identified, even as seedlings, and virtually all seed dispersal is by cassowaries (Mack 1995a). All members of the genus *Aglaiia* are dioecious (Pannell 1992). This particular species produces a large capsule (up to 15 cm diameter) that contains 1–3 large seeds (mean seed size = 113 g). One-, two- and three-seeded capsules are distinguishable by morphology, enabling accurate counts of seed production from fallen capsules. The large seeds, unless removed by dispersers, persist under female trees for at least 6 mo. Rats move some seeds short distances, but do not bury, conceal or completely destroy seeds (Mack 1995b).

Dwarf cassowaries are large (up to 29 kg) flightless ratites found throughout forested New Guinea above 300 m elevation (Beehler *et al.* 1986). They are specialist frugivores and disperse many seeds of many species (A. L. Mack *pers. obs.*; Pratt 1983).

METHODS

Tree distributions

Because the study area was located in a vast tract of continuous forest, the study plot was delineated using natural boundaries (streams, cliffs and ridgetops) in which to search exhaustively for trees. This plot was approximately 260 ha; precise mapping of the area was not possible because of extremely rugged terrain and lack of fine-scale maps and aerial photographs of the area. The plot enclosed 10 km of previously mapped trails. With the assistance of Pawaiian landowners who were thoroughly familiar with the forest, the study area was systematically searched for all individuals of *Aglaiia* large enough to reach the canopy. During the course of other studies in the area (1989–1993), the study area was thoroughly searched several times; certainly nearly all of the mature *Aglaiia* trees in the study area were found.

Mature trees were tagged and measured (DBH or diameter above the buttress for fluted individuals, Clark & Clark 1992). Tree positions were mapped relative to known markers on the mapped trails using compass and tape measure.

Flowering

Flowering is extremely difficult to observe in this species; inflorescences are inconspicuous and ephemeral, and sexes are indistinguishable from the ground. Thus, it was not possible to assess if trees were reproductively mature and active simply by observing flowering. *Aglaiia* seeds have high survivorship and produce vigorous, long-lived seedlings (Mack 1995b). By searching beneath canopies for old seeds, and seedlings, it was possible to determine if trees had produced seeds in recent years. Any tree with evidence of past seed production was considered a mature female (seeds are not dispersed to sites under mature trees, Mack 1995b). All mature females identified in this fashion were 40 cm

diameter at breast height (DBH) or more and had substantial canopy-level branch crowns. Identifying male trees was a problem. *Aglaia* trees were considered males if they were > 40 cm DBH and/or of canopy stature but showed no evidence of prior seed production. Flowering was never observed in any individual (male or female) smaller than 40 cm DBH, nor was evidence found of past fruiting (seedlings from undispersed seeds) under trees < 40 cm DBH. Furthermore, smaller trees were so uncommon (see Results) that if a few flowered they would not substantially alter the conclusions. Little is known of the pollinators or pollination ecology of any *Aglaia* species; small diptera and hymenoptera are most likely the main pollinators (Pannell 1992).

Seed production and seed removal

Data were collected on crop size and seed removal at 22 of 35 mature female trees in the study area during the June–September 1992 fruiting season. The 22 female trees chosen (mean DBH = 79 cm \pm 28.9 SD, range 42–140) were representative of the sizes of female individuals in the population (mean DBH = 76 cm \pm 29 SD) and distributed throughout the study area. After fruiting was complete, fallen capsules under each tree were counted to determine the total number of seeds produced (crop size) and the number of undispersed seeds remaining under 21 of the 22 trees. The difference between the crop size and the number of undispersed seeds is the number of seeds removed.

The study was conducted between May 1990 and July 1993. The species appears to fruit biannually. Data on fruit production and seed removal were collected during the 1992 fruiting season. Data collected in 1990 were incomplete and are not included here but were totally consistent with the results obtained in 1992.

RESULTS

Tree distribution

Sixty-four adult trees were found in the study area. These have a mean inter-tree distance of 88.9 m (SD = 68.9), or approximately one tree per 4 ha (Figure 1). Trees were significantly aggregated ($R = 0.949$, $c = 3.32$, $P < 0.01$) according to the corrected version (Sinclair 1985) of the Clark & Evans (1954) test of spatial dispersion. A complete search was not made for all individuals < 40 cm DBH. Nonetheless, only nine additional individuals were found > 20 cm DBH and < 40 cm DBH; eight of these were < 30 cm DBH. Sub-adult trees were not numerous.

