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Damage tolerance and cotyledonary resource use in the tropical tree *Gustavia superba*

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Explanations for the extremely large seed size of some tropical forest plants are currently lacking. In this study we examine cotyledonary resource use of the tropical tree *Gustavia superba*, and test whether tolerance to damage of either seeds or establishing seedlings might be an important function leading to, or maintaining, its large (> 5 g) seed reserves. We found that seeds of *Gustavia* were both tolerant of insect infestation and were also capable of successful germination after removal of half of their cotyledonary reserves. Simulated complete above-ground herbivory resulted in repeated resprouting (up to 8 times). Resprout shoots were constructed of a small, but fixed proportion of remaining cotyledonary mass regardless of seed size. In the absence of damage, cotyledon reserves were used for onward seedling growth; however, conversion of cotyledon resources was slow, lasting several months. Given high rates of damage to *Gustavia* seeds and seedlings in the field, and the apparent use of cotyledonary reserves to tolerate or recover from it in growing house experiments, we conclude that cotyledonary seed size and morphology in this species is adaptive in surviving pre- and early post-germination hazards.

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The adaptive value of large, persistent seed reserves present in some tropical rain forest trees remains elusive. While large seed reserves have long been thought to be associated with seedling establishment requirements in shady understorey conditions (e.g. Troup 1921, Salisbury 1942, Snow 1971, Foster and Janson 1985; but see Kelly and Purvis 1993, Hammond and Brown 1995) shade persistence does not always correlate with seed size (Augspurger 1984; but see Boot 1996) and some of the smallest seeds (< 1 mg) are produced by shade-tolerant species (e.g. Metcalfe and Grubb 1995). We suggest therefore that the adaptive value of large seed size may not be related to low levels of irradiance per se.

Alternative explanations of large seed reserves are that they afford greater tolerance of pre- and post-germination hazards, such as partial seed predation (e.g. Janzen 1971, 1976, Dirzo 1984, Dalling et al. 1997), and seedling damage from herbivores, falling litter, and trampling (Denslow 1980, Clark and Clark 1985, 1989, 1991, Armstrong and Westoby 1993, Andersson and Frost 1996, Harms and Dalling 1997). Large seed reserves may also allow successful emergence from deeply buried cache sites (Vander Wall 1993), or seed reserves themselves may provide a reward to dispersers (Steele et al. 1993, Andersson and Frost 1996, Grubb 1996). While evidence is accumulating that each of these factors may contribute some selective advantage to large seed size in some species, their relative importance has seldom been assessed for individual species.

In this study we examined the resource allocation patterns in seedlings of the tree *Gustavia superba* (H.B.K.) Berg (Lecythidaceae) in central Panama, and examined whether seed and seedling damage, and scatter-hoarding have selected for, or are important in, maintaining large seed size in this species. Using an experimental and observational approach we assess the applicability of the following predictions for *Gustavia*

that result from either damage tolerance or dispersal advantages: 1) cotyledonary seed reserves are retained after the production of a functional shoot, and regardless of initial seed size; 2) seeds remain capable of germination even after insect infestation, or partial consumption; 3) seeds are capable of producing functional resprout shoots after complete above-ground herbivory; 4) seed reserves of deeply buried seeds (simulating scatter-hoarding) are not entirely used in reaching the soil surface; 5) cotyledonary reserves are retained, rather than used to augment onward seedling growth in the absence of physical damage; 6) resprouting is common for naturally regenerating seedlings in the field.

Methods

Study site and species description

The study was carried out in seasonally moist tropical forest on Barro Colorado Island (BCI), in central Panama. Rainfall on BCI averages 2600 mm yr^{-1}, with a pronounced dry season from January to April (Windsor 1990). The flora, fauna, geology and hydrology of the site are described by Croat (1978) and Leigh et al. (1982).

Gustavia superba is a common sub-canopy tree (10–20 m tall) of lowland Tropical Moist and Wet Forest (sensu Holdridge et al. 1971) of Central America and northern South America (Croat 1978, Prance and Mori 1979). On BCI, Gustavia is a common component of 40–100 yr old secondary forest on the eastern side of the island. During the mid-wet season (May–August) adults of Gustavia produce indehiscent fruits of 150–600 g containing seeds of variable number and size. Sork (1987) reports 5–50 seeds/fruit, and a mass of 3–15 g/seed; Forget (1992) reports an average of 7 viable seeds/fruit and an average mass of 12.6 g/seed, ($n = 50$). Seeds appear morphologically undifferentiated (i.e. no distinct embryo is visible upon dissection), and consist largely of 2–4 (mode = 3) cotyledon segments. Seed germination is hypogeal, with the cotyledons of scatter-hoarded, or otherwise buried seeds remaining beneath the soil. For unburied seeds, the cotyledons turn green on exposure to light; however, since the cotyledons lack stomata, they are unlikely to undertake much photosynthesis (K. Kitajima pers. comm.).

