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Damage Tolerance and Resprouting of Large-Seeded Trees and Lianas on Barro Colorado Island

Traits at the Extreme End of the Seed-Size Continuum

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ABSTRACT. Seed size varies over more than 4 orders of magnitude among Barro Colorado Island (BCI) plants. Traits with so much interspecific variation often play important roles in trade-off-mediated coexistence, interactions with enemies and mutualists, and other community-assembly processes. Here, we focus on the 27 largest-seeded species with diaspores >5 g. These include dicots, monocots, and a gymnosperm from 14 families and 10 orders. Observations and experiments suggest that the ability to resprout after a plant suffers damage and loses tissues—either before or after germination—may be a key ultimate evolutionary explanation for the largest seed sizes. Studies on BCI were among the first to show high levels of tolerance among large-seeded species to seed infestation and damage as well as the capacity of fragments of cotyledonary tissue to differentiate a seedling axis *de novo*. These observations are consistent with patterns found for large-seeded taxa in other tropical forests around the world.

Keywords: *Attalea rostrata*; big seeds; cotyledons; diaspore; functional traits; *Gustavia superba*; *Prioria copaifera*; seed; seed biology; traits

Many ecologists and evolutionary biologists have focused on understanding plant adaptations as causes and consequences of resource allocation patterns, life-history strategies, and habitat associations. The resulting functional trait classifications, such as the Leaf Economic Spectrum and Global Spectrum of Plant Form and Function, clearly organize species into concentrated regions of multidimensional trait space (Wright et al., 2004; Díaz et al., 2016). Seed size figures prominently in some of these classifications, which often include hundreds to thousands of species (e.g., Wright, et al., 2007; Wright, et al., 2010). Even so, seed size is only one characteristic of seeds, and on its own, it cannot account for all aspects of seed biology (e.g., Zalamea, 2024). Some seed traits are restricted to finite portions of the seed-size continuum, and variation in additional seed-biology traits exists at any point along the continuum. For example, Dalling et al. (2020) showed how plant species with similar-size seeds are nevertheless differentiated into groups of taxa that express coherent constellations of intercorrelated traits that together define a set of seed-defense syndromes. In this chapter, we focus on traits of the largest-seeded species on Barro Colorado Island (BCI).

Like several tropical biologists before us (e.g., Garwood, 1979; Sork, 1985; Forget, 1992; Kitajima, 1992), some of our curiosity was drawn toward the "big seeds" on

BCI. Seeds on BCI range in size from the dust-like propagules of several species of epiphytic orchids to comparatively behemoth diaspores of *Gustavia superba* (Lecythidaceae), *Prioria copaifera* (Fabaceae; Lopez, 2024), and *Tontelea passiflora* (Celastraceae), which all generally weigh >10 g, and some of which weigh >100 g (Harms and Dalling, 1997). BCI's largest-seeded taxa (species with diaspores >5 g) are broadly phylogenetically distributed among lineages: the 27 taxa with the largest fresh-mass diaspores on BCI include dicots, monocots, and a gymnosperm from 14 families and 10 orders (Table 1). Some phylogenetic clustering is apparent, with 8 of the 27 largest-seeded taxa in Fabales (a dicot order), 5 in Malpighiales (dicot), and 4 in Arecales (monocot). BCI's largest-seeded taxa have analogs in other biogeographic regions. For example, *G. superba* in Panama is an analog of *Idiospermum australiense* (Calycanthaceae; seed mass up to 225 g) in Australia (Edwards et al., 2001) and of *Carapa surinamensis* and *C. guianensis* (Meliaceae; seed masses up to 40 and 70 g, respectively) in Amazonia (de Souza Ferreira et al., 2017). At the extreme end of the seed-size trait axis, these species often share additional attributes that further distinguish them from small-seeded species.

