Seed damage tolerance and seedling resprouting ability of *Prioria copaifera* in Panamá

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ABSTRACT. Germination and seedling resprouting capacity of the very large-seeded tree species
Prioria copaifera Griseb. (Fabaceae) was studied in the seasonally moist forest of Barro Colorado
Island, Panamá. Seeds with 60% of their cotyledonary mass removed did not suffer a reduced
probability of germination compared to unmanipulated seeds and seeds infested with up to eight
insect larvae germinated às well as uninfested seeds. Unmanipulated seeds were able to consecut-
ively produce up to four functional resprout shoots after excision of the initial, and subsequent,
fully expanded shoots. Even seeds with up to 60% of their reserves removed showed some capacity
to resprout. Less than 10% of seeds we encountered in the field 2 mo after the end of the fruiting
season were in a viable state, with the majority (55%) of mortality attributable to insect or patho-
gen damage. Of the 46 seeds that were viable, 30% had suffered partial removal of seed reserves
similar to our manipulation treatments. These results indicate that *P. copaifera* seeds are capable
of tolerating severe seed and shoot damage. The selective advantage conferred by damage toler-
ance may in part have contributed to the evolution of large seed size in this species.

KEY WORDS: El Cativo, Panamá, *Prioria copaifera*, resprout, seed predation, seed size, seedling
damage

INTRODUCTION

In contrast to most other ecosystems, tropical moist forests typically harbour
some species with extremely large seeds (stored energy reserves > 10 g). While
the adaptive significance of large seed size in tropical forests is not yet well
understood, most authors argue that large seed size is advantageous in the
shady understorey (Foster & Janson 1985, Hammond & Brown 1995, Snow
1971, Troup 1921; but see Kelly & Purvis 1993). For instance, Foster (1986)
argued that large seed reserves might permit prolonged dormancy or quies-
cence of ungerminated seeds under unfavourable light conditions, might be
used for the construction of large amounts of photosynthetic tissue in order to
maintain a positive net energy balance, or might allow seedling growth into
higher light intensity strata. She also argued that, for persistent seedlings in
the understorey, large seed size might be associated with high levels of invest-
ment into chemical defence compounds, or may enhance seedling tolerance to

herbivory and damage by providing energy for tissue replacement. Few of these potential benefits of large seed size have been examined experimentally (Westoby *et al.* 1992).

The persistence of apparently energy rich cotyledons *after* the development of a functional seedling indicates that seed reserves from large seeds are not always immediately exhausted. Growing-house experiments with *Gustavia superba* (Lecythidaceae) have shown that the initial seedling above-ground mass accounts for only about 30% of cotyledonary mass, independent of initial seed size (J. Dalling & K. Harms, unpubl. data). This demonstrates that some large-seeded species may not use all of their reserves to immediately produce the largest possible seedling and this may be a common characteristic of large-seeded species (Harms & Dalling 1997).

Large seed reserves may be an adaptation to high probabilities of pre-germination damage from seed predators, or to high probabilities of physical damage and herbivory to establishing shoots. Most, if not all, large-seeded species suffer attack from insect or vertebrate seed predators, including those that are physically protected by hard seed coats or endocarps (*e.g.*, the palm *Scheelea zonensis* (Bradford & Smith 1977) and the legume *Dipteryx panamensis* (DeSteven & Putz 1984)), or that have hard endosperm (*e.g.*, the 'vegetable ivory palm', *Phytelephas aequatorialis* (Johnson *et al.* 1995)), or that are chemically protected, (e.g., the nutmeg *Virola surinamensis*, that has 15% of dry weight in tannins (Howe *et al.* 1985)). In most cases, intense seed predation probably selects for predator escape through increased seed production, which is neces-sarily concomitant with reduced seed size if the overall reproductive invest-ment remains the same (Janzen 1969, Smith & Fretwell 1974). However, Janzen (1969) noted that in some forest habitats minimum seed size might be set by seedling establishment requirements and that insect seed predation might select for even larger seeds with very high probabilities of germination of the few that survive.

Establishing seedlings, with immature leaves, are especially vulnerable to attack by herbivores (Coley 1983), and all seedlings growing in the understorey and at gap edges are vulnerable to damage from litter fall (Clark & Clark 1991). However, surprisingly few estimates have been made of the intensity and consequences of seedling herbivory or physical damage. In demographic studies that include seedlings, they are generally only recorded as being 'alive' or 'dead' and seedling mortality can rarely be ascribed to specific agents.