Sork (1985, 1987) and Forget (1992) found that seeds of Gustavia are both dispersed (scatter-hoarded) and consumed by rodents on BCI. Forget (1992) found that agoutis (Dasyprocta punctata) usually dig up and consume Gustavia cotyledons after germination. Cotyledons are sometimes carried away from seedlings and partial cotyledon damage occurs (Forget 1992). Seeds are also commonly fragmented before or during the process of removal from the tough, indehiscent fruit (J.

Dalling and K. Harms pers. obs.). Under growing house conditions, even small fragments (1–2 g) of excised cotyledons are capable of producing functional seedlings (Harms et al. 1997). Most fallen Gustavia fruits contain at least some seeds that have been damaged by the clearwing moth Carmenta foraseminis (Sesiidae) (Harms and Aiello 1995).

Effects of insect seed damage on seed germination

All seeds for all experiments were collected from beneath ca 20 trees along Barbour Trail on BCI. In July 1994, we collected 500 seeds from fallen, indehisced fruits. No evidence of insect infestation was apparent on the seeds at the time the study was initiated. Seeds were placed in a growing house under shade conditions (0.4–1.0 mol m^{-2} d^{-1} PAR), and planted on the surface of ten germination trays, watered daily, and censused weekly over the following eight weeks for germination and signs of insect infestation.

Effects of seed size on initial shoot size

In May 1994, we collected 50 seeds exhibiting a natural range in seed size, and accurately measured their fresh masses. Seeds were planted in the growing house (conditions as above). Three weeks after the emergence of the initial sprout we excised the entire above-ground shoot above the cotyledons, dried it in the oven at 70°C for 72 h and measured the dry mass. Seedlings that developed two or more above-ground sprouts simultaneously or that showed signs of insect damage to the cotyledons were excluded ($n = 11$).

Effects of partial cotyledon removal on seedling size and resprouting capacity

In June 1993, we randomly assigned 90 seeds to three categories: unmanipulated, 25% seed (cotyledon) mass removal and 50% seed mass removal. Seeds were reweighed and cut until the appropriate proportion of cotyledon mass had been removed. Seeds were randomly placed on forest soil in three large seedling trays (conditions as above) and watered daily. The initial cohort of seeds to germinate was observed closely to determine the length of time required from the first emergence of an above-ground sprout until the first pair of leaves had just fully expanded (i.e. the shoot was fully functional). This time period (3 wk) was highly consistent among seedlings.

Three weeks after sprout emergence the entire above-ground shoot above the cotyledons was excised from the plant, and dried and measured as above. Since Gustavia leaves are nearly white when they emerge and

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begin expanding (i.e. without chlorophyll) we assume that these excised parts were constructed almost entirely out of the energy reserves of the seed. Observations of one "albino" seed (completely lacking chlorophyll) seem to support this, as it also produced an initial seedling and resprout seedlings similar to those of normal plants. We continued to census seedlings after excision of the shoot and harvested each successive, newly expanded resprout that was produced. We continued the experiment until no new resprouts were produced (59 wk after planting).

Effect of seed burial on initial shoot size and resprouting capacity

Since the scatter-hoarding rodents that disperse *Gustavia* seeds can bury seeds to deep soil layers (up to 8 cm; Smythe 1978, Hallwachs 1986) we examined the capacity of *Gustavia* seeds to establish and resprout from a range of soil depths. In June 1993 we collected 180 seeds (mean = 9.0 g, s.e. = 0.4), and buried seeds at six soil depths (0, 1, 2, 5, 10 and 15 cm). Seeds were buried in 20 cm diameter, 20 cm depth pots in groups of 10 seeds per pot and three pots per treatment. Pots were filled with sieved (5 mm mesh) forest soil and placed in a growing house (conditions as above). Pots were censused weekly and the newly expanded aboveground shoots excised as above, dried and measured. The experiment was terminated after 61 wk when no new resprouts were produced.

