

SHORT COMMUNICATION

## Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas

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In her review of the adaptive value of large seed size for tropical trees of moist forests, Foster (1986) listed several potential advantages of large seeds. One advantage to having large seed reserves may be to enhance seedling tolerance to herbivory and to damage by providing energy and material for tissue replacement (Foster 1986). Phylogenetically independent contrasts of a range of Australian species have shown that large-seeded species generally tolerate defoliation better than smaller-seeded species (Armstrong & Westoby 1993). However, such comparative experiments are lacking for tropical woody species.

The capacity to tolerate herbivory and physical damage may be especially important in tropical forests. Denslow (1980) found severe homopteran damage to the apical meristems of 66% of the seedlings of a bombacaceous tree species of the rainforest in Antioquia, Colombia. Clark & Clark (1985, 1989, 1991) have shown that severe damage from falling debris and herbivores is widespread and common among seedlings in lowland rainforest of Costa Rica. For example, 82% of model seedlings were 'knocked over, flattened, or uprooted' in a 1-y experiment (Clark & Clark 1989). Furthermore, very young seedlings are likely to be especially vulnerable, since many herbivorous insects prefer newly expanded leaves (Coley 1983).

In this study we asked: Are large-seeded woody species of moist tropical forests better able to tolerate severe seedling damage than smaller-seeded woody species? We evaluated this question by determining the resprouting

Table 1. Seed, seedling and resprout characteristics of large-seeded trees from Barro Colorado Island, Panamá. Smaller-seeded species that failed to resprout appear in the footnotes to this table.\* Species are arranged in decreasing order by seed mass.

Species [Family]	Mean seed mass* (g) ± SE (n)	Mean aboveground dry mass of initial seedling (g) ± SE (n)	Mean aboveground dry mass of first resprout (g) ± SE (n)	Mean number of sequential clipping events that yielded ≥ one resprout <sup>c</sup> (Range)	Percentage of germinated seeds that resprouted a given number of times after clipping events (i.e., clipping the initial aboveground shoot and subsequent resprout shoots)		
					≥once	≥twice	>three times
<i>Prioria copaifera</i> Griseb. [Fabaceae]	107.6 ± 4.0 (31)	2.8 ± 0.3 (22)	3.0 ± 0.3 (17)	2.1 (0-4)	81	81	38
<i>Custavia superba</i> (Kunth) Berg [Lecythidaceae]	14.4 ± 1.2 (33)	0.4 ± 0.1 (11)	0.4 ± 0.1 (11)	3.6 (2-8)	100	73	73
<i>Ocotea whitei</i> <sup>a</sup> Woodson [Lauraceae]	7.3 ± 0.3 (45)	0.3 ± 0.0 (45)	0.2 ± 0.0 (37)	N.D. <sup>c</sup>	86	N.D.	N.D.
<i>Beilschmiedia pend- ula</i> (Sw.) Hemsl. [Lauraceae]	5.5 ± 0.1 (45)	N.D.	N.D.	N.D.	26	N.D.	N.D.
<i>Rhacoma acumina- ta</i> (R. & P.) Planch. & Tr. [Clusiaceae]	5.0 ± 0.2 (33)	0.4 ± 0.0 (43)	0.3 ± 0.0 (37)	1.8 (0-3)	91	70	16

\* Smaller-seeded species that did not resprout: *Anacardium excelsum* (Bertero & Balb.) Skeels [Anacardiaceae] 3.85 ± 0.30 g (n = 17); *Dipteryx panamensis* (Pitt.) Reev. & Mell [Fabaceae] 2.73 ± 0.06 g (n = 146); *Viola nobilis* A. C. Smith [Myristicaceae] 2.48 ± 0.03 g (n = 100); *Brosimum alicastrum* (Pitt.) Berg [Moraceae] 1.23 ± 0.02 g (n = 198); *Cybania latifolia* Kunth [Sapindaceae] 0.76 ± 0.06 g (n = 150); *Tachigaita versicolor* Standl. & L. O. Wms. [Fabaceae] 0.69 ± 0.01 g (n = 25); *Ormosia macrocalyx* Ducke [Fabaceae] 0.42 ± 0.01 g (n = 54); *Tetragastris panamensis* (Engler) O. Kuntze [Bursaceae] 0.22 ± 0.02 g (n = 14).

