An Advantage of Large Seed Size: Tolerating Rather than Succumbing to Seed Predators

Andrew L. Mack

Biotropica, Vol. 30, No. 4 (Dec., 1998), 604-608.

BIOTROPICA 30(4): 604–608 1998

An Advantage of Large Seed Size: Tolerating Rather than Succumbing to Seed Predators[1]

Andrew L. Mack[2]

Conservation International, Suite 200, 2501 M St., N. W., Washington, DC 20037, U.S.A.

ABSTRACT

Although large seeds might be more attractive and apparent to seed predators, large seed size could enable tolerance of seed predators. If seeds are large enough to sustain damage that would kill smaller seeds yet still produce viable seedlings, investment above the minimum by the maternal plant could be advantageous. I tested this hypothesis by removing 0–80 percent of the cotyledons of four large-seeded (4–180 g) tree species from Papua New Guinea and monitoring germination and seedling growth for eight months. All species showed little negative effect on seedling size with up to 50 percent removal of cotyledons and the larger species showed a less serious effect on growth than smaller-seeded species above 50 percent removal. Large-seeded species clearly have more than the minimum-required cotyledonary reserves. Observations of viable seedlings with heavily damaged cotyledons suggest that these species withstand attack by rodents and beetles by virtue of their large size.

Key words: cotyledons; germination; herbivory; maternal investment; Papua New Guinea; rodents; seed predation; seed size; tolerance.

TYPICALLY, PLANTS PRODUCE MANY MORE SEEDS THAN GERMINATE; mortality is high at the seed stage of a plant's life history. Hence, there is the potential for selection on seed traits. Seed size is one such trait, affecting several fitness components such as seed dispersal, nutrient reserves, and seed numbers (Mazer 1989; Westoby *et al.* 1992). Large seed size could have a detrimental effect on plant fitness if it increased seed predation (Janzen 1969, Mittelbach & Gross 1984, Kelrick *et al.* 1986). Because of this, large seed size might be viewed as a potential liability (*e.g.*, easier to find and more attractive to seed predators) that must be offset by other advantages such as greater reserves for the embryo.

Here I suggest the hypothesis that large seed size can present anadvantage if it satiates potential seed predators before they damage the embryo: that large seed size acts as a buffer, allowing the seed to be damaged while the embryo grows and becomes a self-sufficient seedling. A maternal investment in endosperm or cotyledonary tissues above the minimum required for sustenance of a vigorous seedling might act as a tolerance trait (Rosenthal & Kotanen 1994), or insurance against the ravages of potential seed predators. I make a simple test of this hypothesis with four species of trees and make suggestions for further investigation.

METHODS

Freshly-fallen seeds were randomly collected from four tree species at the Crater Mountain Biological Research Station, Chimbu Province, Papua New Guinea. With these species, fruit pulp was easily removed by hand without affecting germination (Mack, pers. obs.). All four species exhibit rapid germination and have thick, heavy storage cotyledons. All species have soft testas that are easily penetrated by rats and insects.

It was not possible to obtain adequate sample sizes of fresh seeds from a single tree, so seeds were collected from 2–4 trees for each species and mixed before treatment. After seeds were weighed, different amounts of the cotyledons were ablated with a scalpel. I visually attempted to remove amounts of cotyledon that would span 10–80 percent removal while taking care to avoid damaging or cutting close to the embryo. Then the seeds were reweighed and the actual amount of cotyledon removed was estimated by the weight difference. Seeds were then potted in a shadehouse in a random organization; pot positions were periodically rotated during the study to further minimize any potential position effects. Seedling growth was monitored for eight months.

The species and seeds used in the experiment are listed below with seed measurements from this study and notes on seed dispersers and seed predators based on three years of fieldwork (Mack 1995a, 1995b). Voucher specimens are deposited

---

[1] Received 19 June 1995; revision accepted 2 June 1997.