Effect of complete cotyledon removal on onward seedling growth

In July 1997 we selected 120 undamaged seeds (location as above) to examine the effect of cotyledon removal on subsequent seedling growth. Seed size in this experiment ranged from 9.0 g to 32.1 g (mean = 16.8, s.e. = 0.5). Seeds were assigned to treatments in a stratified random manner to ensure equality of mean seed masses, and planted into individual 2-L pots of forest soil in a growing house (conditions as above). In two cotyledon removal treatments, seedlings were grown for either three weeks or nine weeks after shoot emergence and then seedling height and leaf area were measured and cotyledons were completely removed. Six weeks later height and leaf area were remeasured and seedlings were harvested for total dry mass. Cotyledon removal treatments were paired with controls in which seedlings retained their cotyledons throughout the experiment. Final cotyledon dry mass (at excision or harvest, depending on treatment) was also measured to determine rates of cotyledon resource use.

Field survey of resprouting frequency

In June 1994 we marked 100 newly emerged seedlings (with cotyledons attached and < 6 fully expanded leaves) along Barbour Trail on BCI. In August 1994 we marked an additional 100 seedlings that germinated later in the year along Wheeler Trail on BCI and that were in a similar development stage. In contrast to subsequent years (1995–1997), in 1994 many *Gustavia* seeds germinated on the soil surface without being consumed or scatter-hoarded, and all the seedlings we marked had open cotyledons attached to seedlings and exposed above the soil. Seedlings along Barbour trail were re-censused in August and November 1994, and in January, March, and June 1995 and at Wheeler site in October 1994 and in January, March, and June 1995. At each recensus we recorded the number of remaining cotyledons, and the number of resprouting seedlings.

Statistical analysis

Analyses of variance (ANOVA) were performed using the MGLH procedures in SYSTAT (Wilkinson et al. 1992). Effects of partial cotyledon removal and of seed burial on the initial shoot and subsequent resprout mass, were both analysed by repeated measures ANOVA, using Greenhouse-Geisser adjusted F-tests of between subjects factors. For the partial cotyledon removal experiment, results of analyses performed on the initial shoot and two subsequent versus three subsequent resprouts were very similar, and the analysis for three resprouts is presented here. For the seed burial experiment, analyses are performed on the per pot means of the initial shoot mass and three subsequent resprouts. Kruskal-Wallis non-parametric ANOVA was used to analyse time to seedling emergence.

Effects of complete cotyledon removal on subsequent seedling growth were analysed using analysis of covariance (ANCOVA) of seedling height and seedling leaf area. The covariates (leaf area and seedling height at the time of treatment application) were used after testing for an interaction between the covariate and treatment (the homogeneity of slopes assumption).

Results

Insect infestation and seed germination

Of the 500 seeds collected, 463 germinated within the eight weeks of the study. The remaining 37 seeds completely rotted away, as a result of insect infestation and/or fungal infection. Insect infestation however was not necessarily fatal; one or more of pupae or exit tunnels of the sesiid moth (*Carmenta foraseminis*; Eichlin 1995) were found in 124 of the 463 (27%) of the seeds which successfully germinated.

Table 1. Seed mass, initial seedling mass and resprouting characteristics of whole and cut seeds.

Treatment[1]	Initial seed mass (g ± s.e.) [n][2]	Initial shoot dry mass (g ± s.e.) [n]	First resprout dry mass (g ± s.e.) [n]	Average number of resprouts[3] (range)
Whole seeds	14.4 ± 1.2 [30]	0.43 ± 0.1 [11]	0.39 ± 0.1 [11]	3.6 (2–8)
25% removed	13.1 ± 0.9 [30]	0.41 ± 0.1 [14]	0.23 ± 0.0 [14]	2.7 (0–5)
50% removed	14.7 ± 1.3 [30]	0.32 ± 0.1 [20]	0.22 ± 0.0 [19]	2.1 (0–6)

[1] Cut treatments are exact 25% and 50% reductions in the initial seed masses.
[2] Seed mass prior to cut.
[3] Excluding the initial shoot.

Seedling size and resprouting capacity

There was a strong linear relationship between initial seed mass and the initial shoot mass ($r^2 = 0.85$; df = 1,37; $F = 202.4$; $p < 0.001$). Converting seed fresh masses to dry mass (dry mass = 47.5% fresh mass) indicates that 10% of the seed dry mass is used for construction of the initial above-ground shoot.

