BRIDGING THE GAP: INFLUENCE OF SEED DEPOSITION ON SEEDLING RECRUITMENT IN A PRIMATE–TREE INTERACTION

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Abstract. Frugivores are thought to influence plant recruitment by creating initial seed deposition templates. However, post-deposition processes (e.g., predation) may obscure these initial patterns. Few studies have examined successive life-history stages of animal-dispersed plants to evaluate how initial frugivore seed deposition influences early life stages of plant recruitment. We addressed this issue by quantifying seed removal and seedling recruitment of *Monodora myristica* (Annonaceae), a tropical, low-fecundity, forest tree in Kibale National Park, Uganda. Fruit morphology suggests that this species is dispersed by only the largest arboreal frugivores. We determined which frugivores removed fruit during focal tree watches and quantified seed fate in experiments designed to mimic natural deposition. We estimated stage-specific transition probabilities of survivorship to seedling establishment and determined expected seedling recruitment from each deposition condition. To evaluate spatial and temporal variation, these methods were conducted at two sites, 15 km apart, over two years. Finally, we compared frugivore abundance between sites to expected seedling and standing seedling, sapling, and pole abundances. We found that large-bodied primates were critical for seed dispersal. They were the only frugivores that opened the hard-husked fruits and were estimated to disperse >85% of mature seeds. Seeds placed away from parents had higher germination and establishment probabilities than those under parents, indicating that seed dispersal is advantageous. Single seeds away from parents (mimicking small-bodied primate seed spitting) had the highest cumulative seedling recruitment probability. However, in three of four site-by-year combinations, 86–94% of estimated recruits came from seeds placed in clumps in dung (mimicking large-bodied primates). High recruitment in the latter condition is due to the large number of seeds estimated to be deposited by large-bodied primates. Despite this concordance, germination and establishment probabilities were highly variable between sites and years. Germination was a limiting step in recruitment, and high seed mortality from beetles and rodents indicates the importance of predation. The site with higher frugivorous primate abundance had higher standing seedling abundance, but lower expected seedling recruitment and lower sapling and pole abundances. Thus, even in a system where frugivores are critical for dispersal, spatial and temporal variation in post-deposition processes reduces predictability of frugivore actions on seedling recruitment.

Key words: frugivory; Kibale National Park; primates; seed dispersal; seed predation; seedling recruitment; tropical forest dynamics; Uganda.

INTRODUCTION

Seed dispersal is a key process in plant regeneration. For vertebrate-dispersed plants, the conditions and patterns in which seeds are deposited by their animal dispersers are thought to set the stage for all subsequent plant recruitment (Howe and Smallwood 1982, Schupp and Fuentes 1995). However, seed dispersal is a single step in a multistaged process leading to adult recruitment. Factors that influence later stages, such as seed or seedling predation, may play critical roles in determining recruitment patterns (Augspurger 1983, Barot et al. 1999).

It has become increasingly clear that to better understand the impact of frugivores on plant recruitment,

the intervening stages in the seed dispersal process need to be examined (Herrera et al. 1994, Jordano and Herrera 1995, Schupp and Fuentes 1995, Rey and Alcantara 2000). Recruitment may be limited by processes that occur at any given stage or through the interaction of stages (Jordano and Herrera 1995). Considerable spatial and temporal variation exits in the ecological factors that affect each stage (Willson 1988, Willson and Whelan 1990, Forget et al. 1998). Thus, estimations of recruitment probabilities based on only one or two stages may be misleading. This can result from spatial discordance, where different outcomes occur in different microhabitats, or uncoupling between stages, which occurs when processes affecting one stage are independent of another stage (Jordano and Herrera 1995).

Discordance and uncoupling among stages may make it difficult to predict seedling recruitment based

on seed fall. For example, Jordano and Herrera (1995) found that differences in seed rain in different microsites were unrelated to second-year seedling recruitment despite concordance between other stages (e.g., seedling emergence was positively correlated with second-year seedling survival).

Furthermore, studies that have found spatial discordance or uncoupling between seed deposition and seedling recruitment have focused primarily on wind-dispersed trees (Houle 1995, Houle et al. 2001) or fleshy-fruited trees dispersed by a large coterie of animal species (Herrera et al. 1994, Rey and Alcantara 2000). However, if concordance were ever to be detected in a seed dispersal system, one would expect to detect it in a species where fruit morphology limits access to a small set of dispersers. Although there are few documented cases where a plant species depends entirely on a single species of disperser, large seed size may result in limited sets of dispersal agents (Janzen and Martin 1982, Chapman et al. 1992). In such a system, the ability to detect the influence of disperser activity on subsequent plant recruitment should increase.

We chose to examine the seed dispersal and seedling recruitment processes of an Afrotropical tree species, *Monodora myristica* (Annonaceae), whose fruit morphology strongly suggests the access to its seeds is restricted to a subset of the frugivore community, large-bodied vertebrates. *Monodora myristica* produces large (16 cm diameter), green fruit that contain numerous, large seeds (1.9 cm mean length). The thick, woody husk is difficult to open, initially rendering seeds and pulp inaccessible to smaller frugivores, and the large seed size limits ingestion and endozoochorous dispersal to larger-bodied frugivores. For these reasons, we may expect a relatively predictable ecological relationship, in terms of the effects of dispersers on recruitment, between *M. myristica* and its dispersers.

The objective of this study was to assess whether seed deposition is spatially concordant with seedling recruitment in a system where the ability to detect concordance should be relatively high; namely in a species where fruit morphology limits access to a small set of dispersers. If, contrary to expectation, discordance is found in a simple system such as this, then it is likely to be detected in most systems. To address this objective, we investigated five components of the seed dispersal and seedling recruitment process of *M. myristica*. (1) Using observational data collected at fruiting trees, we assessed which frugivores removed and dispersed the majority of seeds. Since primates are the most common arboreal frugivores in our study system, we expected these frugivores to play an important role. (2) We assessed seed germination and seedling establishment from experiments designed to mimic deposition conditions of the different primates (large vs. small bodied). (3) Using these data, we estimated stage-specific transition probabilities of survivorship to the established seedling stage, for each deposition condi-

tion. We identified the limiting stage in recruitment through examining single stages (Clark et al. 1999, Rey and Alcantara 2000). We then used these stage-specific probabilities to estimate cumulative expected probabilities of seedling recruitment. We expected to find concordance between seed deposition and seedling recruitment.

However, temporal and spatial variation can disrupt the continuity of earlier processes and lead to an overall reduction in the predictability of the demographic consequences of frugivore actions at both early and late stages (Herrera et al. 1994). To examine this aspect, we (4) determined how consistent patterns of seed survival and seedling recruitment were on a regional scale (two sites 15 km apart) over two consecutive fruiting seasons. While several studies have attributed changes in seedling density to changes in disperser abundances (Chapman and Onderdonk 1998, Pacheco and Simonetti 1998, Wright et al. 2000), their findings were contradictory. Thus, we (5) compared frugivorous primate abundance with *M. myristica* standing and expected (based on cumulative probabilities) seedling abundance at the two sites. If primate seed dispersal plays a predominant role, relative to other factors (e.g., seed predation, environmental variation), in influencing early life stages of this species, then seed and seedling survivorship should be greater at the site with greater primate abundance. Consequently, this site should also have higher seedling, sapling, and pole abundances. However, if spatial discordance is prevalent, then it may be difficult to predict seedling patterns based on frugivore deposition patterns and frugivore abundance.

METHODS

Study sites

This study was conducted in Kibale National Park (KNP, 766 km²), western Uganda (0°13′–0°41′ N and 30°19′–30°32′ E), a moist evergreen forest (Chapman and Lambert 2000). Mean annual rainfall at Kanyawara is 1807 mm and falls primarily in two rainy seasons (minimum/maximum daily temperature = 15.5/23.7°C, 1990–1997). Within the park, an elevational gradient from 1590 m in the north to 920 m in the south corresponds to a north-to-south increase in temperature and decrease in rainfall (Seavy et al. 2001). The two sites, Kanyawara (Forestry Compartment K-30) and Dura River, are located 15 km apart on this north–south gradient. Kanyawara is situated at 1500 m and consists of a series of moderately undulating valleys with a mean slope of 15.8°. The Dura site is at 1250 m and has a mean slope of 5.9°. More than 20 years of continuous research have been conducted at Kanyawara, including extensive phenological and primate behavioral data (Struhsaker 1997). A few short-term studies and surveys have been conducted at Dura (reviewed in Struhsaker 1997), and in 1995, long-term monitoring was initiated at this site (Chapman et al. 1997). *Mon-*

odora myristica is found at both sites and preliminary surveys suggested that frugivorous primate densities differed between the sites.

Study species

Monodora myristica, a canopy-level tree reaching 30 m, produces large, green, spherical fruit (mean diameter 16 cm) with a thick (1.8 cm), woody pericarp and numerous (175–750) large seeds (dry mass, 0.92 g [A. Zanne, *unpublished data*]; length, 18.9 ± 2.3 mm [mean ± 1 SD]; width, 12.0 ± 1.1 mm; n = 20 [Balcomb 2001]). Fruiting pedicels may be 25–60 cm long and 1–3.5 cm thick (Verdcourt 1971).

In 1996 and 1997, fruiting started in June, and fruits were present on trees for seven months. Since fruits gradually increased in size during these months and the husk remained green, maturation was assessed once fruits were broken open or eaten by frugivores. Mature fruits were first eaten in November in 1996 and in September in 1997, and by mid-January no fruits remained on trees in either year.