In this study we examined the germination, the initial seedling production, as well as the seed and seedling damage tolerance, of *Prioria copaifera* Griseb. (Fabaceae; voucher specimen T. B. Croat 6860, Missouri Botanical Garden Herbarium). *Prioria copaifera*, known in Panamá as 'El Cativo', is the largest-seeded tree species on Barro Colorado Island (BCI), Panamá, produces single-seeded legumes (Croat 1978), and is one of the most important timber species in Panamá (INRENARE 1990). Although *P. copaifera* typically occurs as the dominant species on seasonally inundated lowland soils (Holdridge & Budowski

1956, Lamb 1953), it also occurs, as on BCI, as a less common component of species-rich forest on well-drained upland soils (Condit *et al.* 1993). Specifically, we examined (i) the capacity of *P. copaifera* seeds to tolerate damage from insect larvae, (ii) whether initial shoot size in *P. copaifera* was positively related to seed mass, or whether smaller seeds compensated for their size by producing disproportionately larger shoots, (iii) the capacity of *P. copaifera* seeds, under growing-house conditions, to resprout after complete shoot removal (simulating severe herbivory or physical damage), and (iv) the frequency and agents of *P. copaifera* seed damage in the field.

STUDY AREA

The study was carried out in seasonally moist tropical forest on Barro Colorado Island (BCI), in central Panamá. Rainfall on BCI averages 2600 mm y^{-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 by Leigh *et al.* (1982). Isolated *P. copaifera* trees grow on BCI in continuously wet sites bordering Lake Gatun, but the most dense stands are found on the well-drained upland plateau of the 50-ha Forest Dynamics Project plot (Condit *et al.* 1993) and on gentle slopes along the AMNH and Wheeler trails.

METHODS

Growing-house experiments

On 23 May 1994, 114 seeds of *P. copaifera* were collected from the ground within a clump of *c.* 20 reproductive individuals along the AMNH trail on BCI. Seeds were weighed and randomly assigned into four treatments: (i) intact seeds with no manipulation, *i.e.*, uncut; (ii) 20% removal (the seed mass was reduced by 20% by cutting off portions of the cotyledons and pericarp distal to the embryo); (iii) 40% removal; and (iv) 60% removal (Table 1).

The uncut and cut seeds were assigned randomly to six 1000-cm^2 seed-trays containing a 2 : 1 mixture of forest soil and sand and placed on a shaded bench

Table 1. Initial and post-cutting mean seed mass (g) for seeds of *Prioria copaifera*, in four seed mass removal treatments, in an experiment to examine resprouting capacity in a growing-house on Barro Colorado Island, Panama.

Treatment % removal	Seed mass	Mean	SD	n	Range
0	uncut	107.6	22.4	31	65.3–145.7
20	pre-cut	96.4	27.9	29	47.8–171.6
	post-cut	75.9	21.4		37.3–133.2
40	pre-cut	90.9	26.4	28	37.4–151.7
	post-cut	55.0	15.9		24.0–85.6
60	pre-cut	86.6	40.0	26	28.6–157.5
	post-cut	30.9	11.7		12.3–70.7

in a fully-screened growing-house in the laboratory clearing on BCI. Mid-day spot measurements of photosynthetically active radiation made over the seedlings on three days with a LI-COR quantum sensor varied between 2–10 μmol m^{-2} s^{-1}. Seed-trays were watered daily and seed germination was recorded weekly. After 3 mo, roots reached the bottoms of the seed-trays and all seeds were transplanted into individual 3-litre plastic pots.

The initial cohort of seeds to germinate was monitored twice-weekly to determine the time required from the emergence of an aboveground sprout until the first leaf pair had just fully expanded (*i.e.*, the shoot was fully functional). This time period (4 wk) was highly consistent among seedlings and subsequently we harvested all shoots at 4 wk after their initial emergence. This allowed us to remove shoot tissue that was almost entirely constructed from seed reserves.