<sup>b</sup> Fresh mass of seed reserves and embryo only.  
<sup>c</sup> The total number of sequential clipping events that resulted in at least one resprout shoot; does not include the first non-resprout seedling shoot that was initially clipped.

<sup>d</sup> Seed reserves had not been completely utilized by the end of the experiment.

<sup>e</sup> Only 44% of the initial seed reserves had been used when the experiment was terminated.  
N.D. = Not determined.

responses of seeds from 13 dicotyledonous tree species on Barro Colorado Island (BCI), Panamá. Mean fresh seed mass (embryo plus storage tissue without seed coat and protective structures) ranged from 0.2–107.6 g among species (Table 1).

In order to test for responses to seedling damage, we placed 24–45 seeds of each species listed in Table 1 in pots filled with forest soil in a screened growing house on BCI. The seeds for each species were collected from the forest floor from beneath several adult trees and were then divided evenly into three lots and placed into three separate 20-cm diameter pots. Once germinated, seeds required a species-specific amount of time to produce seedling shoots with two fully expanded leaves (2–5 wk, depending on the species). After each seedling had produced its first pair of leaves, we clipped off the above-ground shoot at 1 cm above the soil surface, mimicking complete above-ground herbivory or severe damage from falling debris or trampling. Seedlings that subsequently appeared through resprouting were treated in the same manner.

We found that only the largest seeds, all with hypogeal storage organs, are capable of resprouting after damage to the seedling. Five species, each with a mean seed mass of  $\geq 5$  g, resprouted and produced functional new seedlings with at least one pair of fully expanded leaves after clipping (Table 1). Furthermore, many individuals of these large-seeded species were capable of sequentially resprouting many times. In contrast, the eight species with mean seed masses of  $< 5$  g were unable to resprout after clipping (Table 1). All seedlings that failed to resprout perished after clipping.

In agreement with the general pattern of large-seeded, hypogeal species being capable of resprouting, seedlings of *Eperua grandiflora* (Fabaceae) a Neotropical tree, and of *Mucuna andreana* (Fabaceae), a neotropical liana, are capable of resprouting after damage (Forget 1992, Janzen 1976, respectively). Both of these species have large seeds (*E. grandiflora*, 19–84 g; *M. andreana*, 5–10 g) with hypogeal cotyledons.

Failure of the smaller-seeded species (Table 1) to resprout may be due to the complete expenditure of seed reserves in developing an initial functional seedling. In addition, all but one of these eight smaller-seeded species have epigeal cotyledons (*Brosimum alicastrum* has hypogeal cotyledons); the raised cotyledons of these species are as exposed to physical damage as seedling shoots and, if the seedling shoot is lost, cannot contribute to the production of a resprout. In contrast, the five large-seeded species capable of resprouting all have hypogeal storage organs as seedlings, *i.e.*, cotyledons or a modified hypocotyl (as in the case of *Rhedia acuminata*) remain on or below the soil surface after germination.

The seed size that any particular plant species adopts is the result of many (sometimes conflicting) selective pressures, trade-offs, and compromises (Foster 1986, Hammond & Brown 1995, Harper *et al.* 1970, Westoby *et al.* 1992). In order to better understand the outcome of these interactions further studies

are needed to determine the consequences of adopting particular seed sizes under a range of environmental conditions.

Is there a minimum critical seedling size (requiring a minimum seed size) necessary for establishment and survival in the shaded understorey? Kohyama & Grubb (1994) and Metcalfe & Grubb (1995) have demonstrated that some shade-tolerant trees have very small seeds, suggesting that shade-tolerance *per se* may not necessarily impose a minimum critical seed size.

Is there a minimum critical seed size necessary for germinating through leaf-litter of a given depth? Molofsky & Augspurger (1992) found that in a comparison of establishment across six tree species on BCI, smaller-seeded species were more negatively affected by litter.