Initial access to mature fruits is most likely restricted to large-bodied arboreal frugivores. The most common large-bodied arboreal frugivores in KNP are primates. The three largest-bodied primates, chimpanzees (*Pan troglodytes*, 25–40 kg), baboons (*Papio anubis*, 11–50 kg), and grey-cheeked mangabeys (*Lophocebus albigena*, 4–11 kg; Kingdon 1997), have large gape widths and possess large, strong jaws capable of biting through hard fruit husks. Chimpanzees and baboons often swallow large seeds and tend to defecate them undamaged in large clumps in dung (Wrangham et al. 1994, Lambert 1999). Mangabeys typically store large seeds in their cheek pouches and later clean off the pulp and spit the seeds, although they may act as seed predators by masticating *M. myristica* seeds when the fruits are immature (Lambert 1997). The three smaller-bodied frugivorous primates, redtail monkeys (*Cercopithecus ascanius*, 2–6 kg), blue monkeys (*C. mitis*, 4–12 kg), and l'hoesti monkeys (*C. l'hoesti*, 3–10 kg; Kingdon 1997), cannot break open hard-husked fruits and typically do not swallow large seeds, but instead remove the pulp and spit out the seeds (Lambert 1999). Both of the large-bodied avian frugivores in KNP, the Black-and-White Casqued Hornbill (*Ceratogymna subcylindricus*) and the Great Blue Turaco (*Corythaeola cristata*), can swallow large seeds the size of *M. myristica* (Kalina 1988, Sun et al. 1997). Hornbills have been observed regurgitating intact *M. myristica* seeds at their nests (Kalina 1988). However, since there are no published observations of either turacos or hornbills feeding on *M. myristica* fruit, it is unknown if either bird can open the woody exocarp.

Other frugivores may disperse *M. myristica* once the fruits are dropped to the ground. Elephants (*Loxodonta africana*) may be an important disperser; *M. myristica* seeds were recovered in 5.0% of elephant dung in KNP (E. Cochrane, *unpublished data*). African civets (*Civetticus civetta*), palm civets (*Nandinia binotata*), and genets (*Genetta* sp.) are all frugivorous and deposit viable seeds in latrines (Engel 2000). However, seedling recruitment from latrines is low due to repeated use and the fact that these latrines are often located on hard, exposed soil (Pendje 1994).

Little is known about the likely invertebrate seed predators of *M. myristica*, although in general insects can kill a substantial proportion of a plant's seed crop (Crawley 1992). The major vertebrate seed predators of *M. myristica* are likely rodents. Fruits and seeds constitute 48–65% of the diet of the three most common rodents in KNP (*Praomys stella, P. jacksoni*, and *Hybomys univattatus*) (Isabirye-Basuta 1979). Rodents also cache seeds, although little is known about caching behavior of small African rodents. While duikers and bushbuck browse on young leaves and tender shoots (Dubost 1984), their role as tree seedling predators is thought to be minor compared to rodents (Struhsaker 1997).

Crop size and fruit removal

This study was conducted from May 1996 through June 1998, encompassing two fruiting seasons for *M. myristica*. Unless otherwise noted, all methods used at Kanyawara and Dura were identical and repeated for the two fruiting seasons. Since the fruiting season started in June of one calendar year, and seed germination and seedling establishment occurred in the next calendar year; "year 1" and "year 2" will refer to the 12-mo period starting June 1996 and June 1997, respectively.

To quantify crop size and frugivore fruit removal, we monitored the fate of the entire fruit crop for 15 of 41 *M. myristica* trees surveyed at Kanyawara and 18 of 40 trees surveyed at Dura. Due to the large fruit size, we were able to count all fruits. We chose trees that had at least one fruit present in June of each year, and the same trees were used both years. In year 1, we monitored mature fruit fate. In year 2, we observed heavy consumption of immature fruit, and thus we monitored immature fruit. In year 2, we did not quantify removal of mature fruits, although we did estimate mature fruit crop size. We assumed fate of mature fruit was similar between years.

Once a month, from June 1996 to January 1997, we counted the number of intact and partially eaten mature fruits in each focal tree. To determine the fate of fruits removed from the tree since the previous count, we searched under the tree canopy for dropped husks or partially eaten fruit. For each dropped fruit, we recorded the amount of fruit eaten (estimated in 25% increments) and the identity of the likely consumer based on tooth marks. Fruits that disappeared entirely from the tree with no husk remnants on the ground, were assumed to have been removed by large-bodied primates (see *Results*).
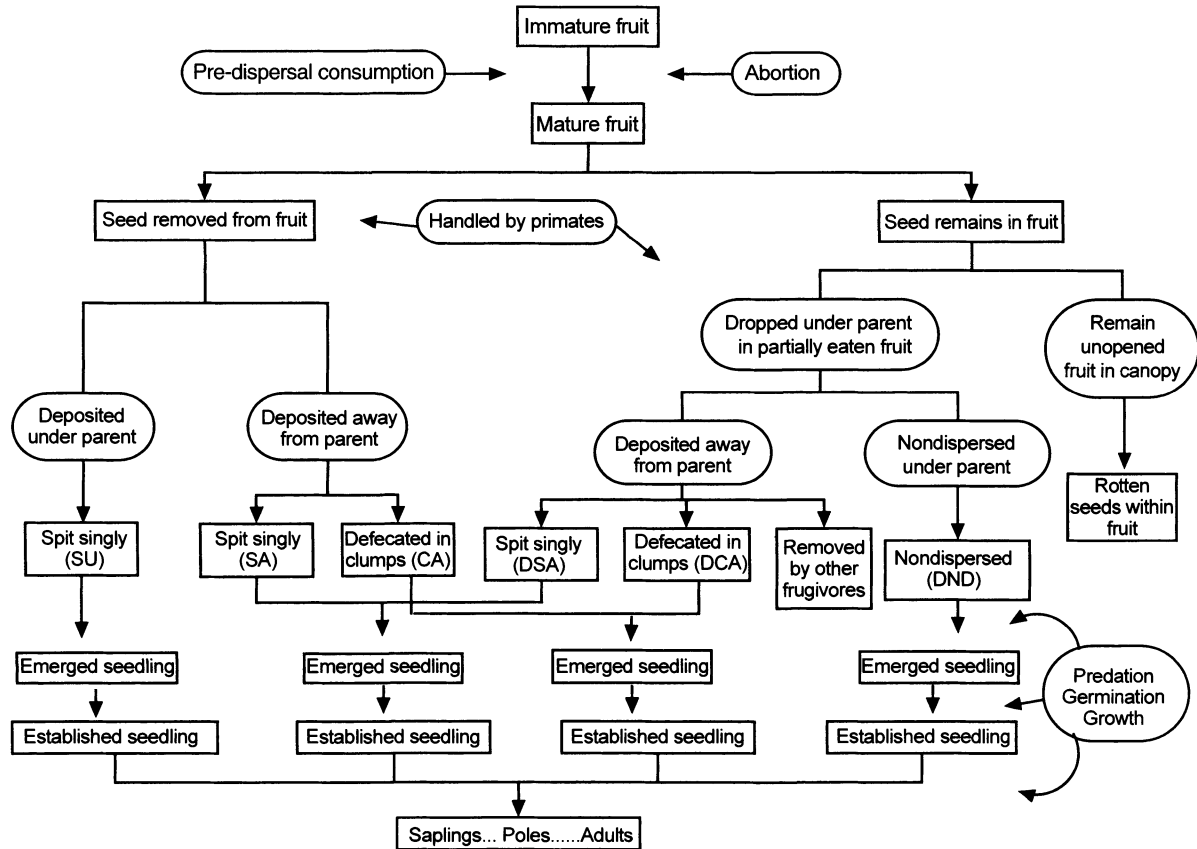
FIG. 1. Fate diagram of *M. myristica* recruitment indicating processes (ovals) influencing the immature fruit/seed to adult stages (boxes). Abbreviations are: SU, seeds spit singly under the parent; SA, seeds spit singly away from the parent; CA, seeds defecated in clumps away from parent; DSA, seeds dropped under parent and subsequently spit singly away; DCA, seeds dropped under parent and subsequently defecated in clumps away; and DND, seeds dropped under parent that remain nondispersed.

Once a month, from June to October 1997, we counted the number of immature fruit in each focal tree and searched under the canopy for evidence of fruit fate. After October, no immature fruits were observed. For each immature fruit found on the ground, we recorded its size and whether it had been removed from the tree by a vertebrate (pedicel ripped at distal end and attached to fruit) or had been aborted (no pedicel attached to fruit, clean abscission mark, and no teeth marks).

We conducted all-day tree watches to determine diurnal frugivore visitation and seed-handling behavior during the peak of mature fruit removal in both years. Three trees were each monitored from approximately 0800–1700 hours at each site on alternating days. Focal trees were selected daily based on high fruit abundance and presence of opened fruits. Observations were collected for 809 h (Dura = 350 h, Kanyawara = 459 h) over 115 d. The tree was scanned once every 15 min for the presence of frugivores. When an animal was seen feeding on a fruit, a feeding sample ([mean ± 1 SD] duration, 40 ± 35 s; range, 4–252 s) was obtained. The following data were collected: type of fruit fed on (whole or already opened), number of bites taken, and whether the seeds were swallowed immediately, spit

out under the parent canopy, spit out in a neighboring tree, or consumed (visibly chewed on). Cercopithecine monkeys often store seeds in cheek pouches and spit them out after oral processing (Lambert and Garber 1998). Thus, if these monkeys left the area before the fate of removed seeds was observed, we assumed these seeds were spit out away from the parent canopy. Since *M. myristica* fruit may contain several hundred seeds, these feeding data were collected to obtain estimates of the proportion of seeds deposited in different conditions (Figs. 1 and 2).