In her review and synthesis of large seeds in tropical forests, Foster (1986) described several potential selective advantages that could account for their evolutionary origin or maintenance. For example, the energy and materials packed into large seeds could fuel the development of a deep tap root, the deployment of leaves into better-lit higher strata of the otherwise-dark understory, or the development of sufficiently extensive photosynthetic surfaces for future positive carbon gain. Large seedlings also could be advantageous for pushing up through a thick litter layer (Molofsky and Augspurger, 1992). Finally, Foster (1986) highlighted the traits that first drew our attention to BCI's largest seeds—that is, their unusual ability to tolerate severe damage—a common occurrence in tropical forest understories (Clark and Clark, 1989)—especially by replacing lost tissues from seed reserves.

SEED DAMAGE AND DAMAGE TOLERANCE IN THE FOREST ON BCI

Our experiments on the damage-tolerance capacity of seeds on BCI were motivated by observations of high rates of both partial seed consumption by vertebrates and insect infestation in some of the largest-seeded species. For *Prioria copaifera*, a survey of seed fate 2 months after dispersal revealed that in a high-density *Prioria* stand on the American Museum of Natural History (AMNH) trail, 30% of seeds that were classed as "apparently viable" had suffered partial seed removal by vertebrate seed predators. Insect infestation of seeds was also high, with 40% of 470 seeds with insect exit holes. *Prioria* seeds on BCI are infested by several insects—most frequently curculionid beetles (*Eubulus fulvosquamis*) but also sesiid moths (*Carmenta* sp.), tortricid moths (*Cryptaspasma persiana*), and an unidentified anthribid beetle and pyralid moth (Gripenberg et al., 2019; Gripenberg, 2024). Germination experiments in the greenhouse

confirmed that *Prioria* seeds can produce viable seedlings even with up to 8 insect exit holes from seed-boring insects, which most likely developed from eggs oviposited in the field before seed collection (Dalling et al., 1997). We do not know the stage of flower or fruit development when oviposition occurs.

Similar patterns characterized *Gustavia superba* (Figs. 1–3), in which exit holes from sesiid moths were observed in 27% of 463 seeds that successfully germinated in the greenhouse (Dalling and Harms, 1999; the moth was *Carmenta*

FIGURE 1. Intact *Gustavia superba* fruit on the forest floor on Barro Colorado Island. The large fruits are generally 7–10 cm in diameter (Pérez, 2008).

FIGURE 2. *Gustavia superba* fruit and seeds partially consumed by an agouti on Barro Colorado Island.

TABLE 1. Fresh diaspore masses for the 27 liana and tree species (indicated by superscripts L and T, respectively) with the largest diaspores on Barro Colorado Island (BCI), each with a fresh diaspore mass greater than 5 g, ordered by increasing mass. Individual diaspores generally have larger masses than their individual seeds per se (e.g., diaspore mass includes legume testas and palm endocarps). Accordingly, the list includes all species with fresh seed masses greater than 5 g on BCI. These data were extracted from S. Joseph Wright's unpublished long-term seed-traits dataset for BCI. Taxonomy was updated according to current names in the Global Biodiversity Information Facility (www.gbif.org) in March 2022; N = number of fresh diaspores measured.