[2] Mailing address: P.O. Box 15, Weikert, Pennsylvania 17885, U.S.A. Email: a.mack@conservation.org

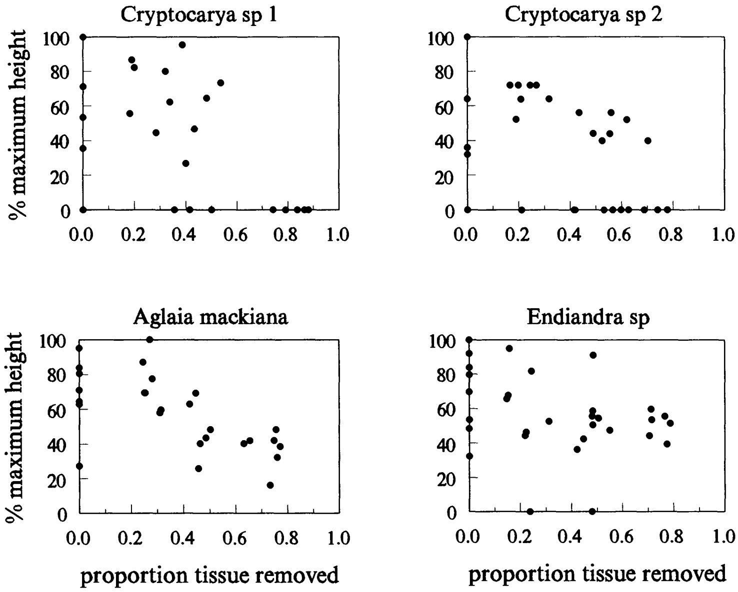

FIGURE 1. Plots of percent of maximum height of seedlings against proportion of cotyledon removed prior to germination. All linear regressions shown were significant ($P < 0.001$). The regression equations for each species are: *Cryptocarya* sp. 1 $y = -72x + 67$, $R^2 = 0.33$; *Cryptocarya* sp. 2 $y = -48x + 52$, $R^2 = 0.15$; *Aglaia* $y = -50x + 76$, $R^2 = 0.40$; *Endiandra* sp. $y = -28x + 66$, $R^2 = 0.11$.

at the Harvard University Herbaria (Cambridge, Massachussetts), University of Papua New Guinea (Port Moresby, PNG), and Forest Research Institute (Lae, PNG).

Aglaia mackiana Meliaceae (voucher AM # 256; see Pannell 1997). This species is primarily cassowary-dispersed. Seed mortality is low but seeds are commonly mined by unidentified beetles and gnawed by rats (mostly *Rattus verecundus*). Initial seeds: $\bar{x} = 116.6$ g, SD = 26.6, range = 61–169 g, $N = 28$.

Endiandra sp. Lauraceae (voucher D. D. Wright # 71). This species is dispersed by cassowaries and flying foxes (*Dobsonia moluccensis*). Seeds are gnawed by rodents and beetles (*Onthophagus* near *latenasutus* Arrow Scarabenae) [voucher deposited Academy of Natural Sciences] that chew 1 cm diameter tunnels through the cotyledons. Initial seeds: $\bar{x} = 126.1$ g, SD = 30.4, range = 58–184, $N = 32$.

Cryptocarya sp. 1 Lauraceae (voucher AM # 13). This, the smallest species studied, is dispersed in large numbers by cassowaries, but other frugivorous birds also disperse seeds. Seeds are not commonly attacked by insects or rats. Initial seeds: $\bar{x} = 5.3$ g, SD = 1.0, range = 3.3–7.5, $N = 26$.

Cyptocarya sp. 2 Lauraceae (voucher AM # 277). This species is dispersed by cassowaries as well as bats and hornbills (*Rhyticeros plicatus*). Some seeds are attacked by rats and beetles but less so than the previous species. Initial seeds: $\bar{x} = 8.8$ g, SD = 2.5, range = 5.1–13.5 g, $N = 31$.

