

Seed Removal and Seed Fate in *Gustavia superba* (Lecythidaceae)¹

Pierre-Michel Forget²

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama

ABSTRACT

The fate of the large (mean 12.6 g) seeds of *Gustavia superba*, an understory tree, was analyzed on Barro Colorado Island (BCI), Panama. Eight hundred thread-marked seeds were placed on the ground at two contrasting 1-ha forest sites (*Gustavia*-rich vs *Gustavia*-poor) during two periods (June and July) of the fruiting season of *G. superba*. These months correspond to maximum food availability on BCI. On average, 85.5 percent of the seeds were removed within 28 days, 47.5 percent and 3.8 percent of them being found scatterhoarded (buried) by agouti (*Dasyprocta punctata*) and gnawed by rodents, respectively, within 10 m of their origins. The effect of site and the interaction of site with month significantly affected seed removal rates, but not scatterhoarding rates. Proportions of seeds removed were greater where *G. superba* trees were rare. Because freshly fallen seeds were not infested by bruchid weevils, unburied and germinating seeds provide an abundant short-term food supply for terrestrial mammals. Burying seeds allowed agoutis to later consume cotyledons of germinating seeds from mid-August throughout October, when food is scarce on BCI. Overall seed dispersal effectiveness (% seed dispersal multiplied by % seedling survival) contrasts dramatically between forest sites, being 10.1 percent and 0.75 percent at *Gustavia*-rich and *Gustavia*-poor areas, respectively. This result suggests that predator-disperser satiation occurred, maybe due to greater *G. superba* seed availability and other alternative food supply, allowing greater *G. superba* seedling survival at the *Gustavia*-rich area.

Key words: agouti; Barro Colorado Island; *Gustavia superba*; Panama; seed dispersal; seed predation; seed removal.

SEED REMOVAL BY TERRESTRIAL RODENTS often represents seed predation (Janzen 1969, 1970, 1971), but some proportion of removed seeds may reflect seed dispersal, *i.e.*, seeds buried by scatterhoarding animals (Morris 1962, Smith & Reichman 1984, Price & Jenkins 1986, Vander Wall 1990). This proportion has remained an obscure issue (Forget 1990). The rate of seed removal, and perhaps also that of seed dispersal, might be influenced by the level of predator-disperser satiation, depending on availability of food resources and seasonal fruit diversity at the community level (Janzen 1970, 1971; Rankin 1978; Vandermeer *et al.* 1979; Boucher 1981; De Steven & Putz 1984; Hallwachs 1986; Sork 1987; Schupp 1990; Forget & Milleron 1991). In general, seed removal in a given species seems to be greater in the community where this species occurs at low density, thus limiting its ability to survive to adulthood (Rankin 1978, Boucher 1981).

However, for large-seeded and scatterhoarded plant species, seed removal may not accurately estimate real seed predation by terrestrial mammals (Rankin 1978). The fate of seeds of rodent-dispersed species could vary with seed features such as

size, nutrient content, perishability, toxicity and edibility, dormancy and germination delay, as well as overall fruit supply over the rodent home range depending on habitat, especially in the neighborhood of fruiting trees. Further, fates could change between seasons or years. All these characteristics may finally determine the way rodents eat, bury, retrieve, or abandon seeds. Consequently, it would be inappropriate to debate about the relationships between rodents and plants without taking into account these criteria and the complex interactions that may appear.