Is there a minimum critical seed size (combined with the appropriate seedling morphology) necessary for a seedling to be capable of resprouting? We have shown that in a sample of BCI's tree flora, only the very large-seeded species (embryo plus seed reserves  $\geq 5$  g) with hypogeal storage organs are able to tolerate extreme seedling damage by resprouting. Furthermore, many large seeds are capable of producing multiple, sequential resprouts, suggesting that much of the seed reserves in these species may be unnecessary for the production of the initial seedling. Further studies are needed to determine the generality of each of these patterns.

When all potential advantages of having large cotyledons are considered, are most large-seeded species similar to *Quercus robur* in which the advantages of large cotyledons seem to be due mostly to the attraction of seed dispersers as opposed to enhancing seedling performance (Andersson & Frost 1996)? Given the great range in seed sizes, even among shade-tolerant tropical woody species (Foster & Janson 1985, Metcalfe & Grubb 1995), the relative influences of the many potential advantages of large seed reserves are likely to differ among individual species. For example, for a given species, the component of fitness not due to resprouting probably follows a curve of diminishing returns with increasing seed size. The fitness gains from increasing seed size due to resprouting may also be characterized by a curve of diminishing returns. However, if the returns from tolerance of herbivory and damage are greater than the returns from other advantages at the largest seed sizes, then advantages due to resprouting may explain the evolution of seed sizes beyond those that would arise if resprouting did not occur.

If damage tolerance confers an advantage on very large seeds, an answer to the question, 'Why are very large-seeded species (*i.e.*, embryo plus seed reserve mass  $\geq 5$  g) rare in forests outside the tropics?', remains to be determined. In addition, since large seeds require hypogeal storage organs to resprout, comparative phylogenetic studies are needed to assess the extent to which hypogeal seedling morphology facilitates the evolution of large seed size and *vice versa*.

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## LITERATURE CITED

- ANDERSSON, C. & FROST, I. 1996. Growth of *Quercus robur* seedlings after experimental grazing and cotyledon removal. *Acta Botanica Neerlandica* 45:85–94.
- ARMSTRONG, D. P. & WESTOBY, M. 1993. Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. *Ecology* 74:1092–1100.
- Clark, D. B. & Clark, D. A. 1985. Seedling dynamics of a tropical tree: impacts of herbivory and meristem damage. *Ecology* 66:1884–1892.
- CLARK, D. B. & 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. & CLARK, D. A. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology* 79:447–457.
- COLEY, P. D. 1983. Herbivory and defense characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53:209–233.
- DENSLOW, J. 1980. Notes on the seedling ecology of a large-seeded species of Bombacaceae. *Biotropica* 12:220–222.
- FORGET, P.-M. 1992. Regeneration ecology of *Eperua grandiflora* (Caesalpinaceae), a large-seeded tree in French Guiana. *Biotropica* 24:146–156.
- FOSTER, S. A. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review* 52:260–299.
- FOSTER, S. A. & JANSON, C. H. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66:773–780.
- HAMMOND, D. S. & BROWN, V. K. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropical forests. *Ecology* 76:2544–2561.
- HARPER, J. L., LOVELL, P. H. & MOORE, K. G. 1970. The shapes and sizes of seeds. *Annual Review of Ecology & Systematics* 1:327–356.
- JANZEN, D. 1976. Reduction of *Mucuna andreana* (Leguminosae) seedling fitness by artificial seed damage. *Ecology* 57:826–828.
- KOHYAMA, T. & GRUBB, P. J. 1994. Below- and above-ground allometries of shade-tolerant seedlings in a Japanese warm-temperate rain forest. *Functional Ecology* 8:229–236.
- METCALFE, D. J. & GRUBB, P. J. 1995. Seed mass and light requirements for regeneration in Southeast Asian rain forest. *Canadian Journal of Botany* 73:817–826.
- MOLOFSKY, J. & AUGSPURGER, C. K. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73:68–77.
- WESTOBY, M., JURADO, E. & LEISHMAN, M. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology & Evolution* 7:368–372.

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