All but one of the 90 seeds used in the partial cotyledon removal experiment germinated. Although the time taken from planting to the emergence of an above-ground shoot varied from 2 to 21 wk, the median time to germination (4 wk) was the same for all treatments. Many of the seedlings ($n = 42$) produced multiple resprouts concurrently after one of the sequential resprout removals. Although these represent a large proportion of our data, they are excluded from subsequent analyses since the concurrent production of multiple resprout shoots is likely to affect patterns of resource allocation in a way that differs from allocation in individuals with sequentially produced shoots.

Both cut and uncut seeds were capable of resprouting multiple times; uncut seeds produced up to eight sequential above-ground resprouts, and cut seeds up to six resprouts (Table 1). Just as the initial shoot size is related to seed mass, it appears that resprout size is related to the size of the remaining seed reserves of the plant. Thus, as each sequential resprout is produced the size of the subsequent resprout diminishes (Fig. 1, Table 2, within subjects 'shoot'). Whole seeds produced larger shoots than seeds with half of the cotyledon mass removed (Tukey HSD, post hoc test, $p < 0.05$), but interestingly, partial removal of seed reserves did not alter the allocation pattern of seed reserves to shoots (Table 2, Treatment × shoot interaction is not significant; slopes parallel in Fig. 1). In effect, large seeds with partially removed cotyledons behaved like smaller seeds.

Effect of seed burial

Seed burial, in contrast, did affect the timing of seedling emergence (Kruskal-Wallis test = 14.6, df = 5, $p < 0.05$). Seeds placed on the soil surface produced shoots faster (median = 5 wk) than seeds buried in the soil (median = 12 wk), and seeds buried at 15 cm depth (median = 30

wk) were slower to emerge than seeds buried in the soil at ≤ 10 cm (median = 8 wk). Seed burial had little effect on either the initial shoot size or resprouting capacity except at a depth of 15 cm. The initial shoot sizes were significantly different across the burial treatments (one-way ANOVA; df = 5,12; $F = 3.3$, $p < 0.05$), but post hoc tests showed that only the mean shoot mass of plants in the 15 cm depth treatment was smaller than for shoots of seeds buried at depths of ≤ 5 cm. Similarly, although there was a significant effect of burial depth on the total shoot mass produced (one-way ANOVA; df = 5,12; $F = 3.3$, $p < 0.05$), this was only significant for comparisons with the 15 cm treatment.

Cotyledon removal and seedling growth

The removal of cotyledons three weeks after shoot emergence had a small, but significant, effect on leaf area production (ANCOVA df = 1,93, $F = 4.4$, $p < 0.05$), and whole plant biomass (ANCOVA df = 1,93, $F = 7.2$, $p < 0.01$), but not on seedling height 6 wk later (Fig. 2). In contrast, cotyledon removal 9 wk after shoot emergence had no effect on seedling size. However, after 9 wk only a quarter of the original cotyledonary dry mass remained, as opposed to nearly half after three weeks (Fig. 3).

Seedlings of *Gustavia* showed strong periodicity in their growth; leaves were produced in flushes rather
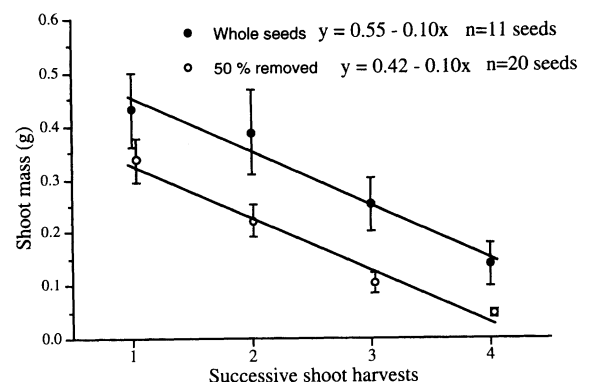

Fig. 1. Mass of sequentially harvested, above-ground shoots for seeds with intact cotyledons, and seeds with 50% of cotyledon mass removed. Data for seeds in the 25% removal treatment are omitted for clarity. Error bars are 1 s.e.

Table 2. Repeated measures ANOVA of cut treatment (whole seeds, 25% cotyledon removal and 50% removal) on the size of sequentially cut resprout shoots. Only data for seedlings that produced three resprouts are included.