Species	Family	Order	Mean ± st. dev. (g)	N
Andira inermis [T]	Fabaceae	Fabales	5.06 ± 5.52	28
Hymenaea courbaril [T]	Fabaceae	Fabales	5.27 ± 1.22	100
Socratea exorrhiza [T]	Arecaceae	Arecales	5.35 ± 1.41	30
Bactris major [T]	Arecaceae	Arecales	5.61 ± 1.71	20
Symphonia globulifera [T]	Clusiaceae	Malpighiales	6.03 ± 1.47	14
Brosimum utile [T]	Moraceae	Rosales	6.76 ± 2.38	25
Garcinia madruno [T]	Clusiaceae	Malpighiales	6.84 ± 1.49	76
Calophyllum longifolium [T]	Calophyllaceae	Malpighiales	6.84 ± 2.42	20
Macropsychanthus wilsonii [L]	Fabaceae	Fabales	7.00 ± 1.92	57
Fevillea cordifolia [L]	Cucurbitaceae	Cucurbitales	7.83 ± 2.12	36
Cuervea kappleriana [L]	Celastraceae	Celastrales	8.29 ± 1.17	13
Mucuna mutisiana [L]	Fabaceae	Fabales	8.43 ± 0.82	35
Beilschmiedia tovarensis [T]	Lauraceae	Laurales	8.58 ± 2.56	25
Quararibea pterocalyx [T]	Malvaceae	Malvales	9.14 ± 3.00	66
Astrocaryum standleyanum [T]	Arecaceae	Arecales	9.69 ± 1.55	25
Licania platypus [T]	Chrysobalanaceae	Malpighiales	9.87 ± 3.02	25
Gnetum leyboldii [L]	Gnetaceae	Gnetales	10.27 ± 1.76	40
Ocotea whitei [T]	Lauraceae	Laurales	13.32 ± 3.36	10
Gustavia superba [T]	Lecythidaceae	Ericales	13.35 ± 4.55	100
Attalea rostrata [T]	Arecaceae	Arecales	15.50 ± 4.41	25
Dipteryx oleifera [T]	Fabaceae	Fabales	15.94 ± 3.72	46
Entada gigas [L]	Fabaceae	Fabales	29.29 ± 7.24	47
Fairchildia panamensis [T]	Fabaceae	Fabales	33.88 ± 7.26	67
Omphalea diandra [L]	Euphorbiaceae	Malpighiales	37.58 ± 5.61	37
Prioria copaifera [T]	Fabaceae	Fabales	38.30 ± 19.98	30
Tontelea passiflora [L]	Celastraceae	Celastrales	68.93 ± 21.49	56
Pouteria fossicola [T]	Sapotaceae	Ericales	125.61 ± 48.58	22

foraseminis, Harms and Aiello, 1995). *Gustavia* seed production and survival in the field shows very high interannual variation. In some years, almost all seeds are consumed or scatter-hoarded, whereas in other years, seeds remain inside the indehiscent fruit, but germinate after the fruit material rots (J. W. Dalling, pers. obs.). In a field survey in 1994, when many *Gustavia* seeds germinated on the soil surface without being removed, 56% of 200 marked seedlings remained alive 10–12 months later, even though 21% of these survivors had been damaged and had resprouted.

COTYLEDONARY RESOURCE USE IN LARGE-SEEDED TREE SPECIES

The capacity for BCI's largest-seeded species to tolerate herbivory and physical damage was explored by Harms and Dalling (1997) in 13 tree species that varied in seed mass from 0.2 to 107 g. To simulate natural damage, each seedling shoot was excised 1 cm above the ground once the seedling had produced its first pair of fully expanded true leaves. As expected, species with epigeal germination (foliose or storage cotyledons borne >1

FIGURE 3. Old *Gustavia superba* fruit in the lab clearing on Barro Colorado Island. This fruit was never opened by an agouti; the adult *Carmenta foraseminis* (Sesiidae) moths that emerged from the seeds within this fruit left their pupal exuviae lodged in the fruit exocarp.

cm above the ground) were unable to recover following the cutting treatment. In contrast, the 5 species with hypogeal germination (cotyledons remaining on or below ground) and with seed mass >5 g successfully produced an aboveground resprout. Furthermore, 3 of these species survived sequential clipping events to produce resprouts multiple times. Therefore, some large-seeded species with hypogeal germination initially retain sufficient cotyledonary reserves to recover from aboveground damage that occurs soon after initial shoot formation. Short-term retention of cotyledonary reserves is likely to be an important tolerance trait because newly produced shoots and leaves that lack fully developed chemical and physical defenses are especially susceptible to herbivory (Coley, 1983; 2024).