To examine the role of seed reserves after extreme herbivory or physical damage, 4-wk old shoots were cut off at the base of the stem, close to the cotyledonary connection. The harvested shoots were dried in an oven at 60 °C for 1 wk and were weighed. Resprout shoots were treated in the same way, with each subsequent resprout shoot harvested 4 wk after its emergence above the soil. The experiment ended when no new shoots were initiated (after 38 wk). We noticed that insect exit holes (holes made by emerging insects that must have been present inside the seeds when they were collected) appeared through the pericarps of some of the seeds during the course of the experiment. Therefore, upon termination of the experiment, seeds were examined for insect damage and all insect exit holes through the pericarp of each seed were counted.

Field observations

In early August 1994, *c.* 2 mo after the fruiting season, and 1 mo after the last seeds had germinated in the growing-house, we examined all *P. copaifera* seeds within four haphazardly-placed 25-m^2 plots beneath the same stand of *P. copaifera* trees from which we collected seeds for the experiments on the AMNH trail on BCI. Seeds were categorized as vertebrate-killed, non-viable, apparently viable, and germinated, and the number of insect exit holes visible through each pericarp was recorded. Vertebrate-killed seeds included all large seed fragments (>75% of pericarp remaining) from which the cotyledons were missing. Tooth marks were apparent on many of these seed fragments. Although *P. copaifera* pericarps are relatively resistant to decay and may remain on the soil surface for 6 mo after dispersal, we may have underestimated predation in the vertebrate-killed category because some seeds may have been completely destroyed by seed predators. Non-viable seeds had intact pericarps, but the entire cotyledonary mass was rotten. Apparently-viable seeds contained at least some viable cotyledonary tissue. Some apparently-viable seeds had suffered partial cotyledon removal by vertebrates and, in each of those cases, an estimate was made of the proportion of cotyledonary mass that had been

removed. Germinated seeds showed at least some shoot and/or root development. All seeds were examined for insect exit holes.

Data analysis

Chi-squared tests were used for comparisons of seed germination among treatments and for comparisons of seed germination with and without insect exit holes. Effects of initial seed size and insect infestation on shoot size were examined using multiple linear regression. Effects of partial seed mass removal on shoot size were examined by analysis of covariance (ANCOVA), using post-cut treatment seed size as the covariate and Tukey's *post-hoc* HSD tests for between-treatment comparisons. Comparisons of successive shoot masses were made using repeated-measures ANOVA. Seeds which produced more than one resprout shoot simultaneously were excluded from regression and ANOVA analyses of total shoot mass because resource allocation to concurrently produced shoots may differ from allocation to consecutively produced shoots.

<div align="center">RESULTS</div>

Growing-house experiments

Seed size in our sample from beneath *P. copaifera* trees was extremely variable (mean = 96.1 g, SD = 27.7, range 28.6–171.6, n = 114). Consequently, mean seed size post-cutting in all seed mass removal treatments was still within the natural range of seed size for this species (Table 1). Seed mass removal had no effect on the proportion of seeds germinating ($\chi^2 = 2.10$, df = 3, P>0.05; Table 2).

At the end of the growing-house experiment, seed-boring insect exit holes were found in 27% of the *P. copaifera* seeds. All exit holes were similar (4 mm diameter), even though two insect species are involved in causing damage to these seeds. Several exit holes had pupal cases left behind by sesiid moths (probably *Carmenta surinamensis* Eichlin (Lepidoptera: Sesiidae); Harms & Aiello 1995), and one emerging beetle was captured and identified as *Eubulus* sp. nov. (Coleoptera: Curculionidae) (Henry Stockwell, *pers. comm.*). Several seeds had

Table 2. Number of germinating seeds, insect-damaged seeds, and mean number of resprouts of *Prioria copaifera* in each seed mass removal treatment in a growing-house on Barro Colorado Island. The 'total-germinated' column includes insect-damaged seeds.

Percentage of seed mass removed	Total planted	Total germinated	Mean number of resprouts	Insect damaged	
				Germinated	Ungerminated
0	31	22	2.1	9	2
20	29	22	2.0	7	2
40	28	17	1.2	6	4
60	26	16	0.9	1	0
Total	114	77		23	8