Source	df	MS	F
Between subjects			
Cut treatment	2	0.17	3.6*
Error	21	0.05	
Within subjects			
Shoot	3	0.44	30.8***
Shoot × Cut treatment	6	0.03	2.2
Error	63	0.01	

* $P < 0.05$, *** $P < 0.001$.

than continuously, and the interval between flushes was sufficient that many seedlings produced no new leaves between the time of cotyledon removal and harvest. For the 3-wk cotyledon removal treatment, significantly more seedlings failed to flush new leaves (10 out of 25) than for the 3-wk control treatment (3 out of 26; Yates-corrected $\chi^2 = 11.1$, df $= 1$, $p < 0.001$). The pro-

Fig. 3. Mean percentage (+ 1 s.e.) of remaining cotyledonary dry mass for seedlings with cotyledons removed after 3, 9, and 15 wk. The initial dry mass was calculated assuming a 52.5% seed moisture content. Line drawn by eye.

portion of seedlings flushing new leaves was not different between the 9-wk cotyledon removal and control treatments (6 out of 18 and 11 out of 31, respectively).

Cotyledonary use and resprouting in the field

Naturally recruiting *Gustavia* seedlings in 1994 showed relatively high survivorship. Ten and twelve months after the initial censuses, 60% and 53% of seedlings were still alive at Wheeler and Barbour sites, respectively (Table 3). Most seedlings lost their cotyledons gradually. At Barbour site 31% of seedlings, and at Wheeler site 28% of seedlings lost one or more, but not all their cotyledons in the first two months. Cotyledons either rotted away, were mobilized by the plant, or were lost. Cotyledon loss presumably occurred because the brittle attachment between stem and cotyledon was broken, or because cotyledons were excised. Few seedlings resprouted in the first two months when cotyledons were still attached, but after 10 months 16% and 27% of the surviving seedlings at the two sites had resprouted at least once.

Discussion

Gustavia appears to be another example of a large seeded tree that is remarkably tolerant to insect seed predators (Janzen 1971, 1976, Forget 1992). Results for this species appear to be broadly similar to those for *Prioria copaifera* (Dalling et al. 1997); seed germination appeared to be relatively little affected by infestation by moth larvae, and seeds with as much as half of their cotyledonary reserves removed germinated as well as intact seeds. Seed damage tolerance, however, may be the result of morphological or chemical adaptations as much as size alone. In oaks (*Quercus* spp.), for example, chemical defences of the seed reserves are concen-
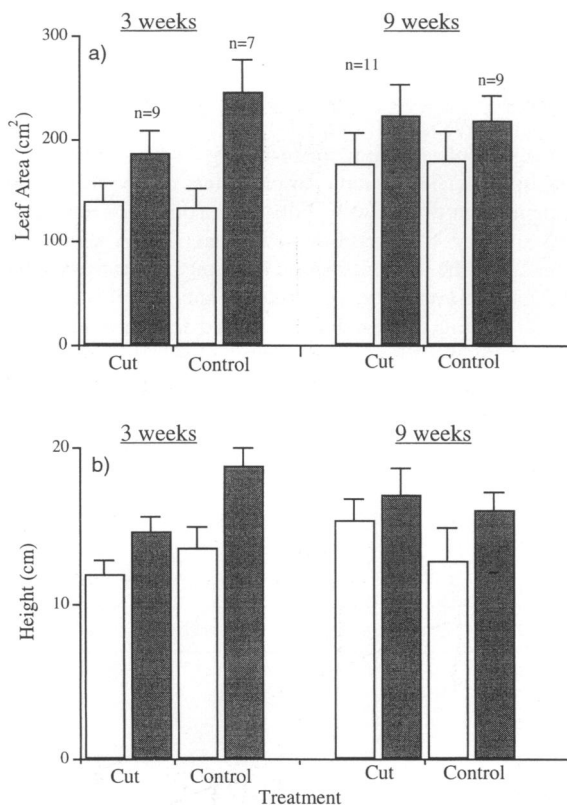

Fig. 2. a) Mean leaf area and b) mean total biomass (+ 1 s.e.) of seedlings in two treatment groups. In the cut treatment cotyledons were excised from the plant 3 or 9 wk after above-ground shoot emergence. In the control treatment, cotyledons were left on the plant and could contribute to seedling growth. Open columns indicate values at the time the cut treatments were applied, and grey columns values 6 wk after treatment application.
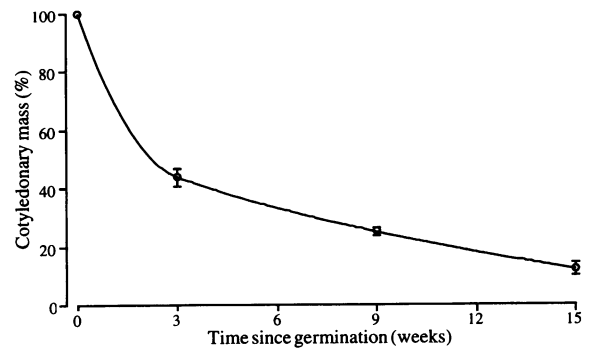
trated in the apical region of the acorn around the embryo resulting frequently in only partial consumption of the seed (Steele et al. 1993). In *Gustavia*, the seed consists of two or three fleshy cotyledon segments, with no clearly differentiated region containing a developed embryo. Presumably meristematic tissue is spread throughout the cotyledons because even small cotyledonary fragments are capable of generating seedlings (Harms et al. 1997).