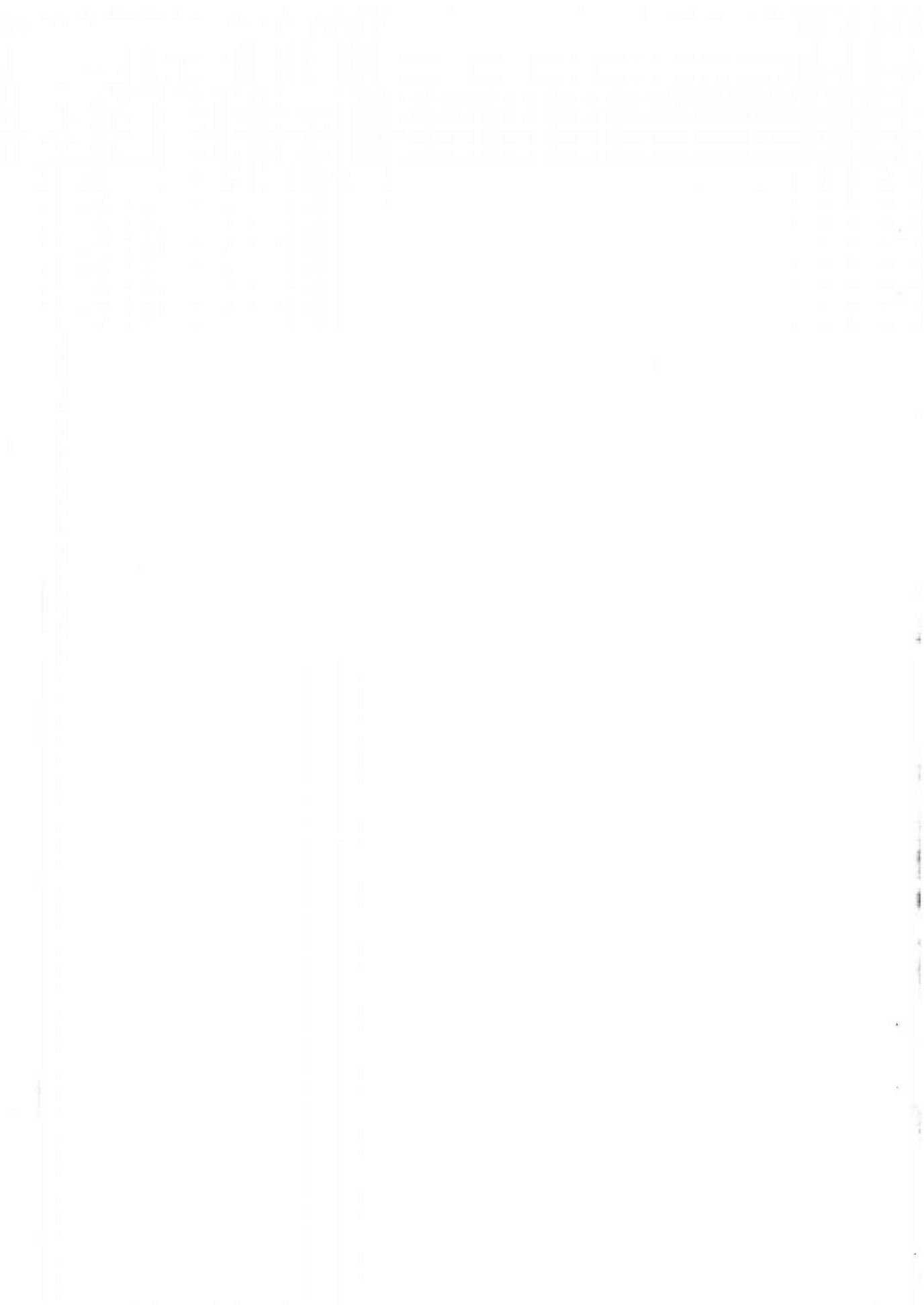
In order to analyze the crucial factors that influence seed removal by rodents, and survivorship of buried seeds, the fates of removed seeds of *G. superba* were determined in Barro Colorado Island (BCI), Republic of Panama. The main question addressed in this paper is: how does the removal rate and fate of *G. superba* seeds vary across site and during the *G. superba* fruiting season? I also briefly discuss the reward gained by the rodents while caching *G. superba* seeds, and the advantages for *G. superba* to be dispersed by "gardening" rodents.