Based upon growth rates, color of leaves, and size and texture of the cotyledons, the different species were judged to have depleted cotyledonary reserves and to be fully self-sufficient at approximately 185 days for *Aglaia*, 230 days for *Endiandra*, 165 days for *Cryptocarya* sp. 2, and 145 days for *Cryptocarya* sp. 1. I used the height of the tallest seedling of each species at these times to represent the observed maximum height and divided the height of each seedling by this value to yield the percent of maximum height for each individual (Fig. 1). This value enables across-species comparisons because the maximum height of the four species differed (99 cm for *Endiandra*, 62 cm for *Aglaia*, 22 cm for *Cryptocarya* sp. 1, and 25 cm for *Cryptocarya* sp. 2). Analysis of other measures (*e.g.*, actual heights or growth rates at different censuses) did not cause substantive changes in the results reported here.

RESULTS

I had predicted that the two smaller *Cryptocarya* species would show a more pronounced negative

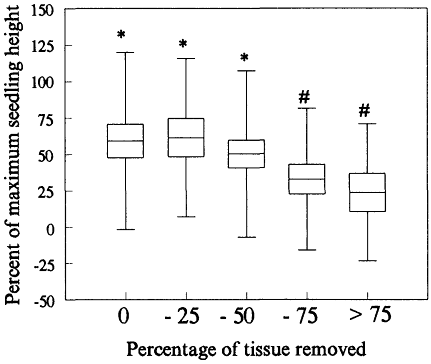

FIGURE 2. Hi-lo plots of percent of maximum seedling height among seedlings with different amounts of their cotyledons ablated. The central horizontal line represents the mean, the box represents ± 2 SE and the whisker represents ± 2 SD. Those categories with identical symbols (* or #) did not differ significantly (SNK test; see Results).

effect due to cotyledon ablation. The effect of proportion removed on seedling height was stronger in the smallest-seeded species (the largest negative regression coefficient) but the other small *Cryptocarya* species had a regression coefficient similar to that of the much larger *Aglaia* seeds (Fig. 1). However, removal of large amounts of cotyledon (>50%) caused greater mortality in the two smaller-seeded *Cryptocarya* species than in the two large-seeded species ($\chi^2 = 11.25$, df =1, $P < 0.001$; Fig. 1).

I pooled the data for all species and divided the seeds into five classes: those with 0, > 0 and ≤ 25, > 25 and ≤ 50, > 50 and ≤ 75, and > 75 percent removal. A one-way ANOVA revealed that there was a significant effect on the dependent variable, relative growth, due to amount of removal ($F = 6.48$, $SS = 1.97$, df = 4, $P < 0.0001$). Student-Newman-Keuls tests showed that the relative growth among all seeds with 0–50 percent of the cotyledon removed did not differ significantly, but that those with > 50 percent removal had significantly smaller seedlings than those with < 50 percent ($P < 0.01$; Fig. 2).

The overall pattern is evident in a three-dimensional plot of the data (Fig. 3). A surface was fitted to the plot using the distance-weighted least squares method with tension relaxed to 0.15 (SYSTAT, Wilkinson 1990). The upturned surface for large seeds indicates that the effect of cotyledon ablation on large seeds is less pronounced than for small seeds and the drop in growth and survivorship occurring around 50 percent removal is also evident in the lower right portion of the contour surface (Fig. 3).

DISCUSSION

Studies of seed predation have sometimes found that rodents prefer "large" seeds (Mittelbach & Gross 1984, Westoby *et al.* 1992). Alternatively, large seeds could prevent predation by small seed predators such as ants (Thompson 1987, Westoby *et al.* 1992). Studies of the benefits of large seeds have focused on the size and vigor of resulting seedlings (*e.g.*, Zhang & Maun 1993). However, the literature on this topic (reviewed by Westoby *et al.* 1992) mostly deals with temperate floras where virtually all species have seeds weighing less than 5 grams (*e.g.*, Baker 1972, Mazer 1989, Westoby *et al.* 1992, Jurado *et al.* 1991). Little attention has been devoted to the possibility that large seeds enable plants to tolerate damage (Rosenthal & Kotanen 1994), probably because few studies have examined floras where truly large seeds occur.