Like other large seeded species on BCI (Harms and Dalling 1997), the expansion of the initial seedling of *Gustavia* required use of only a fairly small proportion of the total cotyledonary reserves (10% for the above-ground shoot). This phenomenon has also been observed for oaks, in which the cotyledons have been considered 'over-sized' for the germination process (Sonesson 1994, Andersson and Frost 1996). In fact, among *Gustavia* seeds of widely varying mass, and in seeds where cotyledonary reserves were removed prior to germination, the same proportion of seed reserves were allocated to forming the initial fully expanded seedling. This apparent pattern of partial seed reserve allocation may simply result from constraints on the rate at which seed reserves are mobilized, but also suggests an adaptive explanation whereby seed reserves are retained in case the newly formed seedling is damaged. In support of this view we found that simulated herbivory (removal of the entire above ground shoot) resulted in rapid resprouting. Furthermore, repeated resprouting was possible as each new shoot used the same, consistent proportion of remaining cotyledonary reserves.

We can exclude the possibility that large seed size in *Gustavia* is simply the result of resource needs to emerge from deep burial following scatter-hoarding, as suggested by Vander Wall (1993), as our experiment showed that within the range of natural scatter-hoarding (1–8 cm burial depths; Smythe 1978, Hopkins and

Graham 1983, Hallwachs 1986) burial did not affect the seedling size or the resprouting capacity of the plant. Seed burial at 15 cm however did affect both the timing of shoot emergence and the size of the initial shoot, though burial at depths this great may be rare under natural conditions.

How long are cotyledonary reserves retained by the seedling? Our study suggests that the importance of cotyledon reserves for resprouting may be limited to the first few weeks following shoot emergence. Comparison of seedling growth with and without cotyledon removal showed that cotyledons contributed slightly to subsequent seedling growth three weeks after shoot emergence, but the contributions had mostly disappeared by 15 wk post-emergence. Cotyledon use may in part be determined by the seedling's light environment, with perhaps more rapid assimilation of seed reserves in deep shade, or perhaps cotyledons persist longer if seeds are buried, and less prone to desiccation. Nonetheless, the contribution of cotyledons during the first few weeks of shoot emergence may be critical as this would be predicted to be the period when the probability of damage is highest; tissue loss to herbivores in tropical forests tends to be much higher on young leaves than on toughened fully expanded leaves (Coley and Barone 1996).

Detailed studies of seed fate of *Gustavia* carried out by Sork (1985, 1987) and Forget (1992), however, do not report observations of browsing and resprouting in this species. They may simply have missed the phenomenon; in the growing house resprout seedlings grew very quickly, often becoming fully expanded within six weeks of the original cut. Certainly, browsing and resprouting appear to be a likely explanation of Sork's (1987) finding that seedlings exposed to mammals were shorter than those within mammal exclosures. Since Sork's recensuses of seedlings were conducted only every 5–6 months, evidence of resprouting may have been difficult to detect.

Table 3. Survival, cotyledon loss, and resprouting frequency for naturally recruiting *Gustavia* seedlings at two sites on BCI. Barbour (BAR), $n = 100$ seeds, and Wheeler (WHE), $n = 100$ seeds.

		Census period					
	Site	Jun 94	Aug 94	Nov 94	Jan 95	Mar 95	Jun 95
Surviving seedlings	BAR	100	93	64	62	57	53
	WHE	–	100	92	76	63	60
With cots[1]	BAR	100	65	0	0	0	0
	WHE	–	100	57	0	0	0
Mean cots[2]	BAR	2.6	1.4	0	0	0	0
	WHE	–	2.4	1.3	0	0	0
Resprouts[3]	BAR	0	3	4	9	13	14
	WHE	–	0	1	10	12	17
Resprout (%)[4]	BAR	0	3	6	11	16	16
	WHE	–	0	1	13	17	27

[1] Number of seedlings with cotyledons attached.
[2] Mean number of cotyledon segments attached.
[3] Total number of seedlings with resprout shoots.
[4] Percent of seedlings alive in each census period resprouting.