STUDY SITE AND SPECIES

BCI (9°09'N, 79°51'W) is a tropical moist forest (2616 mm rainfall/yr, Rand & Rand 1982) ranging in age from approximately 100 years to several

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² Present address: Laboratoire d'Ecologie Générale, Muséum National d'Histoire Naturelle de Paris, 4 Avenue du Petit Château, 91800 Brunoy, France.



centuries (Foster & Brokaw 1982, Piperno 1990). The climate is seasonal with a long, stressful dry season from late December through mid-April that alternates with a wet season, having peak rainfall in October–November. A description of the flora, the fauna, and the ecology of BCI can be found in Croat (1978), Leigh *et al.* (1982, 1990), Eisenberg (1989), Emmons and Feer (1990).

G. superba is a conspicuous, nonpioneer (*sensu* Swaine & Whitmore 1988), understory tree (10–20 m tall) ranging from southwestern Costa Rica, throughout Panama, into northwestern Colombia (Prance & Mori 1979). In Panama *G. superba* flowers February–April during the dry season, and fruits mature in June–July, early in the wet season (Mori & Kallunki 1976, Smithsonian Environmental Science Program [ESP], Don Windsor, pers. comm.). Mature fruits are indehiscent, globose, 3.0–10.0 cm in diameter, green to yellow, with a pulpy orange mesocarp, and contain an average of 7 viable seeds (range 1–22, $N = 100$ fruits randomly collected along T-Barbour trail). Seeds are polygonal, brown, odoriferous, 1.0 to 3.5 cm in length, weighing 12.6 g (range 6.7–20.3 g, random sample of 50 seeds collected along T. Barbour trail). Predispersal seed predation is due to an unidentified moth (Sesiidae, Aegeridae) (P.-M. Forget, pers. obs.). Rotting of fruits on the ground mostly results from infestation by these unidentified larvae. Nevertheless, seeds not decomposed may remain on the ground after the whole mesocarp has rotted away, and rapidly rot within two–four weeks (see Sork 1985). Postdispersal predation on these seeds by bruchid beetles, or any other insect, has never been observed at the study site.

The Central American agouti (*Dasyprocta punctata*) and the red-tailed squirrel (*Sciurus granatensis*) have often been observed eating the mesocarp, but rarely the seeds of *G. superba* (Smythe 1970, Glanz *et al.* 1982, Smythe *et al.* 1982). These rodents store *G. superba* seeds in terrestrial burial (agouti) or arboreal (squirrel) caches (Smythe 1970, Heaney & Thorington 1978, P.-M. Forget, pers. obs.). I don't know if *G. superba* seeds on BCI are consumed by nocturnal rodents such as spiny rat (*Proechimys semispinosus*)—they may hoard seeds in burrow—and paca (*Agouti paca*). It is not known whether other grazing mammals are predators of germinated seeds or seedlings. Although fruits may be dropped (I do not consider this seed dispersal) by white-faced monkeys (*Cebus capucinus*) that feed on the mesocarp (*e.g.*, Hladik & Hladik 1969), only agoutis are reliable seed dispersers of *G. superba* (Smythe 1970).

Seed germination and long-term seedling survival have been studied in detail by Sork (1985, 1987). Burial increases speed of seedling emergence (called germination by Sork 1985, 1987), buried and unburied seeds taking 7 and 9 weeks, respectively. Thus, given the timing of fruiting, seedling emergence may peak in August–September, late in the wet season when overall food availability and the number of species fruiting is low (Smythe 1970, Foster 1982). Survival of buried seeds is greater where rodent population density is low, and does not seem to be affected by year-to-year variations in crop size (Sork 1987). Seedling mortality is mainly caused by rodents that dig up germinating seeds and consume the fleshy cotyledons (Sork 1987, this study).