Initial observations of resprouting success motivated more detailed follow-up studies with *Gustavia* and *Prioria*. These experiments explored the ability to recover from both seed and seedling damage, in species with large hypogeal cotyledons. In *Prioria*, seeds with 60% of initial reserves removed in a cutting treatment had a similar germination probability to intact seeds and remained capable of resprouting following shoot clipping. Furthermore, intact seeds retained sufficient seed reserves to produce up to 4 sequential resprouts (Dalling et al., 1997). For *Gustavia*, seedlings produced up to 8 sequential resprouts and cut seeds (up to 50% of seed mass removed) had >98% germination success (Dalling et al., 1999). Analysis of the seed and seedling shoot mass relationship showed that both intact seeds and seeds with 50% of their mass removed had almost identical responses to the shoot-clipping treatment. In both cases a consistent fraction of remaining seed mass (~10%) was allocated into each successive shoot. Overall, cotyledonary resource allocation from

Gustavia was remarkably invariant. Barberis and Dalling (2008) further found that cotyledon mass was used or reallocated at similar rates across a range of seed sizes and in both sun and shade, with ~20% of initial cotyledon mass remaining 9 weeks after true leaf development. They concluded that the changes in cotyledon mass in this species reflected a gradual transfer of stored reserves from the cotyledon to the roots (or shoots in the case of resprouting). Thus, although cotyledons are important for recovery from damage during establishment, their direct contribution toward undamaged seedling shoot growth appears to be somewhat limited after expansion of the first true leaves.

REGENERATION CAPACITY OF EXCISED SEED FRAGMENTS

Initial greenhouse experiments revealed the surprising capacity for *Gustavia* to generate seedlings from seed fragments. In a follow-up study, Harms et al. (1997) cut a single cotyledon from each of 35 recently germinated *Gustavia* seeds into half-sections that were proximal and distal to the embryonic axis. More than half of these excised cotyledons developed into new seedlings. Furthermore, seedlings did not just arise from differentiation of existing embryonic tissues; in 20% of the cotyledons, seedlings sprouted from both halves. Similar sprouting capacity has been observed on BCI for the large-seeded liana *Tontelea passiflora* (J. W. Dalling and K. E. Harms, pers. obs.) and in Australia for the tree *Idiospermum australiense* (Edwards et al., 2001). A further analysis of the germination capacity of cut cotyledons found similar responses for 7 Australian rainforest species with storage cotyledons and hypogeal germination (Harrington et al., 2005). While lacking anatomical evidence, these authors argued that this widespread germination capacity reflected somatic embryogenesis from potential meristematic buds that are scattered throughout cotyledonary tissue.

The capacity to develop an embryonic axis from cotyledonary tissue likely reflects an adaptation to survive partial seed consumption by insect and mammalian seed predators. As noted previously, seeds of *Gustavia* and *Prioria* are frequently partially eaten by vertebrates or are heavily infested by moths and beetles that use only a fraction of the seed's reserves during larval development. In addition, on BCI, scatter-hoarding rodents, such as agoutis (*Dasyprocta punctata*), frequently damage *Gustavia* seeds when extracting them from their indehiscent fruits, when digging up developing seedlings, or when moving seeds from cache to cache (Forget, 1992; Jansen et al., 2012). Furthermore, for species that lack the cotyledonary sprouting potential described here, scatter-hoarders can manipulate seeds to prevent germination and prolong seed availability. Jansen et al. (2006) reported that in French Guiana, red acouchies (*Myoprocta acouchy*) deliberately pruned the radicle and epicotyl of seeds of *Carapa procera* (Meliaceae), which prevented both further seedling development and cotyledonary decay, thus allowing seed reserves to be stored (and then consumed) over a longer period.