Large cotyledons or endosperm can protect the embryo by satiating potential seed predators before these agents damage the embryo. "Satiation" here includes both physically filling the rodent's gut or reaching some maximum tolerable amount of toxic secondary compounds contained in the consumed tissues. In the largest species studied, up to 141 g of cotyledons could be removed without killing the seed. This amount could certainly satiate most seed-gnawing rodents at the study site. Eleven species of rodent have been recorded at the site (D. D. Wright, pers. comm.). Nine of these typically weigh less than 120 g, one species averages 212 g, and one species weighs over 500 g on average (Flannery 1995). Viable, partially-gnawed seeds are commonly found (Mack, pers. obs.). Likewise, large seed size makes it unlikely that rodents will carry seeds to a cache site. In an Australian rain forest, very large seeds are less likely to be moved by rodents than smaller seeds (Osunkoya *et al.* 1994). After grazing on a seed, it is likely a rodent will abandon it. Established seedlings of the two largest species in this study are commonly found growing from partially-gnawed seeds (Mack, pers. obs.).

The situation is similar where beetles mine the storage tissue. If the storage tissue is large in volume, tunnelling scarab beetles can extensively feed and tunnel through this tissue without lethally encountering the seed embryo. Heavily-mined cotyledons were commonly observed on young seed-

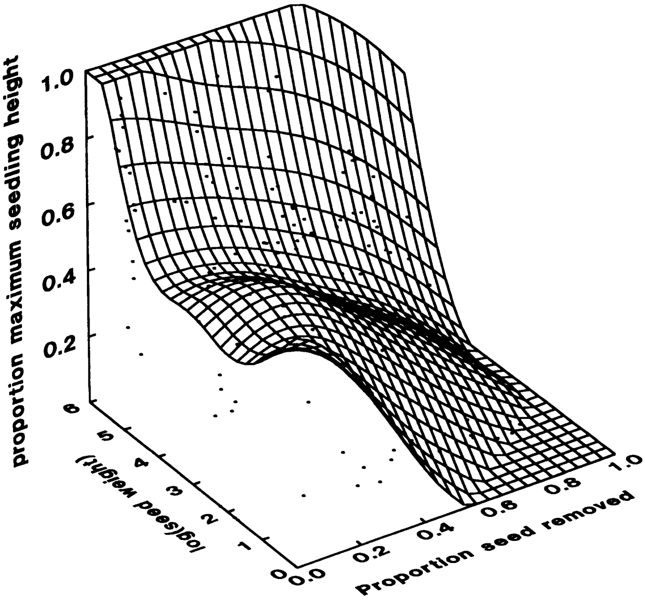

FIGURE 3. Three-dimensional plot of initial seed size (z axis), proportion of seed ablated (x axis) and percent of maximum height of seedlings (y axis). Data for all four species are pooled (N = 117) and a contour surface fitted with a distance-weighted least squares procedure.

lings of the two largest species. This advantage would only apply to species that exhibit rapid germination and do not remain dormant longer than it would take for a lethal amount of tissue to be damaged.

In all four species studied, seedling growth was not significantly different among seeds that had 0–50 percent of the cotyledon removed (Fig. 3), suggesting there is greater maternal investment in the cotyledons among these species than the minimum necessary to produce a healthy seedling. Despite heavy damage, seeds still yield viable seedlings (Figs. 1 and 3).

There are several caveats. Seedling growth was measured in a shadehouse, not under true field conditions; and the effect of cotyledon removal in the field could differ. However, numerous field observations (pers. obs.) of healthy seedlings with heavily damaged cotyledons indicate that these species can thrive despite levels of damage comparable to those of the manipulated seeds in this study. I did not measure naturally-occurring levels of damage. This would have meant weighing fresh seeds and re-weighing them later (losses due to boring beetles are otherwise difficult to measure) after weeks in the field. This creates complications because germinating seeds would need to be uprooted and other factors (*e.g.*, dessication, metabolism) significantly affect weight change over longer time periods than the manipulation. Such analyses were beyond the scope of this study but should be incorporated into further examinations. Lastly, only a few species were studied here. Future studies should examine a large number of unrelated species; ideally, the contour of a plot such as Figure 3 should be derived from mean values for different-sized species.