Fate of dropped fruits

Large-bodied primates often drop opened *M. myristica* fruit underneath the parent canopy. Seeds may subsequently be dispersed by terrestrial frugivores, be preyed upon, or germinate under the parent. To determine the fate of dropped seeds, we placed a section of fruit husk (~5 × 10 cm) with 20 pulp-covered seeds in the center of a tracking station (1 × 1 m plot cleared of vegetation and smoothed over with dirt) placed at a randomly selected location under the canopy of a fruiting tree. At each site, 13 such stations were established in year 1, from 6 to 8 January 1997 (at the end of the
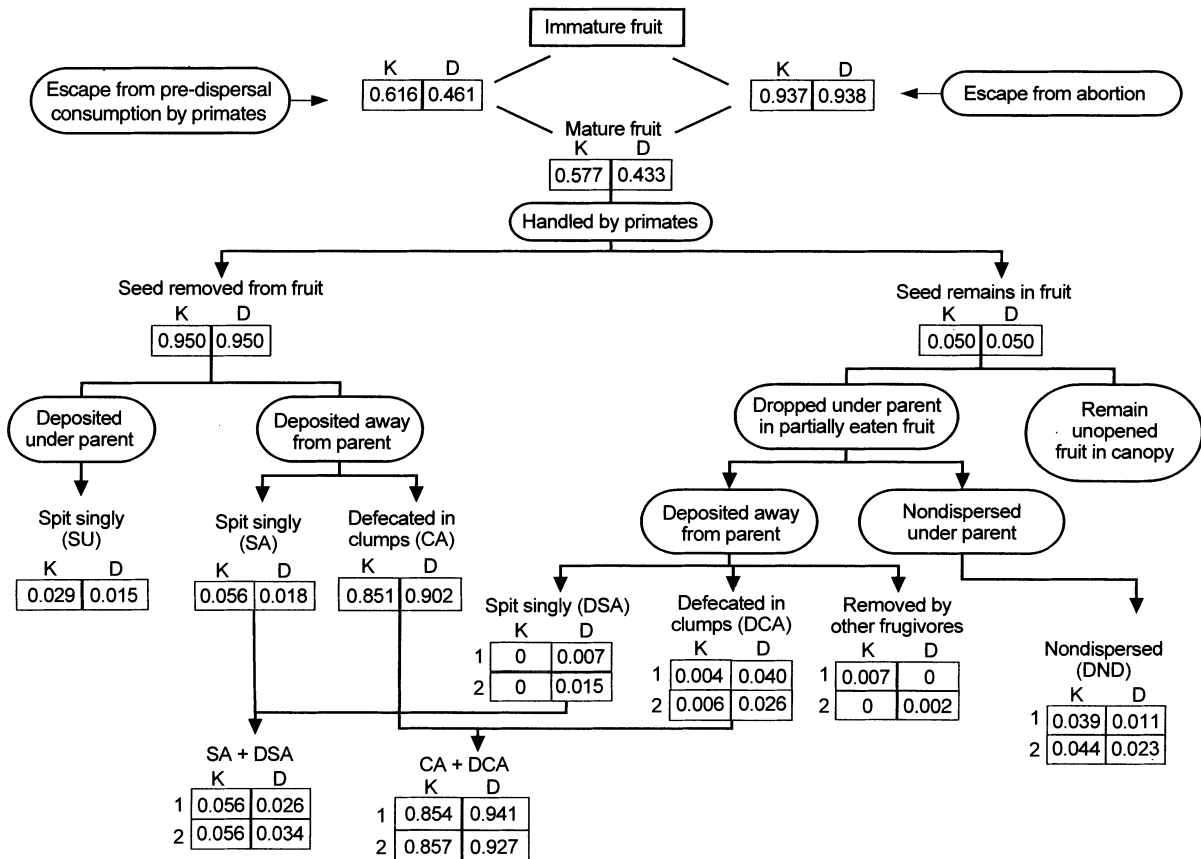
FIG. 2.   Diagram of stage-specific probabilities for *M. myristica* fruit maturation, and seed removal and deposition by primates at Kanyawara (K) and Dura (D) in each year (1 and 2). Probabilities are extrapolated from data on fruit crop counts and frugivore feeding samples (see *Methods* and Table 1 for details). Symbols for deposition conditions are defined in the legend for Fig. 1.

fruiting season), and 13 in year 2, from 27 October to 10 November 1997 (in the peak of the fruiting season). The stations were checked once a day for seven days, then once a week for a month, and then once a month until all seeds had been removed or had died. If any seeds produced seedlings, their fate was followed until 13 mo after the start of the experiment.

The identity of the seed remover was determined by (1) teeth marks in the pulp, husk, or seeds; (2) pieces of outer seed coat left behind (small rodents); and (3) footprints in the dirt. Teeth marks of large primates, small primates, squirrels, and small rodents were distinguished based on measurements of teeth from skulls. We assumed primates were seed dispersers (Lambert and Garber 1998) and rodents were seed predators. Given the variability in caching behavior that occurs on small spatial scales (Forget et al. 1998) and the lack of data on African seed-caching behavior, we assumed all removed seeds were killed. Insect infestation of seeds was determined by presence of entry or exit holes—eggs may have been laid pre- or post-dispersal. Seeds were considered dead once they were soft. These data were used to obtain estimates of the proportion of seeds in dropped fruits that subsequently remained un-

der the canopy or were dispersed away from the canopy (Figs. 1 and 2).

Post-deposition fate of seeds through to seedling survival

To quantify the fate of seeds processed by primates, we established experiments that simulated conditions under which primates deposit seeds. Small-bodied primates typically spit out single seeds cleaned of pulp under or within ten meters of the canopy of parent trees, while large-bodied primates typically swallow seeds and deposit them undamaged in large clumps in dung (Lambert 1999). These experiments were established at both sites in January 1997 (year 1) and November 1997 (year 2).

To mimic a seed-spitting frugivore, we obtained seeds from ripe fruit and removed pulp. We placed 10 single seeds at random locations under each of 10 fruiting *M. myristica* trees at each site (*n* = 100 seeds per site per year) and 120 single seeds per site at 10 m intervals, 1 m off of trails (seven transects at Kanyawara, five at Dura) avoiding conspecifics. For both experiments, a small section of leaf litter was cleared and a seed placed on the soil surface and marked with

flagging tied 1 m above. In year 2, thread was glued to seeds and one end was tied to vegetation to minimize seed loss by factors other than predation.

A typical chimpanzee defecation weighs 80 g (range 1–350 g) and contains a mean of 10.7 intact *M. myristica* seeds (Wrangham et al. 1994). To mimic deposition by large-bodied primates, we placed 10 seeds collected from baboon dung in 60 g of fresh baboon dung from which all large seeds had been removed. Twenty-four stations were established per site in year 1 and 26 in year 2. Stations were established on the same transects as the single seed experiment. A stratified-random design was used such that five seeds-in-dung stations were present on each transect and were separated by 10–40 m. A small section of leaf litter was cleared and seeds in dung were placed on the soil surface.

For all three experiments (spit singly under, spit singly away, clumped in dung), seeds were monitored weekly for the first month and then monthly for 13 mo. Seeds were monitored for fungal attack, beetle infestation, and rodent predation. Seeds that disappeared were assumed to have been eaten by rodents (Chapman 1989). Dung beetles also remove seeds from dung. In Kibale, dung beetle movement of larger seeds is primarily accomplished by a burrowing beetle, which tunnels under the dung pile (Shepherd and Chapman 1998). Thus, when seeds were removed from dung, we searched the soil under the station to a depth of ~10 cm. These seeds were reburied and checked on each subsequent monitoring.

Seeds that germinated (defined as the production of a radicle) were monitored monthly until 13 mo after the start of the experiment. Seedlings were categorized as "emerged seedlings" while they were physically attached to the seed. Once it was no longer attached to the seed and its root was firmly in the soil it was deemed an "established seedling." Upon production of a shoot, seedling height (measured as aboveground stem length) and cause of death (desiccation, herbivory, crushed from fallen branches, or unknown) was recorded.

Plant size-class densities and survivorship of seedlings and saplings

The number of *M. myristica* seedlings (small, <0.2 m tall; large, 0.2–0.5 m tall), saplings (0.5–2.0 m tall), poles (>2.0 m tall and dbh < 20 cm), and adult trees (dbh ≥ 20 cm) were quantified at both sites from July 1996 to October 1997. Plots (50 × 60 m) were placed at 50 randomly selected points along a 4-km loop route (see Methods: *Frugivorous primate abundance*). The (single) trail was used as the central axis for each plot. No individuals were included within 0.5 m of either side of the trail, and this area was discounted in calculating overall densities. Adult tree density was determined within the entire plot. Due to expected greater density of stems with decreasing size class, subplots, oriented along the central axis of the plot, were used

to measure densities of small seedlings (ten 1 × 1 m subplots every 4 m), large seedlings and saplings (one 4 × 20 m subplot), and poles (one 10 × 20 m subplot). Subplots were combined to obtain one value per plot. For all individuals, except adults, distance to the edge of the canopy of the nearest adult conspecific, if present within the plot, was estimated.

Growth rate and survival of seedlings and saplings were quantified by monitoring the first five individuals of each size class encountered in the first 30 plots. For some size classes, sample size was increased by including individuals outside the plots. A total of 355 individuals (Kanyawara: 36 small seedlings, 58 large seedlings, 47 saplings; Dura: 99 small seedlings, 100 large seedlings, 15 saplings) were tagged. Surveys were conducted approximately every 5 mo for 18 mo (mean interval for plot surveys = 148 ± 54 d, range 25–235 d) to assess survival and growth. Relative height growth rate (RHGR) was determined as $(\ln[H_2] - \ln[H_1])/(H_2 - H_1)$, where H_1 is the initial height and H_2 is the final height. This accounts for differences in initial plant sizes (Hunt 1982, Hutchings 1997).

Frugivorous primate abundance

Diurnal frugivorous primate abundance was assessed by line transect (Chapman et al. 1988, Whitesides et al. 1988). At both sites, a 4-km loop route was established, and censuses were conducted biweekly from June 1996 to July 1997 (Kanyawara, $n = 26$; Dura, $n = 23$). Censuses were conducted from ~0700 to 1400 hours at a speed of ~1 km/h. Data collected included primate species observed, time of observation, straight line distance between the animal and observer (visually estimated), and mode of detection. Since chimpanzees construct individual sleeping nests each night leaving evidence of their presence and numbers, their abundance was determined by counts of nests from the line transects (marked nest counts [Plumptre and Reynolds 1996]). For details regarding density estimates for the chimpanzees and five cercopithecine primates see Balcomb et al. (2000) and Chapman et al. (2000), respectively.