METHODS

THE STUDY AREAS.—The study area is located at R. C. Shannon trail area where the forest is old, but close to a patch of young regrowth (Foster & Brokaw 1982; R. Foster, pers. comm.). Two 1-ha areas (sites 1 and 2) about 200 m apart were delimited, each being crossed by five parallel trails 100 m long and 25 m apart. These sites were chosen in November 1989 because they represent two contrasting situations *versus* density in *G. superba*, *Dipteryx panamensis* (Papilionaceae) and *Astrocaryum standleyanum* palm, three major resources of both agoutis and squirrels on BCI (Smythe 1970, Glanz *et al.* 1982, Smythe *et al.* 1982, Giacalone-Madden *et al.* 1990). At site 1, referred to as the *Gustavia*-rich area (an old forest site near trail marker 500 m), several small aggregations of *G. superba* grew, presumably reflecting long-past large natural disturbances in this area (see Foster & Brokaw 1982; R. Foster, pers. comm.). In the 1990 dry season 16 flowering trees were inventoried at this plot. *D. panamensis* and *A. standleyanum* are absent or at low density, respectively. At site 2, referred to as the *Gustavia*-poor area (an old regrowth near trail marker 200 m), the relative absence of *G. superba* (scattered trees grew near the area) contrasts with the presence of six big *D. panamensis* trees >30 cm in diameter (possibly relictual from human disturbance in this area), and a dense population of *Astrocaryum standleyanum* palms. Broadly, the most diverse forest is at the *Gustavia*-rich area.

EXPERIMENTAL DESIGN.—The experiment follows a two-treatment split-plot factorial design. The first treatment factor is forest site (*Gustavia*-rich vs *Gustavia*-poor), the second factor is fruiting period (June

TABLE 1. ANOVA results of percent of seed removal and scatterhoarding of *G. superba* for the effect of forest site (Gustavia-rich and Gustavia-poor areas) and month (June and July) at 28 days after seed placement. Data were arcsine square root transformed. Degrees of freedom indicate which error term was used.

Source of variation	df	Removal		Scatterhoarding	
		MS	F	MS	F
Site	1,38a	3205.62	4.53*	2722.0	3.74
Season	1,38b	343.2	1.39	329.44	0.06
Site × Season	1,38b	3241.1	13.14***	1631.81	0.32
Depot (Site)	38a	706.2		726.92	
Season × Depot (Site)	38b	246.5		5028.99	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

vs July). Seeds were collected in mid-June and mid-July from freshly fallen fruits found on the ground several hundred meters from the study area. Seeds showing infestation holes by moth larvae were excluded. Intact seeds were marked with a white thread 60 cm long passing through the cotyledons (Forget 1990). Twenty depots (four per trail) of ten grouped seeds ($N = 200$ seeds per site per experiment) were placed randomly. The experiment was replicated twice approximately four weeks apart, 13 and 16 June (early to mid-fruiting) and 14 and 18 July (late-fruiting) at sites 1 and 2, respectively. The same locations were used for replication. By 28 days after the beginning of each experiment, seeds remaining on the ground were removed by the experimenter (first experiment) or left on the ground (second experiment) in order to follow long-term destiny of unburied seeds. The average spacing between depots on trails was 14.8 ± 16.6 m ($N = 5 \times 3$ intervals per trail; range 5–68 m) at *Gustavia*-rich area, and 15 ± 14.8 m ($N = 15$ intervals; range 2–49 m) at *Gustavia*-poor area. Seeds were censused daily and marked seeds were searched for and caches labeled within 10 m where a majority of seeds was likely to be buried (see Hallwachs 1986, Forget 1990). In *G. superba*, this distance class limit appears to be a good balance between the necessity to retrieve a large number of seeds versus the amount of time necessary to survey all forty sites during the two months of intensive study. Seeds could not be set out on all plots on the same day because, especially late in the fruiting season, one could not find enough intact seeds before rodents removed them. These two replicated experiments were assumed to correspond to high and low levels in the decrease of overall abundance and diversity of available fruits (Smythe 1970, Foster 1982).

Survival of cached seeds and germinating seeds was measured by 10 October, approximately 3 and

4 months after the beginning of July and June replicates, respectively. By this date, seedlings of most buried seeds may have emerged (Sork 1985). The effectiveness of seed dispersal by terrestrial rodents reflects both the proportion of seeds removed and buried, and the proportion of buried seeds that survive until establishment. I used as an index of this effectiveness percent of seeds buried within 28 days of placement times percent of seedlings surviving to mid-October. Because all removed seeds were not retrieved by the experimenter, this index is an underestimate. Nonetheless, both the proportion of seeds buried > 10 m away and the proportion of their seedlings which survived may vary proportionately with the index of dispersal effectiveness (see Sork 1984, Forget 1990). The underestimate might then be consistent among plots and replicates.