Population sex ratio

Twenty-nine mature male and 35 mature female trees were found (Figure 1). The male : female ratio, 0.81, is not significantly different from 1:1 ($\chi^2 = 0.56$, $P > 0.1$). The mean distance between a female tree and the nearest male tree

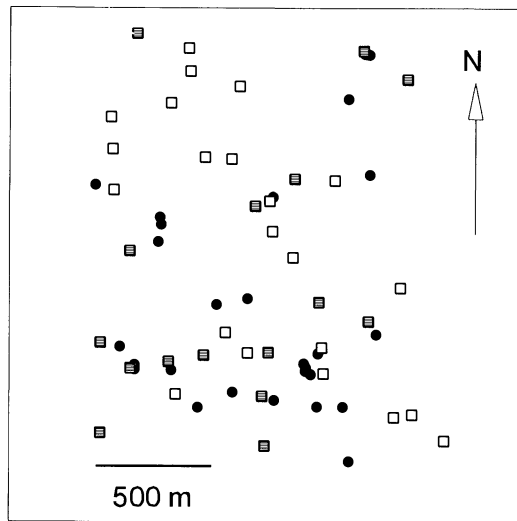


Figure 1. Map of the Crater Mountain study area in Papua New Guinea showing the locations of all *Aglaia* aff. *flavida* trees ≥ 40 cm DBH. Male trees are designated by filled circles, monitored female trees by open squares and unmonitored female trees by filled squares. The northern edge of the study area was bordered by impassable cliffs.

was 232 m (SD = 168), and the mean distance between a female tree and the second-nearest male tree was 316 m (SD = 153). If proximity to a female affects male mating success, some males were likely to have high success (close to several females), whereas some males were likely to have low mating success (not close to any females). In this sample, 14 male trees were the nearest males to the 22 female trees: one male was the closest male to six females, one to three females, one to two females and 11 males were closest to 11 individual female trees. There was no significant difference in size (DBH) of male versus female trees (female mean DBH = 72, SD = 29; male mean DBH = 69, SD = 26).

Seed production

Seed crop size differed greatly among female trees (mean = 151, SD = 163, range = 10–520, $n = 22$). Crop size was not significantly correlated with tree size as measured by DBH rank (Spearman's $r_s = 0.215$, $P > 0.05$). For example, two trees less than 55 cm DBH produced seed crops greater than 100, whereas five trees greater than 60 cm DBH yielded seed crops less than 50 (Figure 2).

The 22 monitored trees produced a total of 3312 seeds. Five female trees produced 63.2% of the seeds in this total. Crop size was negatively correlated with distance to nearest male tree (Spearman's $r_s = -0.421$, $P < 0.05$). Seven of the 10 females less than 200 m from a male tree produced seed crops greater than 100 and only one of 12 female trees over 200 m from a male tree produced a seed crop greater than 100 seeds (Figure 3). The correlation between crop size and the mean distance of the two nearest male trees ($r_s = -0.431$) was not much stronger than the correlation to the nearest male.

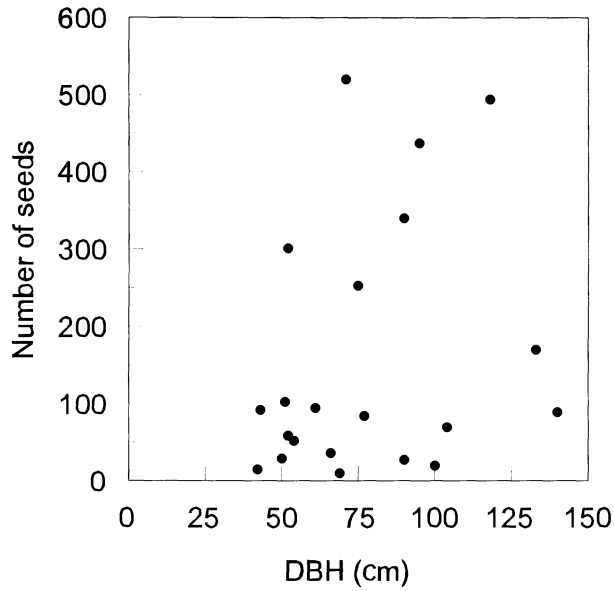


Figure 2. Relationship between crop and tree (DBH) sizes of 22 female *Aglaiia* aff. *flavida* trees showing no significant correlation between size of tree (DBH) and crop size.