Overall probability of dispersal and seedling recruitment

To determine the probability of an immature seed becoming an established seedling, we constructed a fate diagram of stages and processes influencing *M. myristica* recruitment (Fig. 1). We then determined stage-specific and cumulative probabilities of seeds passing from one stage to the next (Figs. 2 and 3). To calculate seed fate probabilities from immature seed to seed deposition stage (Fig. 2) we used the fruit as the unit of entity since either all seeds (when immature), or an estimated proportion (when mature), underwent a given fate. For seeds to become mature they must escape being aborted and being eaten by vertebrates. Thus, we calculated the probability that seeds became mature as the product of the proportion of immature fruits per tree that escaped abortion and the proportion that escaped pre-dispersal consumption by vertebrates.

Figure 3 diagram data

Under parent / Away from parent

Stage	Site·Year	Nondispersed (DND) K	DND D	Spit singly (SU) K†	SU D	Spit singly (SA + DSA) K†	SA+DSA D	Defecated in clumps (CA + DCA) K†	CA+DCA D
Germination probability	1	0	0	0.040	0.010	0.358	0.067	0.213	0.021
	2	0.131	0.125	0.590	0.560	0.817	0.692	0.865	0.692
Emerged seedling probability	1	--	--	0.500	0	0.442	0.250	0.366	0
	2	0.189	0.190	0.356	0.143	0.755	0.422	0.736	0.315
Established seedling probability	1	--	--	0.500	--	0.421	0.500	0.322	--
	2	0	0.075	0.238	0.125	0.662	0.257	0.647	0.247

Cumulative probability of seedling recruitment (Site·Year), columns K, D for each condition:

Year	DND K	DND D	SU K	SU D	SA+DSA K	SA+DSA D	CA+DCA K	CA+DCA D
1	0	0	0.010	0	0.067	0.008	0.025	0
2	0	0.002	0.050	0.010	0.408	0.075	0.412	0.054

Expected seedling density/tree (Site·Year):

Year	DND K	DND D	SU K	SU D	SA+DSA K	SA+DSA D	CA+DCA K	CA+DCA D
1	0	0	0.6	0	8	0.4	52	0
2	0	0.1	5	0.8	80	12	1437	237

Expected seedling density/m^2 (Site·Year):

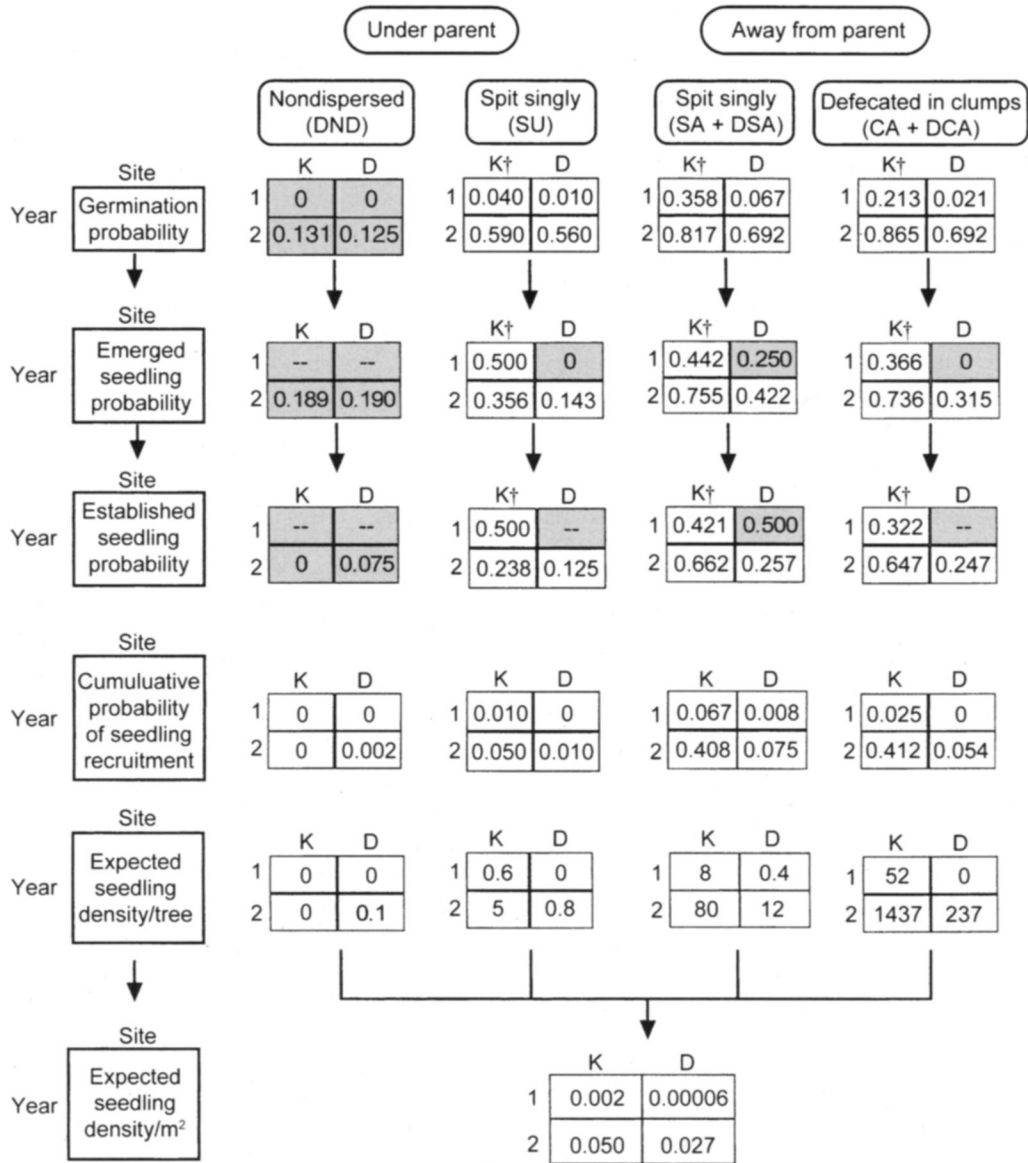| Year	K	D
1	0.002	0.00006
2	0.050	0.027

FIG. 3. Diagram of stage-specific recruitment probabilities for *M. myristica* seed germination, seedling emergence, and seedling establishment for each seed deposition condition (see Fig. 1 legend for definitions) at Kanyawara (K) and Dura (D) in years 1 and 2. Within each stage and condition, site and year effects were tested. If the test was significant ($P < 0.05$), a dagger (†) indicates which site or year was greater. Shaded boxes were not analyzed due to small sample size.

Once fruits were mature, they were handled by primates and seeds were either removed from the fruit and deposited under or away from the parent canopy, or seeds remained in the fruit and were dropped under the parent (Fig. 1). Those dropped under the parent either remained nondispersed or were subsequently removed and deposited away from the parent. We calculated the probabilities that seeds were removed by primates and other frugivores and deposited in different conditions (spit singly under [SU], spit singly away [SA], defecated in clumps away [CA], dropped then spit singly away [DSA], dropped then swallowed and defecated in clumps away [DCA], or dropped and remain non-dispersed [DND]; Figs. 1 and 2, Table 1). Since it is not feasible to follow the fate of every seed, and since individual frugivores were not followed once they left the vicinity of the tree, we made a number of assumptions when calculating these probabilities. If a small-bodied primate moved out of the area before seed fate was observed, we assumed the seeds were spit away. This could overestimate the probability of SA. Since only large-bodied primates removed entire fruits (see *Results*), we assumed that seeds from such fruits (M) were swallowed and defecated away from parent trees. Since it is possible that chimpanzees only consume part of a fruit they carry away, this may overestimate the

TABLE 1. Calculations of the probability that a seed was dispersed and deposited in different conditions by frugivores that fed on *M. myristica* fruits (see Figs. 1 and 2).

Deposition condition	Probability for all a frugivores feeding on fruits	Probabilty for frugivore i
Spit singly under (SU)	$p(SU) = \sum_{i=1}^{a} p(SU)_i$	$p(SU)_i = N \times C \times J$
Spit singly away (SA)	$p(SA) = \sum_{i=1}^{a} p(SA)_i$	$p(SA)_i = N \times C \times K$
Defecated in clumps away (CA)	$p(CA) = \sum_{i=1}^{a} p(CA)_i$	$p(CA)_i = M + (N + O + N \times C)(1 - J)$
Dropped, then spit singly away (DSA)	$p(DSA) = \sum_{i=1}^{a} p(DSA)_i$	$p(DSA)_i = O \times D$
Dropped, then swallowed and defecated in clumps away (DCA)	$p(DCA) = \sum_{i=1}^{a} p(DCA)_i$	$p(DCA)_i = O \times E$
Dropped and remain nondispersed (DND)		$p(DND) = O \times F$

Note: N = (no. partially eaten fruits in tree/total no. fruits in tree) × proportion of fruit that was eaten (set at 0.5 since the majority of partially eaten fruits [26/37] were estimated to be half eaten); C = no. records of frugivore i feeding from partially eaten fruits in tree/total no. feeding records from partially eaten fruits for all frugivores; J = no. records of frugivore i spitting seeds under parent canopy/total no. records of fate of seed removed by frugivore i; K = no. records of frugivore i spitting seeds away from parent canopy/total no. records of fate of seed removed by frugivore i; M = no. intact fruits entirely removed by frugivore i/total no. fruits in tree; O = (no. partially eaten fruits on the ground/no. fruits in tree) × proportion of fruit that was eaten (set at 0.5); D, E, and F = mean no. seeds from the dropped fruit experiment that were removed by small-bodied primates (spit singly away), removed by large-bodied primates (defecated in clumps away), or remained nondispersed under the canopy, respectively. Since the fruit experiment was conducted in both year 1 and 2, D, E, and F, differ for the two years (see Fig. 2).

probability of CA. Although we assumed rodents consumed seeds, they could potentially scatter-hoard seeds, resulting in our underestimating survival of seeds dropped then dispersed away from parent trees (DSA or DCA).