Data were analyzed with a fully crossed ANOVA with two fixed effects of forest site and fruiting period, and a random effect of depot nested within site (see also Sork 1987 for similar analysis). The split-plot factorial analysis contains a mixture of between- and within-blocks effects. By incorporating the random effect, the appropriate error term was used for calculation of the F -statistic. The main effects and interactions among the main effects were tested against different error terms. The degrees of freedom listed in the results (Table 1) indicate which error term was used. Data were arcsine square root transformed.

RESULTS

On average, 85.5 percent of seeds were removed within 28 days, 47.5 percent and 3.8 percent of them being found buried and gnawed, respectively, within 10 m of their origin. However, sites and the interaction of site with month treatment significantly affected seed removal (Table 1). Sites had a greater effect on percent of seeds removed than did month

(Fig. 1). Neither sites, nor months had a significant effect on proportion of seeds scatterhoarded (Table 1). However, if month effect is removed, seed removal and scatterhoarding rates appear lower (one-way ANOVA, $F = 6.25$, $df = 1$, 78 , $P = 0.01$) and greater (one-way ANOVA, $F = 4.80$, $df = 1$, 78 , $P = 0.029$) at *Gustavia*-rich and *Gustavia*-poor areas, respectively (see Fig. 1).

Seeds were often buried less than 5 m from the origin. For instance, at one site where two depots were set 2 m apart, the average dispersal distance to the center of the two depots was $4.1 \pm SD 2.7$ m (range 0.3–9.3 m, $N = 15$ seeds retrieved within 10 m). Only one seed was found up to 10.80 m. The proportion of seeds gnawed was low at both forest types and mostly occurred once the remaining seeds germinated on the ground. The high proportion of lost seeds (41% and 55.5% at *Gustavia*-rich and *Gustavia*-poor areas, respectively) may be the consequence of terrestrial and arboreal rodents which may hoard seeds out of visibility, *i.e.*, in burrows, logs, trees, or farther than 10 m. Because of these mixed effects, the proportion of seeds lost was not analyzed for the effect of forest site or month.

All unremoved seeds were rooted after four weeks. Two months later (mid-October), no germinated unburied seeds of the second replicates had survived, they were all destroyed by the gnawing of rodents. Sometimes, marked cotyledons were found buried beside the origin but they were retrieved later by animals, and destroyed. Extremely low survival at *Gustavia*-poor area (Fig. 1) made ANOVA analysis useless. Overall survival and seed dispersal effectiveness contrast dramatically between forest sites (Fig. 1). On average, dispersal effectiveness was 10.1 percent and 0.75 percent at *Gustavia*-rich and *Gustavia*-poor areas, respectively.

DISCUSSION

The level of seed removal observed during this study is entirely consistent with that of Sork (1987) at a BCI site (site C) with an equivalent density of *G. superba* trees, and, from the viewpoint of rodent population, maybe also a similar situation though population densities are variable between years (see Giacalone-Madden *et al.* 1990, Glanz 1990). Nonetheless, I found that removal of unburied *G. superba* seeds essentially reflects seed dispersal by agoutis, not predation. Nor surprisingly, survival rate of seeds buried by animals in my study is nearly that of seeds buried by experimenter in Sork (1987, Fig. 3, p. 1344). Therefore, most of the points