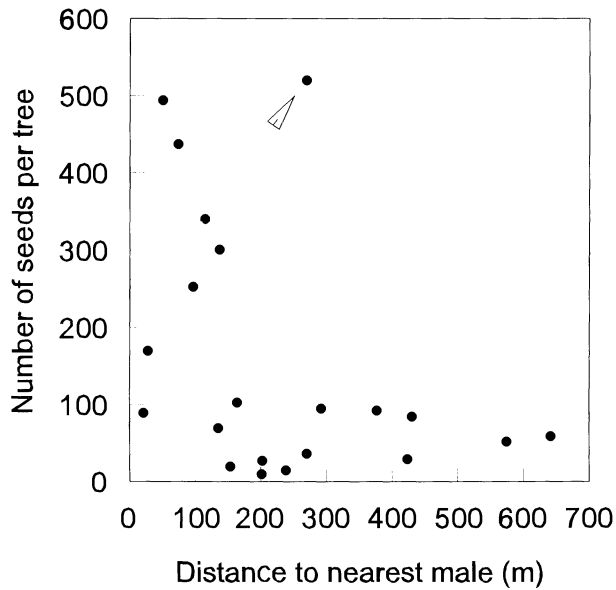


Figure 3. Crop sizes of 22 female *Aglaiia* aff. *flavida* trees and the distance to the nearest male tree. Large crops (> 100 seeds) occurred on female trees within 200 m of a male tree. The tree marked with an arrow is an exception (see Discussion).

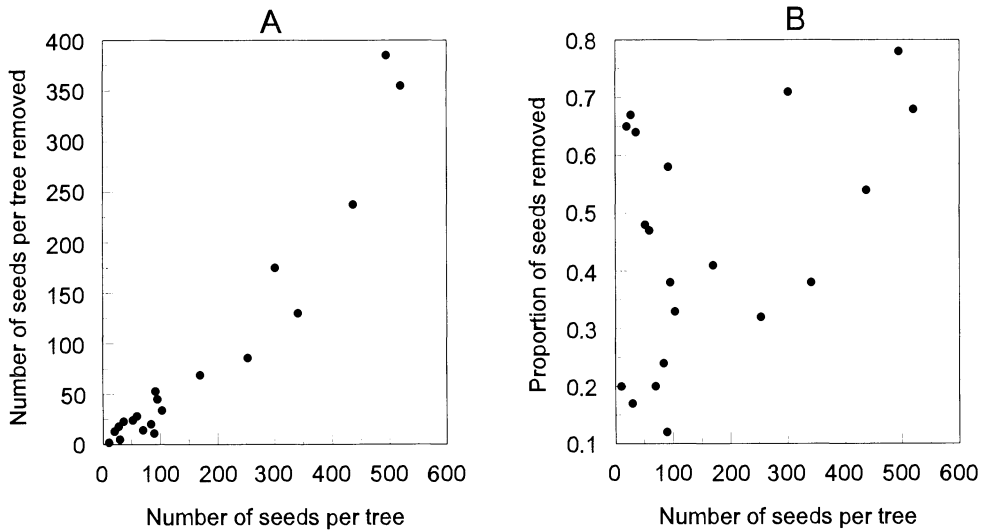


Figure 4. Relationship between number (A) and proportion (B) of seeds removed by vertebrate dispersers and crop size for 22 trees of *Aglaia* aff. *flavida*. Missing undispersed seeds during counts would inflate estimated removal, especially for trees with small crops. Elimination of such errors would strengthen the correlation.