This study adds a potential advantage to large-seededness to those described by Foster (1986) in a review of large-seeded tropical trees. Maternal investment in storage tissue might increase fitness through tolerance of otherwise lethal levels of herbivory (predation) in smaller seeds as well as the recognized advantages to seedling vigor. A large number of studies have addressed the variety of factors that can affect the evolution of seed size and the trade-offs in maternal investment in seed size versus seed number (reviewed by Shaanker *et al.* 1988). These data are not intended to claim that large seeds have evolved in these species solely due to a selective benefit to large seeds surviving damage. However, this potential benefit of large-seededness merits further study. Many experiments measuring seed size versus number have been conducted in controlled greenhouse environments where seed predators are excluded. Where there are seed "predators" that reject seeds upon satiation, there could be significant selection in favor of seeds that exceed the satiation threshold. Future studies of maternal trade-offs in seed size versus number should examine this aspect, particularly with very large-seeded species.

ACKNOWLEDGMENTS

I thank the University of Papua New Guinea for sponsoring my residency in PNG and the Wildlife Conservation Society, the Douroucouli Foundation, and the National Science Foundation (BSR 89–0399) as principal financial supporters. I thank K. Ickes and J. H. Jessen for help in the field, Ronda J. Green, S. J. Mazer and D. D. Wright for comments on the manuscript, and B. D. Gill for identifying a beetle specimen.

LITERATURE CITED

Baker, H. G. 1972. Seed mass in relation to environmental conditions in California. Ecology 53: 997–1010.

Flannery, T. F. 1995. Mammals of New Guinea. Cornell University Press, Ithaca, New York.

Foster, S. A. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. Bot. Rev. 52: 260–299.

Janzen, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. Evolution 23: 1–27

Jurado, E., M. Westoby, and D. Nelson. 1991. Diaspore weight, dispersal, growth form and perenniality of central Australian plants. J. Ecol. 79: 811–830.

Kelrick, M. I., J. A. MacMahon, R. R. Parmenter, and D. V. Sisson. 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use. Oecologia (Berl) 68: 327–337.

Mack, A. L. 1995a. Seed dispersal by the Dwarf Cassowary, *Casuarius bennetti,* in Papua New Guinea. Ph. D. Dissertation, University of Miami, Miami, Florida.

———. 1995b. Distance and non-randomness of seed dispersal by the dwarf cassowary, *Casuarius bennetti.* Ecography 18: 286–295.

Mazer, S. J. 1989. Ecological, taxonomic, and life history correlates of seed mass among Indiana dune angiosperms. Ecol. Monogr. 59: 153–175.

Mittelbach, G. G., and K. L. Gross. 1984. Experimental studies of seed predation in old-fields. Oecologia (Berl) 65: 7–13.

Osunkoya, O. O., J. E. Ash, M. S. Hopkins, and A. W. Graham. 1994. Influence of seed size and seedling ecological attributes on shade-tolerance of rain-forest tree species in northern Queensland. J. Ecol. 82: 149–163.

Pannell, C. 1997. In press. A new, cassowary-dispersed, species of *Aglaia* (Meliaceae, section Amoora) from Papua New Guinea. Kew Bull.

Rosenthal, J. P., and P. M. Kotanen. 1994. Terrestrial plant tolerance to herbivory. Trends Ecol. Evol. 9: 145–148.

Shaanker, R. U., K. N. Ganeshaiah and K. S. Bawa. 1988. Parent-offspring conflict, sibling rivalry, and brood size patterns in plants. Annu. Rev. Ecol. Syst. 19: 177–205.

Thompson, K. 1987. Seeds and seed banks. New Phytol. 106: 23–34.

Westoby, M., E. Jurado, and M. Leishman. 1992. Comparative evolutionary ecology of seed size. Trends Ecol. Evol. 7: 368–372.

Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT, Evanston, Illinois.

Zhang, J., and M. A. Maun. 1993. Components of seed mass and their relationships to seedling size in *Calamovilfa longifolia.* Can. J. Bot. 71: 551–557.