Paradoxically, Sork (1987) and Forget (1992) both found that seedling damage and mortality in *Gustavia* were mainly caused by rodents that dig up germinating seedlings expressly to consume the cotyledons. Sork (1987) found that seedlings continued to be dug up by predators for more than a year after germination; Forget (1992) found that agoutis (*Dasyprocta punctata*) ate or nibbled on *Gustavia* cotyledons up to four months after seedlings germinated. If cotyledon reserves are particularly attractive to some herbivores, then why would they be retained for so long by the plant rather than mobilized? Perhaps a trade-off exists between the advantages of resprouting from cotyledons as against the additional predation risks associated with retaining them. Older seedlings that lack cotyledons are also capable of resprouting, which suggests that at some point in ontogeny a shift occurs in the location of stored reserves used for resprouting from cotyledons to roots.

Alternatively, if little resprouting from cotyledons does occur in the field, then large seed size in *Gustavia* may simply represent a dispersal reward, as suggested by Steele et al. (1993) for oak species. Since *Gustavia* seeds are primarily dispersed by scatter-hoarding agoutis (Forget 1992), large seeds may indeed have a dispersal advantage. Hallwachs (1994), found that agoutis cached proportionally more acorns and coconut chunks as weight increased, and hoarded heavier units further away. Our field data on *Gustavia* however do not suggest any dispersal advantage, perhaps because the year we carried out our study was atypical. 1994 appeared to be an extremely good fruiting year for *Gustavia* on BCI, and had the third highest total annual seed fall to sixty 0.25-m² seed traps recorded between 1986 and 1997 (S. J. Wright unpubl.). This super-abundance of fruit in 1994 presumably meant that many *Gustavia* seeds escaped dispersal/predation and germinated on the soil surface. In contrast, Forget's (1992) study was conducted in 1990, which had the lowest total fruitfall 1986–1997. Whereas > 50% of unburied seedlings survived one year in this study, none of Forget's unburied seedlings survived > 2 mo.

We have suggested that tolerance to cotyledon damage and the retention of cotyledonary reserves after full leaf expansion are general features shared by many tree species with seed reserves > 5 g and hypogeal germination (Harms and Dalling 1997, Dalling et al. 1997). The primary functions of large seed reserves in these species may therefore be for dispersal and for damage tolerance rather than for the tolerance or avoidance of unfavourable light conditions. The ability to manipulate *Gustavia* seed size without affecting either germination success or the seed-size to seedling size relationship indicates that this species would be ideal for further investigations of the dispersal versus establishment advantages of large seed size in scatter-hoarded species.

References

Andersson, C. and Frost, I. 1996. Growth of *Quercus robur* seedlings after experimental grazing and cotyledon removal. – Acta Bot. Neerl. 45: 85–94.

Armstrong, D. P. and Westoby, M. 1993. Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. – Ecology 74: 1092–1100.

Augspurger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. – J. Ecol. 72: 777–795.

Boot, R. G. A. 1996. The significance of seedling size and growth rate of tropical rain forest tree seedlings for regeneration in canopy openings. – In: Swaine, M. D. (ed.), Ecology of tropical forest tree seedings. UNESCO Paris and Parthenon Carnforth, pp. 267–282.

Clark, D. B. and Clark, D. A. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. – Ecology 66: 1884–1892.

Clark, D. B. and Clark, D. A. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. – Oikos 55: 225–230.

Clark, D. B. and Clark, D. A. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. – J. Ecol. 79: 447–457.

Coley, P. D. and Barone, J. A. 1996. Herbivory and plant defenses in tropical forests. – Annu. Rev. Ecol. Syst. 27: 305–335.

Croat, T. R. 1978. Flora of Barro Colorado Island. – Stanford Univ. Press, Stanford, CA.

Dalling, J. W., Harms, K. E. and Aizprúa, R. 1997. Seed damage tolerance and seedling resprout ability of *Prioria copaifera* ('El Cativo'). – J. Trop. Ecol. 13: 617–621.

Denslow, J. S. 1980. Notes on the seedling ecology of a large-seeded species of Bombacaceae. – Biotropica 24: 146–156.