SEED DISPERSAL MAY FACILITATE OR FAVOR LARGE SEED SIZE

Janzen and Martin (1982: 19) evocatively described the large fruits that the Pleistocene "gomphotheres ate." Many of these fruits contain large, well-protected seeds, which mega-herbivore seed dispersers would have swallowed, defecated, and thereby dispersed. Even so, unless seeds themselves are the dispersers' reward, dispersal despite large seed size would not on its own provide the selective advantage to drive the evolution of exceptionally large seed sizes. In contrast, if large seed size enhances dispersal, for example, if scatter-hoarding rodents were to preferentially disperse larger seeds, selection could favor larger seeds. Several studies have now shown this to be the case. Hallwachs (1994) found that agoutis in Costa Rica cached proportionally more acorns or chunks of coconut endosperm with increasing size, and Jansen et al. (2004) observed that red acouchies in French Guiana removed larger *C. procera* seeds faster and farther, and they were more likely to scatter-hoard them, resulting in a higher probability of seedling establishment for larger seeds.

TRAIT SIMILARITIES AMONG THE LARGE-SEEDED SPECIES

Seed character syndromes reflect the co-occurrence or interdependency of traits that influence dispersal, dormancy, and germination requirements. For example, small-seeded species have advantages in fecundity—and consequently dispersal to many sites—that are offset by lower probabilities of seedling emergence and establishment success, as well as lower tolerance to drought, shade, or litter cover (Foster, 1986; Dalling and Hubbell, 2002; Engelbrecht et al., 2006; Muller-Landau, 2010). More recently, seed defenses have been integrated into these syndromes in recognition of the role that seed chemical and physical traits play in shaping seed dormancy and interactions with predators and pathogens (Dalling et al., 2020). Although absolute seed toughness tends to increase with seed size, investment in physical defenses is especially effective in small seeds (Fricke and Wright, 2016). The smallest seeds on BCI require 2000 times more energy per gram to break than the largest seeds, and the toughness advantage of small seeds reflects a physical scaling relationship independent of selection on defense traits. Therefore, for very large seeds, maximizing seedling recruitment by excluding seed predators through physical defenses may be less effective than tolerating them. It is notable that many of the largest-seeded tree and liana species on BCI lack especially hard protective structures. More generally, very large (>10 g) physically protected diaspores appear to be primarily a characteristic of palms (e.g., *Astrocaryum*, *Attalea*, *Phytelephas*), although very hard endocarps do occur in several non-palm large-seeded species on BCI (e.g., *Dipteryx panamensis* [Fabaceae], *Pouteria fossicola* [Sapotaceae], *Vantanea occidentalis* [Humiriaceae]).

However, even some palms may have evolved traits to tolerate partial consumption. Double-seeded endocarps are not uncommon in *Attalea rostrata*, in which each seed is separated by a hard septum. We once observed a 2-seeded endocarp produce a bruchid (inferred from the adult emergence hole) from 1 seed and a seedling from the other (Harms and Dalling, 2000). In any case, very little is known about potential chemical defenses in the largest tropical seeds, let alone the potential trade-offs between chemical defenses and resprouting abilities or other traits.

TOLERANCE TRAITS OF LARGE-SEEDED SPECIES MAY CONTRIBUTE TO COEXISTENCE

Despite its general absence from global assessments of plant traits, resprouting is an important phenomenon in tropical plant biology (e.g., Green and Juniper, 2004a, 2004b; Baraloto and Forget, 2007) and may be a crucial element in the trade-offs that could shape much of community assembly and plant coexistence in the high-diversity tropics. For example, resprouting ability could be an important component of the "competitive ability" in Rees and Westoby's (1997: 116) competition-colonization trade-off model for plant coexistence or of the tolerance of environmental stressors in Muller-Landau's (2010) tolerance-fecundity trade-off model. In saplings and sub-canopy trees in lowland and montane forests of Panama, stem-resprouting ability recently has been shown to be correlated with wood nutrient storage (Heineman et al., 2021). Similarly, here we highlight the importance of seed stores for seedling resprouting. Damage tolerance could help equalize recruitment success across the more-than-4-orders-of-magnitude variation in seed size observed in tropical forests because of opposing relationships between seed size and fecundity, and seed size and establishment probability.

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