more than one exit hole and one seed germinated with eight exit holes. When all mass removal treatments were pooled there was no effect of insect infestation on seed germination (Yates-corrected $\chi^2 = 0.73$, df = 1, P>0.05).
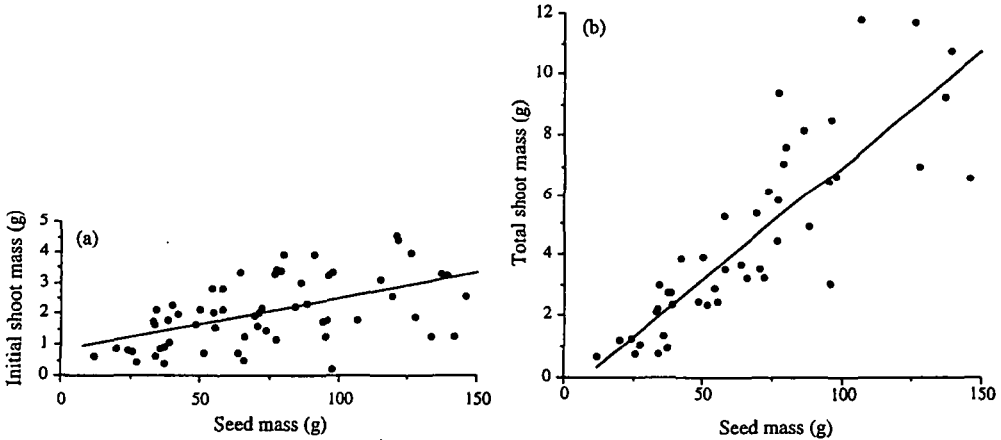

Figure 1. Relationship between (a) initial seed mass (fresh weight after manipulation) and initial shoot mass (dry weight), for seeds in all treatments (y = 0.83 + 0.02x, $r^2 = 0.27$, P<0.001, n = 60), and (b) initial seed mass and total shoot mass, for seeds in all treatments (y = –0.52 + 0.08x, $r^2 = 0.71$, P<0.001, n = 46), of *Prioria copaifera* in a growing-house on Barro Colorado Island. Seeds that failed to produce resprout shoots or that produced two or more resprouts concurrently were excluded.

P. copaifera seeds showed a remarkable capacity to resprout following excision of the initial shoot (Table 2). Uncut seeds produced an average of 2.1 sequential resprouts after excision of the initial and subsequent shoots and three seeds produced four sequential functional resprouts. For seeds that germinated, uncut seeds resprouted significantly more times than cut seeds (Mann-Whitney U-test, $n_{uncut} = 22$, $n_{cut} = 55$, P<0.01), but even seeds with 60% of their seed reserves removed showed some resprouting capacity (Table 2).

For uncut seeds, the size of the initial shoot was not related to seed mass ($r^2 = 0.03$, P>0.05, n = 22) and the total mass of shoots produced (initial shoot plus all subsequent resprout shoots) was only weakly related to seed size ($r^2 = 0.37$, P<0.05, n = 15). When seeds in the cut treatments that resprouted were also included, both initial shoot mass. Figure 1a; see legend for statistics) and the total mass of shoots; Figure 1b) were significantly positively related to seed mass, so that seeds with part of their cotyledonary mass removed produced smaller initial shoots and less total shoot mass. Adding the number of insect exit holes (a measure of insect damage to the seed) as a second factor in regressions of seed mass versus shoot mass did not improve the fit of the regression models.

There was a significant effect of the seed treatment on both the initial shoot mass (F = 5.75; df = 3,73; P<0.01) and on the total mass of shoots produced (F = 4.36; df = 3,57; P<0.05), though in both cases significant differences were

restricted to comparisons between uncut and cut seeds (Tukey's HSD, $P<0.05$), rather than between cut treatments (Tukey's HSD, $P>0.05$). Initial shoot mass was not significantly greater than the mean mass of the first and second resprout shoots produced for uncut seeds alone ($F = 1.39$; $df = 1,12$; $P>0.05$; Figure 2). Initial shoot mass was significantly greater than the mean mass of the first and second resprout shoots when all treatments were combined ($F = 8.85$; $df = 1,33$; $P<0.01$; Figure 2). Too few seeds produced three or four resprout shoots for statistical comparisons to be made.
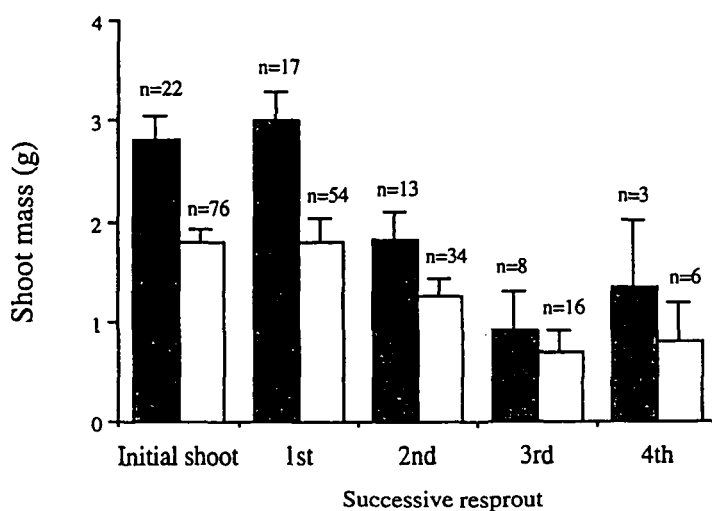