Dirzo, R. 1984. Herbivory a phytocentric overview. – In: Dirzo R. and Sarukhán J. (eds), Perspectives in plant population ecology. Sinauer, Sunderland, MA, pp. 141–165.

Eichlin, T. D. 1995. A new Panamanian clearwing moth. – J. Lepid. Soc. 49: 39–42.

Forget, P.-M. 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). – Biotropica 24: 408–414.

Foster, S. A. and Janson, C. H. 1985. The relationship between seed size and establishment conditions in tropical woody plants. – Ecology 66: 773–780.

Grubb, P. J. 1996. Rainforest dynamics: the need for new paradigms. – In: Edwards, D. S., Booth, W. E. and Choy, S. C. (eds), Tropical rainforest research: current issues. Kluwer, Dordrecht, pp. 215–233.

Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). – In: Estrada, A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Junk, Dordrecht, pp. 285–304.

Hallwachs, W. 1994. The clumsy dance between agoutis and plants: scatterhoarding by Costa Rican dry forest agoutis. – PhD dissertation, Cornell Univ.

Hammond, D. S. and Brown, V. K. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropical forests. – Ecology 76: 2544–2561.

Harms, K. E. and Aiello, A. 1995. Seed-boring by tropical clearwing moths (Sessiidae): aberrant behavior or widespread habit? – J. Lepid. Soc. 49: 43–48.

Harms, K. E. and Dalling, J. W. 1997. Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. – J. Trop. Ecol. 13: 481–490.

Harms, K. E., Dalling, J. W. and Aizprúa, R. 1997. Regeneration from cotyledons in *Gustavia superba* (Lecythidaceae). – Biotropica 29: 234–237.

Holdridge, L. R., Grenke, W. G., Hatheway, W. H., Liang, T. and Tosi, J. A., Jr. 1971. Forest environments in tropical life zones. – Pergamon Press, New York.

Hopkins, M. A. and Graham, A. W. 1983. The species composition of soil seed banks beneath lowland tropical rainforests in North Queensland, Australia. – Biotropica 15: 90–99.

Janzen, D. H. 1971. Escape of juvenile *Dioclea magacarpa* (Leguminosae) vines from predators in a deciduous forest. – Am. Nat. 105: 97–112.

Janzen, D. H. 1976. Reduction of *Mucuna andreana* (Leguminosae) seedling fitness by artificial seed damage. – Ecology 57: 826–828.

Kelly, C. K. and Purvis, A. 1993. Seed size and establishment conditions in tropical trees; on the use of taxonomic relatedness in determining ecological patterns. – Oecologia 94: 356–360.

Leigh, Jr., E. G., Rand, S. A. and Windsor, D. M. 1982. The ecology of a tropical forest: seasonal rhythms and long-term changes. – Smithsonian Inst. Press, Washington.

Metcalfe, D. J. and Grubb, P. J. 1995. Seed mass and light requirement for regeneration in South-East Asian rain forest. – Can. J. Bot. 73: 817–826.

Prance, G. T. and Mori, S. A. 1979. Lecythidaceae. – Flora Neotrop. Monogr. 21.

Salisbury, E. J. 1942. The reproductive capacity of plants. – Bell, London.

Smythe, N. 1978. The natural history of the Central American agouti (*Dasyprocta punctata*). – Smithson. Contrib. Zool. 257: 1–52.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating in birds. – Ibis 113: 194–202.

Sonesson, L. K. 1994. Growth and survival after cotyledon removal in *Quercus robur* seedlings grown in different natural soil types. – Oikos 69: 65–70.

Sork, V. L. 1985. Germination response in a large seeded Neotropical tree species, *Gustavia superba* (Lecythidaceae). – Biotropica 17: 130–135.

Sork, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. – Ecology 68: 1341–1350.

Steele, M. A., Knowles, T., Bridle, K. and Simms, E. L. 1993. Tannins and partial consumption of acorns: implications for dispersal of oaks by seed predators. – Am. Midl. Nat. 130: 229–238.

Troup, R. S. 1921. The sylviculture of Indian trees. Vol. 1. – Oxford Univ. Press, Oxford.

Vander Wall, S. B. 1993. A model of caching depth: implications for scatterhoarders and plant dispersal. – Am. Nat. 141: 217–232.

Wilkinson, L., Hill, M. and Vang, E. 1992. SYSTAT: Statistics, Version 5.2 Ed. – Evanston, IL.

Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panamá. – Smithson. Contrib. Earth Sci. 29: 1–145.