For each seed deposition condition, we determined stage-specific probabilities of seed germination, seedling emergence, and seedling establishment in each site and year from the seed experiments (Figs. 1 and 3). We calculated the probability of making it through three stages: (1) germination (survival of seeds to germination), (2) seedling emergence (survival of germinated seedlings to establishment), and (3) seedling establishment (survival of established seedlings until 13 mo after the initiation of the experiment). These were calculated as (1) the mean number of seeds that germinated divided by the total number of seeds in the experiment, (2) the mean number of seedlings that survived the emerged seedling stage divided by the number of seeds that germinated, and (3) the mean number of seedlings that survived until 13 mo after the initiation of the experiment divided by the number of emerged seedlings. We then calculated cumulative probability of seedling recruitment as the product of the three stage-specific probabilities (Fig. 3).

We estimated the number of seedlings per tree expected to recruit as the product of the mean seed crop size (250 seeds/fruit; Lambert 1999) and the probabilities that seeds were deposited in (Fig. 2) and seedlings recruited to each condition (Fig. 3). To estimate expected seedling density for each population, we multiplied the sum of the number of seedlings per tree for

each condition by adult tree density and proportion of trees fruiting that year.

Statistical analyses

Data were analyzed with generalized linear models (PROC GENMOD, SAS Institute 1998), a categorical data analysis procedure analogous to ANOVA. In cases where the response variable was binary (e.g., fruit fate [eaten or not], seed fate [alive or dead]), a logistic regression model with binomial error distribution was used (Agresti 1996). Most of the analyses included two main effects, site and year, and the site-by-year interaction. For spit singly seeds, a third main effect, location (under vs. away), as well as all possible two-way interactions, were included. In all experiments, the fate of each seed was given a score of 1 or 0 for each dependent variable (e.g., germinated or not, removed by rodents or not). Since the station was the unit of replication, these scores were compiled as number of "successes" over number of seeds in each station (1, 10, or 20). For example, germination was assumed to be a dichotomous factor with a binomial distribution. The dependent variable was logit transformed as part of the logistic regression analysis; the logit transformation is the natural logarithm of the ratio of the proportion of successes to failures (Sokal and Rohlf 1995).

For the analysis of each dependent variable, the significance of each main effect and interaction term was assessed through likelihood ratio tests, which compare the likelihood of a more complex model with the likelihood of a simpler model. If removing a factor or interaction term from the more complex model results

in only a small increase in deviance, then the more complex model does not fit the data significantly better than the simpler model, and the term is deleted from the model (Crawley 1993). One assumption of logistic regression is that fates of all seeds are independent of each other. Since seeds are nested within stations and stations are nested within trails or trees, this assumption may be violated. Violations of this assumption (or other assumptions such as that all seeds within a station have the same inherent survival and germination rates) can result in underestimating the true variance, which would lead to greater Type II error rates. Such violations can be detected by comparing the variance of residuals with that of a binomial distribution, the distribution assumed for logistic regression. The conservative assumption is that data are overdispersed (have higher variance than the binomial distribution would assume) as a result of clustering due to nonindependence of seed fates. A scaling factor is estimated to account for the differences in variances. The scaling factor is applied to the deviance for each observation and has the effect of making tests of significance more conservative (Crawley 1993). Applying the scaling factor functions in a similar way to including the effects of "station" and "trail" or "tree" as a block (random effect), and accounts for such nuisance variation within the framework of a generalized linear model.

For count-type response variables, a log-linear model with Poisson error distribution was used (Agresti 1996). PROC GENMOD (SAS Institute 1998) was used to analyze effect of site, year, and site-by-year on fruit crop size, and effect of site on density of seedlings, saplings, poles, and trees.

All other data were analyzed using the SPSS statistical package (SPSS 1999). For between-site differences in proportion of trees fruiting and proportion of seedlings and saplings surviving we used Pearson chi-square and G tests of independence, conditional on fixed row totals (Sokal and Rohlf 1995). Yates' correction for continuity was applied due to low sample size resulting in some expected cell frequencies of less than five (Sokal and Rohlf 1995). All statistical tests shown, with the exception of the t test, have one degree of freedom and thus degrees of freedom are not presented. In addition, all values are presented as the mean $\pm$ 1 SE, unless otherwise noted.

RESULTS

Fruit crop size and removal

Monodora myristica trees produced similar mature-fruit crop sizes at both sites within a given year (year 1, Kanyawara = 7.93 $\pm$ 11.99 fruit/tree [mean $\pm$ 1 SD], N = 15 trees; Dura = 6.41 $\pm$ 10.11 fruit/tree, N = 17 trees; year 2, Kanyawara = 16.36 $\pm$ 25.98 fruit/tree, N = 14 trees; Dura = 13.42 $\pm$ 12.65 fruit/tree, N = 12 trees; effect of site, χ^2 = 0.43, P = 0.51). However, trees produced larger fruit crops in year 2 (χ^2 = 5.37, P = 0.02). The increase in fruit crop size

from year 1 to 2 was consistent between sites (i.e., the site-by-year interaction was nonsignificant; χ^2 = 0.00, P = 0.98). When fruit crop was defined as number of immature and mature fruits combined (data available only for year 2) there was still no difference between sites (Kanyawara = 26.47 $\pm$ 34.06 fruit/tree, N = 15 trees; Dura = 20.67 $\pm$ 14.25 fruit/tree, N = 18 trees; χ^2 = 0.63, P = 0.43).

The proportion of trees that carried fruit to maturity did not differ between sites for either year 1 (Kanyawara = 39.0%, N = 41 trees; Dura = 45.0%, N = 40 trees; χ^2 = 0.19, P > 0.05) or year 2 (Kanyawara = 34.1%, N = 41 trees; Dura = 27.5%, N = 40 trees; χ^2 = 0.15, P > 0.05). However, adult density was higher at Dura (3.6 $\pm$ 4.0 trees/ha) than at Kanyawara (1.0 $\pm$ 1.9 trees/ha; χ^2 = 19.53, P < 0.001).

In year 2, 50.2 $\pm$ 28.7% and 66.3 $\pm$ 33.8% of *M. myristica* fruit crops at Kanyawara and Dura, respectively, were lost prior to maturation (χ^2 = 1.68, P = 0.19). Primate fruit consumption was the primary cause of immature fruit loss at both sites, with mangabeys consuming 47.9 $\pm$ 29.6% and 55.8 $\pm$ 35.1% of fruit crops at Kanyawara and Dura, respectively (χ^2 = 1.53, P = 0.22). Abortion was relatively low and did not differ between sites (Kanyawara = 2.4 $\pm$ 4.3%, Dura = 10.5 $\pm$ 24.1%; χ^2 = 0.00, P = 0.97). Although overall, 97.0% of trees (32/33) experienced some level of immature fruit consumption, only 33.3% and 50.0% of trees at Kanyawara and Dura, respectively, lost immature fruit due to abortion.

In year 1, all mature fruit were bitten into or removed by large-bodied primates. Chimpanzees and baboons together were responsible for removing 76.3 $\pm$ 32.5% and 79.6 $\pm$ 29.1% of mature fruit crops at Kanyawara and Dura, respectively (effect of site: χ^2 = 2.31, P = 0.13). The remaining mature fruits were partially ($\sim$50%) consumed, and either left attached to the tree (Kanyawara = 19.8 $\pm$ 29.7%; Dura = 11.4 $\pm$ 26.1%; χ^2 = 4.23, P = 0.04) or dropped below the parent canopy (Kanyawara = 3.9 $\pm$ 7.0%; Dura = 9.0 $\pm$ 17.7%; χ^2 = 0.00, P = 0.99). From observations on nonfocal trees, the few fruits not handled by primates remained attached to the tree and eventually turned black and rotted.

Frugivores were in the vicinity of focal fruiting trees on all observation days, although visitation rates were low (12.6% of 3288 15-min scans, Table 2). All species of frugivorous primates fed from ripe fruits in focal trees, except the l'hoesti monkey, which is secretive. Chimpanzees and mangabeys were the only frugivores observed biting through the husk of unopened mature fruits (Table 2); teeth marks on fallen fruit indicated that baboons can also open fruits. Chimpanzees primarily swallowed pulp and seeds and rarely spat seeds under the parent (Table 3); they also occasionally carried away whole fruit. Based on dung collections, it was evident that baboons also swallowed seeds in large quantities. In contrast, the cercopithecines never swallowed *M. myristica* seeds whole. Mangabeys, the larg-

TABLE 2.   Interactions between frugivores and fruiting *M. myristica* trees from focal tree observations conducted at Kanyawara and Dura.

| | Kanyawara | | | | |
| Species | Days present in area (%) ($n = 62$ d) | Scans present in tree (%) ($n = 1877$ scans) | Feeding rate | | No. times observed opening fruits |
			Bites/min†	n	
Chimpanzee	45.2	1.7	9.1 ± 4.1	52	18
Baboon	4.8	0	⋯	⋯	⋯
Mangabey	53.2	5.0	11.4 ± 5.1	25	4
Redtail monkey	53.2	3.1	7.0 ± 3.0	37	0
Blue monkey	48.0	2.0	6.9 ± 4.7	20	0
L'hoestis monkey	8.1	0.1	0	⋯	0
Great Blue Turaco	77.4	0.2	20	1	0
Black and White Hornbill	85.5	0	⋯	⋯	⋯
Squirrel	14.5	0.1	0	⋯	0

Notes: Presence in the area was indicated by sightings and calls of frugivores in the vicinity of the focal tree. For frugivores that were never observed in the focal tree, no feeding data were recorded (⋯).

† Mean ± 1 SD.

est of the cercopithecines, were primarily responsible for depositing single spit seeds away from the parent, although on one occasion they were observed eating mature seeds. Redtail monkeys processed pulp and spat the majority of mature seeds directly under the parent, while blue monkeys deposited single spit seeds both under and away from the parent with roughly equal frequency. The only other frugivore observed feeding on fruit was the Great Blue Turaco (Table 2), which fed on pulp from open fruit, and did not drop or remove seeds in the process.

Fate of dropped fruits

Removal of experimental seeds and pulp from under the parent generally occurred within the first week. More seeds were removed at Kanyawara than at Dura and in year 1 than 2 (Tables 4 and 5). There was no year-by-site effect (Table 5), indicating that the decrease in removal from year 1 to 2 was consistent between sites. Because experiments were established at different times during the fruiting season in the two years, seasonality may also contribute to interannual differences.