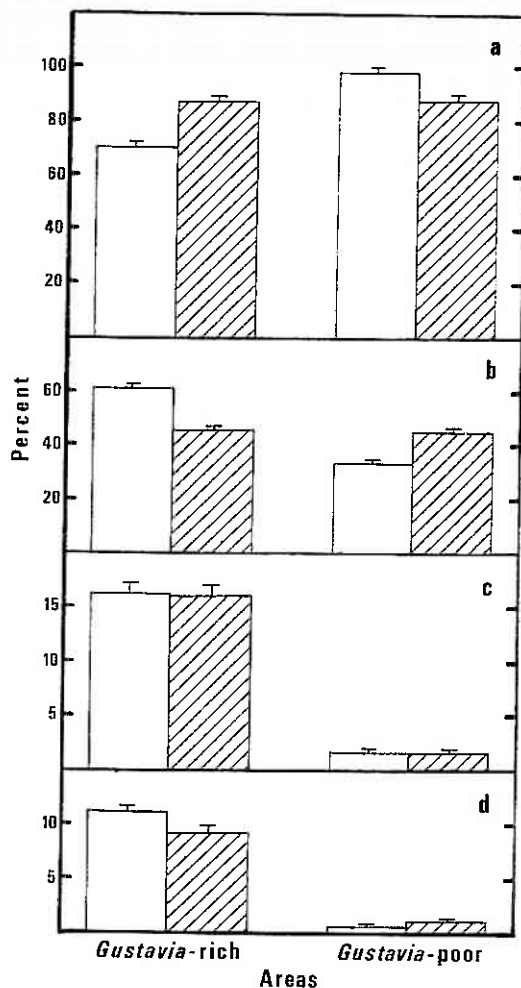


FIGURE 1. Mean (\pm SE) of the percent of *G. superba* seeds removed by animals (a) Seed removal; of the percent of removed seeds that were found buried within 10 m from the origin (b) Seed dispersal; of the percent of buried seeds that survived throughout mid-October (c) Seed survival, and (d) overall effectiveness (Dispersal times Survival) of seed dispersal by rodents in June (empty) and July (hatched) at *Gustavia*-rich and *Gustavia*-poor areas.

discussed by Sork (1987) still hold, although one might consider separately, and without any possible comparison, removal of unburied seeds on the one hand, and seed survival of buried seeds on the other, though in some instance, the latter case may correspond to short-term secondary burial before final consumption.

Sork (1987) suggested that seed survival at a given site might be a function of the population level of predator-dispersers, mostly terrestrial rodents, and seasonal use of their home range de-

pending on occurrence of other alternative food sources (see also Smythe 1978). In addition, my study suggests that, if, as in other studies (Rankin 1978, Boucher 1981, Forget & Milleron 1991) seed removal rate is higher where *G. superba* trees are rare, fate of buried seeds may also vary widely between forest types as a function of *G. superba* density, of forest age with the same level of rodent population, and of type of rodent food supply, all of which may largely determine location of animal home range in a given habitat (Smythe 1978).

During *G. superba* fruiting, agoutis and squirrels mostly consume *A. standleyanum* seeds and shift progressively to *Scheelea zonensis* seeds that are often available in patches below the parent palms (Glanz *et al.* 1982; Smythe *et al.* 1982; Smythe 1989; Forget & Milleron, pers. obs.; Forget & Munoz, pers. obs.). In June–July, agoutis also dug up seedlings of many species that are emergent (see Garwood 1982), and then consumed their persistent cotyledons (P.-M. Forget, pers. obs.). Therefore, despite a decrease in overall fruiting tree diversity (Foster 1982), *G. superba* bears fruits when the food supply is abundant and when agoutis are foraging over less of their home range, and spending more time resting and nursing (Smythe 1970, 1978). Satiation of rodents (Janzen 1970) over the home range of rodents seems to be responsible for lower seed removal rate at *Gustavia*-rich area, especially in June. Nevertheless, scatterhoarding of *G. superba* seeds was high at both study sites in June and July. This result is consistent with the observation of Smythe (1978) that scatterhoarding occurs more frequently toward fruit-biomass peak at the community level, and suggests that *G. superba* trees, which are usually scattered at a low density in the old forest, might have evolved a fruiting pattern which maximizes seed dispersal by agoutis encountering single multiple-seeded fruits (Smythe 1970). Given the fact that agoutis do not consume freshly fallen seeds, the pulpy mesocarp might be viewed in the modern age (see Janzen & Martin 1982, Hallwachs 1986), indeed, as a favorable adaptation to attract the contemporary seed dispersers, which, in turn may bury seeds in order to eat their cotyledons later.