Seed removal

The mean number of seeds removed per tree was 81 (SD = 113.4, N = 22 trees) and the mean proportion taken was 0.43 (SD = 0.211). The majority of dispersed seeds came from a minority of the trees; 74.1% of seeds removed were from five trees (23.8% of trees in the sample) with large seed crops. The number of seeds removed was strongly correlated with total crop size ($r_s = 0.911$, $P < 0.001$; Figure 4A). The correlation between crop size and proportion removed was not significant ($r_s = 0.29$, $P > 0.19$; Figure 4B). Proportion of seeds removed was not correlated with distance to the nearest female tree ($r_s = 0.01$, $P > 0.9$), nor with distance to the nearest female tree with a large ($\mu 100$ seeds) fruit crop ($r_s = 0.01$, $P > 0.4$). Thus, distance and crop size of neighbouring conspecific trees appeared to have little effect on seed removal. Missing undispersed seed during counts would inflate estimated removal, especially for trees with small crops. Elimination of such errors would strengthen the correlation.

DISCUSSION

Fecundity

Because data on pollinators, flower production or pollen movement could not be collected, firm conclusions cannot be drawn regarding how many male trees contribute to a female tree's seed set, nor regarding the exact relationship between male–female distance and seed set. Nonetheless, the data are sufficient to warrant consideration. Provisional conclusions should be tested with population genetic and paternity analyses of this and other low-density, dioecious tree species.

Although trees frequently exhibit a positive correlation between stem diameter and crop size (e.g. Bullock & Bawa 1981, Howe & De Steven 1979), *Aglaia* trees did not. For example, the fifth smallest tree produced the fourth largest seed crop in the sample. Instead, crop size was determined by the proximity to the nearest potential pollen donor (Figure 3) as has been found for several other dioecious rainforest trees (House 1992). The correlation between crop size and the mean distance of the nearest two male trees was not stronger than with distance to the single nearest male tree. The second-nearest male trees, at an average distance of 316 m, were usually beyond the deduced 200 m range of effective pollen transmission (Figure 3) suggesting most seeds on a female tree come from a single pollen donor. Based on distances to neighbours, some male trees probably donated pollen to several females, but most female trees likely received most of their pollen from single male trees. Trees with large crops had large seedling cohorts beneath them (undispersed seeds from previous crops), and trees that had small crops had small seedling cohorts (Mack 1995b), indicating that observed crop sizes were consistent in previous reproductive episodes.

Another consequence of the low density of males and the apparent threshold in effective pollination distance is that many female trees did not produce large crops even though their size (DBH) suggested greater potential fecundity. Fifty-five per cent of the females were more than 200 m from the nearest male tree. Consequently, a few female trees produced the majority of seeds in the sampled population: 63.2% of the seeds came from five (22.7%) trees. Four of the five most fecund females were < 140 m from the nearest male tree. The fifth tree with a large crop was 269 m from the nearest male tree (Figures 1 and 3) and was located in a region I visited infrequently due to an inhospitable ravine. It is conceivable a closer male tree was overlooked in this area.

These data suggest reproductive success of male trees varied greatly among individuals although it was not directly measured. If the assumption is made that all seeds produced by a female are progeny of the nearest male, then 71% of the seeds produced in this sample came from five of 14 males. Even if some seed set comes from second- or third-nearest males, the general conclusion probably is robust because many of these were also the closest male to other females. Thus, a small number of male trees contribute disproportionately to seed set. An important caveat is that it was impossible to identify unambiguously male trees by their flowers. If small, sub-canopy trees produced male inflorescences the above assumption would be invalid, though this was never observed and sub-adult trees were rare. Plant density and distance to nearest putative pollen donor limit seed set in many plants (Kunin 1992, 1993; Platt *et al.* 1974, Silander 1978). Barrett & Thomson (1982), however, found no inter-sex distance effect in a population of *Aralia nudicaulis* because, they hypothesized, its pollinator was capable of carrying pollen long distances. Studies of distance-density effects on seed set in dioecious tropical rainforest trees are

few, despite the obvious consequences such effects could generate after forest fragmentation (House 1992).

This population was not male biased, unlike many tropical dioecious tree populations (Bawa & Opler 1975, House 1992, Thomas & LaFrankie 1993). The rarity of males contributes to the observed male–female distance effect on seed set. As males become less numerous, male–female distances increase, and the small insects that typically pollinate dioecious tropical trees may have difficulty moving between sexes. Thus, male–female distance should affect seed set most markedly in species, such as *Aglaiia*, that occur in low densities, have female-biased sex ratios and/or have pollinators with limited flight capabilities.