Site strongly affected number of seeds removed by primates and rodents, but year did not (Table 5). Primates removed more seeds at Dura than Kanyawara, and rodents removed more seeds at Kanyawara than Dura (Tables 4 and 5). Greater removal by primates at Dura is in accordance with higher frugivorous primate densities at that site. Civets (Kanyawara, year 1) and red duikers (Dura, year 2) removed only a small percentage of seeds (Table 4).

In year 1, <10% of seeds remained under the parent at both sites. All were infested by curculionid beetles, which led to seed death (Table 4). In year 2, only 1.2% of seeds (3/260) at Dura, and none at Kanyawara, survived under the parent.

Post-deposition fate of seeds through to seedling survival

Single spit seeds.—The two main agents of mortality to single spit seeds were curculionid beetles and ro-

dents (Table 6). Insect holes were seen within one week of the experiment's start. There was a nonsignificant trend in the effect of location (under vs. away from parent) on seed mortality due to beetles (Table 7). There were site and year effects on seed mortality due to beetles (Table 7); beetle infestation was greater at Dura than at Kanyawara and in year 1 than in year 2 (Table 6). Direct evidence of rodents consuming seeds, such as outer seed coat remnants, was relatively rare. However, when consumed and removed seeds were combined, there was an effect of location on seed removal by rodents; more seeds were removed by rodents under the parent than away (Tables 6 and 7). Site and year also affected rodent seed removal (Table 7); removal was greater at Kanyawara than at Dura and in year 1 than in year 2 (Table 6).

Seeds began germinating after 10 wk in year 1, and after four weeks in Year 2, regardless of site or location. Location influenced the probability that seeds germinated (Table 7); seed germination was lower under the parent than away (Table 6). The increased probability of germination away from the canopy was consistent between sites (Table 7). Site and year also influenced seed germination (Table 7). Seed germination was higher at Kanyawara than at Dura, and in year 2 than in year 1 (Table 6). However, proportional changes in germination between years were not consistent, likely due to low germination of seeds in year 1 at Dura away from the parent.

In year 1 at Dura, only one of 100 seeds under the parent germinated; it was infested by curculionid beetles and did not survive (Table 6). Therefore, seedling survival at Dura in year 1 was not analyzed further. At Kanyawara, emerged seedling survivorship was greater away from the parent than under, and greater in year 2 than in year 1 (Table 7). In year 2, survivorship was greater away from the parent than under and greater at Kanyawara than at Dura (Table 7). The main identifiable causes of mortality to emerged seedlings were beetle or rodent damage to the seed upon which the

TABLE 2. Extended.

		Dura		
Days present in area (%) (n = 53 d)	Scans present in tree (%) (n = 1411 scans)	Feeding rate		No. times observed opening fruits
		Bites/min†	n	
49.1	0	...	...	...
43.4	0.3	12	1	0
75.5	0.9	8.6 ± 7.6	17	2
69.8	3.0	6.7 ± 5.3	23	0
0	0	...	...	...
17.0	0.1	0	...	0
50.9	0	...	...	...
66.0	0	...	...	...
7.6	0	...	...	...

emergent seedling was still dependent for its reserves (Table 6). Differences in prevalence of these factors among location, site, and year were not tested due to small sample sizes. However, there appears to be a general trend of greater beetle damage under the parent than away, and in year 1 than in year 2 (Table 6). Rodent predation on seeds with emergent seedlings was more prevalent at Kanyawara and virtually nonexistent at Dura, although there was no consistent pattern with location or year.

At Kanyawara, established seedling survivorship was greater away from the parent than under and did not differ between years (Table 7). In year 2, established seedling survivorship was greater away from the parent than under and greater at Kanyawara than at Dura (Table 7). The two main causes of mortality to established seedlings were desiccation and herbivory. Differences in their prevalences among location, site, and year were not tested due to small sample size (Table 6).

Seeds defecated in clumps.—Primary causes of mortality to seeds in dung differed between sites and varied between years within sites (Table 8). The two main agents of mortality were curculionid beetles and ro-

dents. Beetle holes were seen within three weeks of the experiment's start. Similar to single spit seeds, mortality by beetles was greater at Dura than at Kanyawara and in year 1 than in year 2 (Tables 8 and 9). The decrease in beetle infestation from year 1 to 2 was consistent between sites (Table 9). Beetle infestation was the main cause of seed mortality at Dura in both years, whereas at Kanyawara, beetles infested and killed relatively few seeds in year 1 and none in year 2 (Table 8). In contrast, rodent consumption of seeds was greatest at Kanyawara (Table 8). Direct evidence of rodent seed consumption was rare, however, when consumed and removed seeds were combined, seed removal by rodents was greater at Kanyawara than at Dura and in year 1 than in year 2 (Table 9). Thus, rodent predation was the main cause of seed mortality at Kanyawara in both years, whereas they removed relatively fewer seeds at Dura (Table 8). Although number of seeds buried by dung beetles was relatively low at both sites in both years (Table 8), a greater proportion of seeds were buried at Kanyawara than at Dura and in year 2 than in year 1 (Table 9).

TABLE 3. Fate of *M. myristica* seeds processed by frugivorous primates observed during focal tree watches.

Frugivore and site	N	Seed fate (%)			
		Swallowed	Spit under parent canopy	Spit away from parent canopy	Consumed (killed)
Chimpanzee					
Kanyawara	51	92.2	7.8	0	0
Mangabey					
Dura	15	0	13.3	86.7	0
Kanyawara	22	0	0	95.5	4.5
Redtail					
Dura	15	0	93.3	6.7	0
Kanyawara	27	0	74.1	25.9	0
Blue monkey					
Kanyawara	11	0	45.5	54.5	0

Note: N = number of feeding samples for each species in which seed fate was recorded.

TABLE 4. Fate of *M. myristica* seeds from experiments designed to mimic fruit dropped by primates under fruiting trees at Kanyawara and Dura in year 1 and year 2.

	Kanyawara		Dura	
Fate	Year 1	Year 2	Year 1	Year 2
Seeds removed	99.2 ± 2.8	83.1 ± 28.5	91.5 ± 11.3	65.0 ± 37.4
Primates	7.7 ± 27.7	12.3 ± 30.1	78.8 ± 28.4	50.8 ± 49.2
Other frugivore	14.6 ± 35.7†	0.0	0.0	3.9 ± 13.9‡
Rodents	68.8 ± 47.8	49.6 ± 48.4	12.3 ± 25.2	4.6 ± 15.2
Missing	8.1 ± 27.7	21.2 ± 31.3	0.4 ± 1.4	5.8 ± 13.7
Seeds remaining				
Infested by beetles (dead)	0.8 ± 2.8	5.0 ± 12.4	8.5 ± 11.3	27.7 ± 34.4
Germinated and died	0.0	11.9 ± 18.3	0.0	6.5 ± 9.7
Germinated and survived	0.0	0.0	0.0	1.2 ± 3.0

Notes: Percentages are the mean number of seeds per 20 seeds ± 1 SD. $N = 13$ replicates per site per year.
† African civet.
‡ Red duiker.

The timing of germination for seeds placed in dung was similar to that for single spit seeds. Both site and year strongly affected the number of seeds that germinated (Table 9); germination was greater at Kanyawara than at Dura and in year 2 than in year 1 (Table 8). In year 1 at Dura, only five seeds, all from a single station, germinated and none survived to become seedlings (Table 8). Therefore, seedling survival at Dura in year 1 was not analyzed further. As with single spit seeds, at Kanyawara, emerged seedling survivorship was greater in year 2 than in year 1 (Table 9). In year 2, survivorship was greater at Kanyawara than at Dura (Table 9). There was no trail effect at this stage. Because of the small number of seedlings emerging per station, data regarding causes of mortality were pooled across stations. The main cause of mortality at both sites in both years was beetle infestation of seeds with emergent seedlings (Table 8). Rodent predation of seeds with emergent seedlings was greatest at Kanyawara in year 1 and not observed at Dura. Desiccation

TABLE 5. Effect of site and year on fate of *M. myristica* seeds from fruit experiments under fruiting trees.

Factors and interactions	χ^2	P	Direction
Overall removal			
Site	21.74	<0.001	K > D
Year	12.79	<0.001	1 > 2
Site × year	0.17	0.68	
Removal by primates			
Site	24.44	<0.001	K < D
Year	1.50	0.22	
Site × year	1.73	0.19	
Removal by rodents			
Site	20.38	<0.001	K > D
Year	1.82	0.18	
Site × year	0.03	0.87	

Notes: Directional differences are indicated when $P < 0.05$ (K = Kanyawara, D = Dura, 1 = year 1, 2 = year 2). For means, see Table 4.

of emerged seedlings was prevalent at Kanyawara in year 2 and at Dura in year 1.

At Kanyawara, there was no difference in established seedling survivorship between years, and survivorship was greater at Kanyawara than at Dura in year 2 (Table 9). Desiccation was the major cause of mortality to established seedlings in year 1 (data only available for Kanyawara), while herbivory was the major cause of mortality in year 2 at both sites (Table 8).

Plant size-class densities and survivorship of seedlings and saplings

Monodora myristica density differed between the two sites for all size classes (Table 10). While seedling and tree densities were lower at Kanyawara compared with Dura, sapling and pole densities were higher. At Kanyawara it was rare to see seedlings under conspecifics (only one small seedling in 50 plots), while at Dura this was common (as many as 265 small seedlings were found in a 10-m² area under a conspecific adult). This resulted in a 30-fold difference in small seedling density between sites. However, when only those individuals located away from adult conspecifics were considered, densities of all size classes still differed between sites (Table 10).

Small seedlings under conspecifics had lower survivorship than did those located at least 0.5 m away from the edge of a conspecific adult canopy (data only available for Dura; under $= 40.0\%$, $N = 45$; away $= 63.0\%$, $N = 54$; $\chi^2 = 5.19$, $P = 0.02$). In contrast, large seedlings (0.2–0.5 m tall) did not differ in survivorship between locations (under $= 83.3\%$, $N = 36$; away $= 85.9\%$, $N = 64$; $\chi^2 = 0.12$, $P = 0.73$). Saplings (0.5–2 m tall) were rarely under adults (two saplings at Kanyawara and 0 at Dura), and poles (>2 m tall) were never under adults at either site.