Prance and Mori (1979) reported that *Berbertholletia excelsa* seeds are not immediately harvested by agoutis, but are cached where some of them are able to establish because they are forgotten by the animals (Huber 1910). The same may be true of *G. superba*. The obvious failure of bruchids to eat fresh *G. superba* seeds (a common fact among Lecythidaceae, P.-M. Forget, pers. obs.) suggests that,

as in *G. hexapetala* which seeds are used for making fish poison (Prance & Mori 1979), *G. superba* may be rich in some insect repellent substances. Instead of rotting, seeds germinate on the ground and are not consumed by rodents until later when food availability decreases. Only those buried would have more chance escaping various vertebrate predators, especially those animals unable to dig. Agoutis can consume *G. superba* cotyledons as late as November, but it seems that agoutis progressively lose interest in germinated seedlings. Indeed, from November 1989 throughout June 1990 at *Gustavia*-rich area, a few seedlings were observed which were dug up, and whose cotyledons were superficially nibbled (P.-M. Forget, pers. obs.). Therefore, the period between June and July throughout October represents the crucial phase of establishment in *G. superba*.

Agoutis could not survive in the forest without the occurrence of food plants bearing seeds that, once hoarded, remain available and edible throughout the season of fruit scarcity (Smythe 1978, 1989). The same is conceivable for squirrels. Subsequently, the occurrence of agoutis or any other rodents, as well as the fate of *G. superba* seeds, is more likely to be influenced by the presence or absence of other plants fruiting over the year, than simply by the density of *G. superba* trees (see also Sork 1987). Though many seeds on the *G. superba*-poor area were removed and buried, a disproportionate mortality of seeds and seedlings occurred later on, maybe due to low food supply and to the lack of satiation of predator-dispersers seeking food at this forest site. Conversely, at the *G. superba*-rich area, accumulation of *G. superba* seeds on the ground, and thus satiation of the rodents, might have compensated for the high postdispersal mortality of buried seeds. Although agoutis, as well as other mammals, may simply consume unburied germinating seeds that would have persisted several weeks on the ground, the hoarding behavior in agoutis of *G. superba* seeds appears an efficient adaptation to allow consumption of food reserve, *i.e.*, cached cotyledons, while competing with other rodents during food shortage starting in mid-August (Smythe 1970, 1978). Therefore, abundance of *G. superba* trees in the forest, along with *A. standleyanum*, *S. zonensis*, and other large-seeded species with persistent reserves, *e.g.*, *Gnetum leyboldii* (Gnetaceae), *Hylenaea praecelsa* (Hippocrateaceae), appear to be favorable for an agouti to establish a home range. Conversely, the abundance of *D. panamensis* at *G. superba*-poor area might have determined squirrel preference for this area (P.-M. Forget, pers. obs.), and might explain why despite a higher proportion of removed

seeds, a lower proportion of seeds were found buried.

Saturating the disperser-predator with an abundant population of germinating seeds (buried or not) might increase the chance that seedlings escape post-dispersal predation (Janzen 1970, 1971). The chance of seedling survival might also be enhanced when agoutis, squirrels and other mammals forage more frequently at fruiting *S. zonensis* palm and rely upon its seeds from July throughout December (Glanz *et al.* 1982; Smyrthe *et al.* 1982; Forger & Munoz, pers. obs.). Therefore, the seed dispersal reward gained by *G. superba* is likely to be maximal when the large seeds are dispersed near the parent, *i.e.*, in a habitat where food availability satiated predators while promoting seedling survival. Beside, there may be no advantage for *G. superba* to be dispersed far away in a forest stand where *G. superba* do not occur, and where absence of local satiation would decrease the chance of recruitment. The intermediate dispersal distance seems to be the best alternative for efficient *G. superba* recruitment. This study demonstrates that agoutis play an essential role in dispersing *G. superba*, and, being the main cause of *G. superba* seedling mortality, they may be

active partners in the recruitment maintenance of the ecosystem's tree diversity, which in turn, may allow the animal to survive year-round.

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