Seed removal

Fruit presentation (abscission) by an *Aglaiia* tree is usually extended over a 45–60-d interval (Mack 1995b); trees with large crops generally drop a few fruits daily. Such a ‘steady state’ phenology (*sensu* Gentry 1974) is probably best if disperser numbers are limited and easily satiated. Daily visits by foraging cassowaries to trees with large crops are likely to be rewarded with newly fallen fruits. Visits to trees with small crops (less than 100) are less likely to be rewarded with edible fruits on a daily basis. Thus, in terms of optimal foraging by frugivores (Martin 1985), most visits and most seed removal should occur at trees with predictably reliable (i.e. large) crops.

Most seeds removed among the sample of 22 crops came from the five trees with the largest crops; the 12 trees with the smallest crops accounted for less than 10% of the seeds removed which could have important implications for population genetics. If dispersal increases fitness (Clark & Clark 1984), trees with high seed removal should have high fitness and selection should favour increased crop size. The data suggest crop size is largely a function of distance to the nearest male tree, a non-heritable trait. Any selection caused by cassowary preference for trees with large crops simply favours trees that happen to be near males. It is important, however, to bear in mind that this study covered only one fruiting season. Male trees can come and go in the lifespan of a female; females can have fecundity elevated or lowered with the maturation or demise of near-by males.

Unlike other studies (Denslow 1987, Manasse & Howe 1983, Moore & Willson 1982, Sargent 1990), there was no discernible neighbourhood effect (either positive or negative) on seed removal. The relatively large distances and rough terrain between fruiting trees minimize the impact one *Aglaiia* tree has on another’s removal rate because dwarf cassowaries consume a wide variety of fruits (D. D. Wright, unpubl. data; Pratt 1983) and their movements are constrained by topography (Mack 1995a). There probably are neighbourhood effects that depend on overall (interspecific) fruit availability within topographically defined (not linear–distance) boundaries.

Evolution of dioecy

Bawa & Opler (1975) predicted that dioecious species will occur, on average, in higher densities than hermaphroditic species. It is unlikely that *Aglaia*, at one adult per 4 ha, occurs at higher density than most hermaphroditic species in the area (D. D. Wright, *pers. comm.*). Bawa (1980) and Givnish (1980) proposed that dioecy could evolve in response to a disproportionate increase in fitness of females freed from male costs (but see Thomson & Brunet 1990). *Aglaia* fecundity was not correlated with female size and presumed ability to invest in inflorescences but was related to distance to the nearest male. Seed dispersal did increase with crop size (female investment) (Figure 4A), but the effect was not strongly disproportionate (Figure 4B). An important consideration, however, is that as density of adult trees increases, the effect of male to female distance might be moderated and the advantage to increased female investment could be more pronounced.

Conservation implications

Many economically valuable tropical trees occur at low densities, are selectively logged and require better natural history data to devise viable management practices (Bawa & Krugman 1991, Terborgh 1990). Although this species of *Aglaia* is not logged, many other members of the Meliaceae (mahoganies) are (Rodan *et al.* 1992). Most of the 1992 seed cohort was produced by a few female trees and probably the nearest one or two male trees. Harvesting these individuals could have disproportionate consequences for the regeneration potential of the population. For example, in hypothetical worst-case scenarios, selectively logging five female trees from a population of 36 male and female trees could reduce total seed output by 63.2% and diminish the number of seeds dispersed by 71.4%. Similarly, removing the five male trees nearest these fecund females could result in a 71% reduction in seed set and an 80.4% reduction in seeds dispersed. Conversely, in the best case hypothetical scenarios, removal of five female trees could result in a seed crop reduction of only 2.6% and a 1.2% reduction in number of seeds dispersed. Removal of five male trees could result in only a 10.2% reduction in seed crop and a 4.9% reduction in seeds dispersed. A random selection of trees would fall between these two extremes. One key to a selective harvest plan that minimally affects reproductive output of such populations is to identify and preserve the individuals that contribute the most to the seedling pool.

An important caveat is that this short-term study of a long-lived species did not measure lifetime reproductive success. Thus, conclusions regarding harvest practices should be regarded as tentative. Given the relentless pressure to extract economic gain from rainforests by poor nations, however, extraction practices must be based on short-term studies. Hopefully, if long-term data become available there will still be forests to manage and managers willing to emend extraction practices.

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