Although density of both small and large seedlings was lower at Kanyawara than at Dura (Table 10), small-seedling survivorship and relative-height growth rate (RHGR) over an 18-mo period were greater at Kany-

TABLE 6. Fate of *M. myristica* seeds from experiments where single seeds were placed under and away from parents to mimic spitting by small-bodied primates.

| | Kanyawara | | | | Dura | | | |
| | Year 1 | | Year 2 | | Year 1 | | Year 2 | |
Fate	Under	Away	Under	Away	Under	Away	Under	Away
Seeds	(100)	(120)	(100)	(120)	(100)	(120)	(100)	(120)
Germinated	4.0	35.8	59.0	81.7	1.0	6.7	56.0	69.2
Infested by beetles	37.0	30.0	6.0	1.7	83.0	80.8	35.0	20.0
Rodents†	13.0	2.5	1.0	0.0	6.0	3.3	2.0	2.5
Removed‡	46.0	30.8	33.0	15.0	10.0	9.2	7.0	6.7
Emerged seedlings	(4)	(43)	(59)	(98)	(1)	(8)	(56)	(83)
Survived	50.0	44.2	35.6	75.5	0	25.0	14.3	42.2
Died								
Beetles§	50.0	34.9	1.7	0	100.0	75.0	5.4	0
Rodents§	0	11.6	13.6	6.1	0	0	1.8	0
Herbivory‖	0	2.3	0	0	0	0	0	0
Dessication	0	4.7	0	1.0	0	0	0	0
Unknown	0	2.3	49.2	17.4	0	0	78.6	57.8
Established seedlings	(2)	(19)	(21)	(74)	(0)	(2)	(8)	(35)
Survived	50.0	42.1	23.8	66.2	⋯	50.0	12.5	25.7
Died								
Herbivory‖	0	15.8	9.5	12.2	⋯	0	12.5	8.6
Dessication	50.0	21.1	42.9	9.5	⋯	0	25.0	25.7
Unknown	0	21.1	23.8	12.2	⋯	50.0	50.0	40.0

Notes: At the seed stage, percentages are expressed out of the total number of seeds per site per year (in parentheses). At the emerged and established seedling stages, percentages are expressed with respect to total number of individuals alive at the end of the previous stage per site and year (in parentheses).

† Remains of eaten seeds at the station as evidence.
‡ Seeds removed from the stations (presumably by rodents).
§ Seed destroyed while emerged seedling was still dependent on its reserves.
‖ Stems, leaves, or roots eaten or damaged by either mammalian or insect herbivores.

awara, with a similar trend for large seedlings (Table 11). In contrast, while sapling and pole densities were higher at Kanyawara than at Dura (Table 10), sapling survivorship and RHGR did not differ between sites (Table 11).

Desiccation, although low, was the primary cause of mortality for all size classes at both sites (Table 11). Cause of mortality for remaining individuals was unknown since they disappeared between monitorings.

Primate abundance

Frugivorous primate group density was higher at Dura than Kanyawara for all three large-bodied primates (chimpanzees, Dura = 4.81 nests·km^{-2}·d^{-1}, Kanyawara = 1.78 nests·km^{-2}·d^{-1}; baboons, Dura = 5 sightings, Kanyawara = 1 sighting; and mangabeys, Dura = 3.29 groups/km^2, Kanyawara = 1.13 groups/km^2) and two of the small-bodied primates (red tail monkeys, Dura = 12.19 groups/km^2, Kanyawara = 4.83 groups/km^2; and L'hoesti monkeys, Dura = 5 sightings, Kanyawara = 3 sightings). In contrast, while blue monkeys were present at Kanyawara (1.00 groups/km^2), they were never seen at Dura.

Overall probability of seed dispersal and seedling recruitment

Although immature fruit consumption by primates caused substantial reductions in initial fruit crop, once fruit were mature, the estimated probability that primates removed seeds from mature fruit was high (0.95) at both sites (Fig. 2). The probability of dispersal of seeds away from the parent was greater than 0.90 at both sites. We estimated that seeds had a much higher chance of being defecated by large-bodied primates in clumps in dung (CA + DCA; >0.85), than being spat out singly (SA + DSA; <0.06) at both sites.

The probability that deposited seeds survived each stage (germination, emerged seedling, and established seedling) varied greatly depending on deposition condition, year, and site (Fig. 3). Cumulative probability of seedling recruitment from seeds under the parent was very low. In three year–site combinations, seeds spit singly (SU) had a higher estimated recruitment probability than dropped, nondispersed seeds (DND; Fig. 3). Comparing all four seed experiments, cumulative probability of seedling recruitment was greatest for seeds spit singly away from the parent (SA + DSA) at both sites in both years, although it was equally high for seeds defecated in clumps (CA + DCA) at Kanyawara in year 2.

Despite the high cumulative probability of seedling recruitment from SA + DSA seeds, 86–94% of seedlings contributing to Kanyawara's year 1, year 2, and Dura's year 2 seedling population were estimated to come from seeds in clumps (CA + DCA). In contrast,

the only seedlings projected to recruit into Dura's year 1 seedling population were from single seeds away from the parent (SA + DSA). When the overall seedling recruitment into the population was calculated, seedling density was 33 times greater at Kanyawara than at Dura in year 1, and 2 times greater in year 2.

DISCUSSION

For frugivores to predictably contribute to plant recruitment, the steps leading from seed removal to seedling recruitment must be predictable (Herrera et al. 1994). The more consistently a frugivore visits fruiting trees and disperses intact seeds to good sites, the more likely it will contribute to seedling, and ultimately adult, recruitment (Howe 1989, Jordano 1992, Schupp 1993). This study clearly demonstrates that *M. myristica*, with its large, hard-husked fruit, initially restricts access of its seeds to all but the largest-bodied arboreal primates. Large-bodied primates visited all *M. myristica* trees monitored, removed over 75% of mature fruits, and are estimated to have dispersed over 85% of mature seeds. Only after mature fruits have been handled by large-bodied primates are these seeds accessible to other frugivores. Moreover, mature fruit do not drop from the tree unaided; when the few fruits not handled by these primates eventually fell, the seeds were dead. Thus, large-bodied primates are critical for initiating *M. myristica* seed dispersal.

The frugivorous primate community (including small- and large-bodied species) was estimated to have removed 90–97% of mature *M. myristica* seeds away from the parent tree. This is important since seeds located under parents had lower germination and seedling establishment probabilities than those located away. The lack of *M. myristica* poles under conspecifics further suggests recruitment into the adult population is difficult without seed dispersal. Consequently, dispersal is a critical process for *M. myristica* recruitment.

Although dispersal of seeds away from conspecifics is important for *M. myristica*, the manner in which seeds are deposited also influences the likelihood of seedling establishment. While seeds were most likely to be defecated in clumps, the cumulative probability of seedling recruitment was highest in single spit seeds. This spatial discordance between seed deposition and seedling establishment was evident at Dura in year 1, where we projected 100% of recruiting seedlings to come from single spit seeds. However, in three of four year-by-site combinations, we projected 86–94% of recruiting seedlings to come from seeds defecated in clumps by large-bodied primates. This is because the number of seeds that were likely ingested and defecated by large-bodied primates is greater than those spat singly and this difference is large enough to overcome differences in seed and seedling survival between the two deposition types. Fragoso (1997) similarly found concordance between clumped seed deposition by ta-

TABLE 7. Effect of location (under vs. away), site, and year on fate of *M. myristica* seeds from single-seed experiments.

Seed fate factors and interactions	χ^2	P	Direction
Beetle infestation			
Location	3.16	0.07	
Site	69.65	<0.001	K < D
Year	91.68	<0.001	1 > 2
Location × site	0.15	0.70	
Location × year	1.13	0.29	
Site × year	0.05	0.83	
Rodent removal			
Location	8.44	<0.01	U > A
Site	29.84	<0.001	K > D
Year	10.34	0.001	1 > 2
Location × site	2.56	0.11	
Location × year	0.03	0.86	
Site × year	0.76	0.38	
Germination			
Location	32.08	<0.001	U < A
Site	19.14	<0.001	K > D
Year	183.15	<0.001	1 < 2
Location × site	1.12	0.29	
Location × year	6.78	<0.01	
Site × year	8.25	<0.01	
Emerged seedling survival			
Kanyawara			
Location	21.91	<0.001	U < A
Year	10.17	<0.01	1 < 2
Year 2			
Location	37.57	<0.001	U < A
Site	28.13	<0.001	K > D
Established seedling survival			
Kanyawara			
Location	10.57	<0.01	K > D
Year	2.52	0.11	
Year 2			
Location	12.42	<0.001	U < A
Site	16.09	<0.001	K > D

Notes: Directional differences are indicated when $P < 0.05$ for main effects (U = under parent, A = away from parent, K = Kanyawara, D = Dura, 1 = year 1, 2 = year 2). For means, see Table 6.

pirs and high seedling densities around tapir latrines in a large-seeded Neotropical palm.

Despite concordance between primate seed deposition and seedling recruitment, the magnitude of effects of location, site, and year on all post-deposition stages were highly variable. For example, at Dura, the probability of germination from seeds in clumps varied from 2.1% in year 1 to 69.2% in year 2. Other studies have similarly shown that post-dispersal seed survival varies among habitats and among years (Schupp 1988, 1990, Willson 1988) and that spatial and temporal patterns of seed survival are generally unpredictable (Willson and Whelan 1990). This variation reduces the predictability of demographic consequences of frugivore actions (Herrera et al. 1994). Thus, even in a species that relies on a limited set of frugivores, spatiotemporal

TABLE 8. Fate of *M. myristica* seeds from experiments where 10 seeds were placed in 60 g of baboon dung.

	Kanyawara		Dura	
Fate	Year 1	Year 2	Year 1	Year 2
Seeds				
Infested by beetles	19.2 ± 25.4	0.0	85.0 ± 25.7	23.1 ± 29.5
Consumed by rodents†	23.3 ± 36.3	0.0	0.4 ± 2.0	0.4 ± 2.0
Removed‡	29.6 ± 39.2	12.7 ± 23.1	12.5 ± 24.9	5.0 ± 8.6
Buried by dung beetles§	7.5 ± 19.4	15.0 ± 22.3	1.7 ± 4.8	4.6 ± 11.4
Germinated	21.3 ± 23.7	86.5 ± 22.8	2.1 ± 10.2	69.2 ± 29.7
Emerged seedlings	(51)	(225)	(5)	(180)
Survived	47.1	74.7	0	35.0
Died				
Beetles‖	31.4	2.7	60.0	28.9
Rodents‖	11.8	0.4	0	0
Herbivory¶	0	0.9	0	0
Dessication	0	3.1	40.0	0.6
Unknown	9.8	18.2	0	35.6
Established seedlings	(24)	(168)	(0)	(63)
Survived	29.2	61.9	···	25.4
Died				
Herbivory¶	20.8	13.1	···	46.0
Dessication	33.3	8.3	···	11.1
Crushed#	0	8.9	···	0
Unknown	16.7	7.7	···	19.1

Notes: At the seed stage, percentages are mean number per 10 seeds ± 1 SD. $N = 24$ replicates per site in year 1, and 26 replicates per site in year 2. At the emerged and established seedling stages, percentages are expressed with respect to total number of individuals alive at the end of the previous stage per site and year (in parentheses).

† Remains of eaten seeds at the station as evidence.
‡ Seeds removed from the stations (presumably by rodents).
§ Buried directly under the station by tunneler dung beetles.
‖ Seed destroyed while emerged seedling was still dependent on its reserves.
¶ Stems, leaves, or roots eaten or damaged by either mammalian or insect herbivores.
# Crushed by fallen branches.

variation in post-deposition processes contributes to a lack of concordance between actions by frugivores and subsequent plant recruitment.

Although dispersal is critical for *M. myristica*, these findings suggest that processes occurring post-deposition may also limit recruitment. If the most critical stage in the seedling recruitment process is defined as that stage with the lowest probability (Clark et al. 1999, Rey and Alcantara 2000), then the limiting stage differed with each year by site combination. According to this criteria, the most critical stage was seed germination in year 1 at Kanyawara, emerged-seedling survival in year 1 at Dura, and established-seedling survival in year 2 at both sites. An alternative approach, instead of comparing probabilities among stages within a given year and site, examines the differences in inter-annual survivorship probabilities for each stage within a site. This analysis reveals that the greatest interannual differences within a site occurred in germination probability, and this decreased with progression through the stages. Indeed, analyses of each of the four deposition conditions revealed significant year effects for all stages, except the established seedling stage. Thus, seed germination is the limiting stage regardless of site or year since it sets the

stage for the absolute number of seedlings that emerge. This contrasts with Rey and Alcantara's (2000) findings that seedling establishment was the critical step for a Mediterranean bird-dispersed tree.

If germination is a limiting step for *M. myristica*, then factors affecting this process may also strongly influence recruitment dynamics. In all cases, seeds that failed to germinate were either infested by curculionid beetles or were removed or consumed by rodents, indicating the importance of seed predation in this system. Interestingly, regardless of deposition condition, beetles were the major vector of seed mortality at Dura, while rodents removed most seeds at Kanyawara. Thus, fluctuations in the population dynamics of these animals may differentially affect seedling recruitment at the two sites.

The effect of changes in frugivore abundance on seedling abundance

Given *M. myristica*'s dependency on large-bodied frugivores to initiate seed dispersal, this system, if any, should exhibit a detectable link between disperser and plant abundances. If concordance is prevalent in this system, then the site with higher primate abundance

TABLE 9. Effect of site and year on fate of *M. myristica* seeds from experiments where 10 seeds were placed in 60 g of baboon dung.

Seed fate factors and interactions	χ^2	P	Direction
Beetle infestation			
Site	88.66	<0.001	K < D
Year	77.93	<0.001	1 > 2
Site × year	1.65	0.20	
Rodent removal			
Site	21.05	<0.001	K > D
Year	22.31	<0.001	1 > 2
Site × year	1.53	0.22	
Dung beetle removal			
Site	10.99	<0.001	K > D
Year	4.41	0.04	1 < 2
Site × year	0.07	0.79	
Germination			
Site	18.05	<0.001	K > D
Year	148.94	<0.001	1 < 2
Site × year	2.84	0.09	
Emerged seedling survival			
Kanyawara			
Year	4.52	0.04	1 < 2
Year 2			
Site	23.21	<0.001	K > D
Established seedling survival			
Kanyawara			
Year	0.10	0.76	
Year 2			
Site	6.81	<0.01	K > D

Notes: Directional differences are indicated when $P < 0.05$ (K = Kanyawara, D = Dura, 1 = year 1, 2 = year 2). For means, see Table 8.

greater at Dura than at Kanyawara. However, if primates play a predominant role in determining early life stages we also expected the probability of seedling recruitment to be higher at the site with higher primate density (i.e., Dura). In contrast, survivorship across all stages was consistently greater at Kanyawara, leading to higher expected seedling density at this site.

Positive or negative associations between frugivore and seedling abundances can be caused by processes that operate independently of differences in number of seeds dispersed by frugivores. For example, once seeds germinate, differential growth and survivorship in seedlings among sites may determine number of individuals recruiting to a given size class. In our study, *M. myristica* standing seedlings <0.2 m at Kanyawara survived better and grew faster then did those at Dura. In addition, after an initial burst in height, seedlings may remain within a given size-class for many years (Connell and Green 2000). Thus, densities of seedlings in a given size-class may not represent equivalent recruitment from a single fruiting season at the two sites. Consequently, the lower *M. myristica* standing seedling density at Kanyawara compared with Dura may not result from lower primate densities and subsequently lower seed dispersal rates.

Moreover, Kanyawara, the site with lower frugivorous primate abundance, had higher sapling and pole abundances. Thus, despite the initial importance of these primates to *M. myristica* recruitment, processes affecting later stages, such as light availability, may be more important for the long-term population structure. These effects are difficult to determine without appropriate demographic models on long-term growth and survivorship.

Conclusions

Our study has demonstrated that in a species where fruit morphology restricts frugivore access, such as with *M. myristica*, seed dispersal by large-bodied pri-

should have higher seedling abundance. At first examination this appears to be the case. Frugivorous primate density was three times greater, and *M. myristica* standing seedling density (<0.2 m tall) was four times

TABLE 10. Density of seedlings, saplings, poles, and trees of *M. myristica* at Kanyawara and Dura.

Size class	All locations				Away only			
	Kanyawara	Dura	χ^2	P	Kanyawara	Dura	χ^2	P
Small seedlings (<0.2 m tall)	0.05 ± 0.16	1.47 ± 4.86	27.56	<0.001	0.05 ± 0.16	0.20 ± 0.33	15.29	<0.001
Large seedlings (0.2–0.5 m tall)	0.05 ± 0.08	0.36 ± 0.85	24.75	<0.001	0.05 ± 0.08	0.12 ± 0.15	10.55	<0.001
Saplings (0.5–2.0 m tall)	0.018 ± 0.018	0.008 ± 0.015	11.27	<0.001	0.017 ± 0.017	0.008 ± 0.015	10.59	<0.001
Poles (>2.0 m tall and <20 cm dbh)	0.005 ± 0.007	0.0002 ± 0.001	54.42	<0.001	0.005 ± 0.007	0.0002 ± 0.001		
Trees (≥20 cm dbh)	1.0 ± 1.9	3.6 ± 4.0	19.53	<0.001				

Notes: Density estimates are given for individuals in all locations and those located >0.5 m away from the edge of an adult conspecific canopy. Density estimates are mean no. individuals/m² for small seedlings and poles and no. individuals/ ha for trees (±1 SD).

TABLE 11. Relative-height growth rate (RHGR), survivorship, and causes of mortality, over 18 mo, of small seedlings, large seedlings, and saplings located at least 0.5 m away from adult conspecific canopies.

Size class (height)	N	RHGR (cm·cm⁻¹·yr⁻¹)	P†	Survived (%)	Test	Died (%)			
						Desicca-tion	Herbivory	Crushed	Unknown
Seedlings (<0.2 m)									
Kanyawara	35	0.23 ± 0.18		88.6	$G = 6.27$	5.7	0	0	5.7
Dura	54	0.04 ± 0.46	0.04	63.0	$P = 0.01$	5.6	3.7	1.9	25.9
Seedlings (0.2–0.5 m)									
Kanyawara	57	0.08 ± 0.13		96.5	$G = 3.06$	0	0	0	3.5
Dura	64	0.01 ± 0.25	0.09	85.9	$P = 0.08$	4.7	0	0	9.3
Saplings (0.5–2.0 m)									
Kanyawara	46	0.05 ± 0.08		91.3	$G = 0.08$	2.2	0	0	6.5
Dura	15	-0.06 ± 0.34	0.25	93.3	$P = 0.77$	0	0	0	6.7

Note: Percentages are expressed with respect to total number of individuals monitored per size class (N).
† Values based on Mann-Whitney test.

mates is a critical factor in the recruitment process. However, despite the general concordance between seed deposition and seedling recruitment, it is difficult to predict patterns of seedling recruitment due to spatial and temporal variation in post-deposition processes that influence later stages. For example, we found seed predation, seed germination, and seedling emergence varied markedly between sites, years, and deposition conditions. Such fluctuations can result in spatial and temporal variation in seedling recruitment patterns. Thus, the relative importance of seed deposition in generating subsequent patterns may vary between years and sites. Other studies have similarly found that initial seed-dispersion patterns can be obscured by variation in post-deposition seed survival, germination, and seedling recruitment (Herrera et al. 1994, Houle 1998, Rey and Alcantara 2000, Wenny 2000). This study has demonstrated that this is the case even for a fruit-frugivore system where one would expect the link between disperser activity and later stages in plant recruitment to be apparent.

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