Figure 2. Mean (± 1 SE) dry mass of the initial shoot produced and of subsequent resprout shoots for uncut *Prioria copaifera* seeds only (solid bars) and for seeds in all treatments combined (open bars) in a growing-house on Barro Colorado Island.

Field census

Damage levels of *P. copaifera* seeds sampled in the field were high. Of the 470 seeds sampled, the largest proportion (55%) was non-viable, with intact pericarps but no cotyledonary contents, suggesting destruction by insects and/or pathogens. Another 36% of the seeds had been killed by vertebrates. Only 8% of the seeds were in an apparently-viable condition, containing at least some healthy cotyledonary material, and only 1% of seeds had germinated. Of the 46 seeds we recovered that were in the 'apparently-viable' or 'germinated' categories, 30% had suffered removal by vertebrates of 10 to 80% of their seed reserves.

The infestation rate by insects that feed in and emerge from seeds of *P. copaifera* in the field was 40% (190 out 470 seeds had insect exit holes). Seeds with exit holes had, on average, 1.5 exit holes/seed. Since we counted exit holes through pericarps, some of which were partially eaten or partially decayed, the infestation rate by these insects may be an underestimate. Furthermore, insects that fed within seeds, but that never emerged, went undetected.

DISCUSSION

Even though most of the seeds from *P. copaifera* trees are quite large, seed size in *P. copaifera* is highly variable (Table 1). Westoby *et al.* (1992) observed that species have adopted many different seed sizes within particular habitats, but seed size also often varies considerably within species, both among trees and within the crop of a single tree. For example, on BCI mean seed sizes among 46 trees of *Virola surinamensis* (Myristicaceae) varied between 1.34 g and 4.04 g (Howe & Richter 1982) and viable seeds of *G. superba* can range between 1.8 g and 24.5 g (J. Dalling & K. Harms, unpubl. data). Clearly trees do not always (or are unable to always) produce a single optimal seed or seedling size (Geritz 1995).

Like many tropical trees (Janzen 1969), *P. copaifera* has high seed mortality in the field. Two months after the end of the fruiting season in August 1994, fewer than 10% of seeds we encountered in the field had germinated, or were in an apparently-viable state. Nonetheless, growing-house experiments show that not all seed damage is necessarily lethal; seeds infested by *Eubulus* beetles and sesiid moths had the same probability of germinating as uninfested seeds. In addition, seeds with 60% of their cotyledon reserves removed had the same probability of germinating as intact seeds. Furthermore, seeds of all sizes and in each of the partial cotyledon removal treatments produced functional shoots and seedlings were able to survive repeated aboveground biomass removal through resprouting.

The capacity of seeds to survive insect infestation and to subsequently produce functional shoots has only rarely been reported (Cipollini & Stiles 1991, Hartshorn 1983, McHargue & Hartshorn 1983), yet we predict that it is a common occurrence, particularly among species with large seeds. On BCI, at least three other species can tolerate seed infestation; *G. superba* seeds survive infestation by sesiid moth larvae (Harms & Aiello 1995; J. Dalling & K. Harms, unpubl. data), cotyledons of seedlings of *Beilschmedia pendula* (Lauraceae) are frequently infested by beetle larvae (J. Dalling & K. Harms, *pers. obs.*), and *Scheelea zonensis* (Palmae) seeds occasionally survive bruchid larval infestation (K. Harms & J. Dalling, unpubl. data).

For *P. copaifera*, additional field experiments are needed to determine the relative importance of insect infestation versus herbivory in controlling seedling establishment. Seed consumption and herbivory may also vary geographically and between years. Janzen (1969) found no evidence of bruchid damage to seeds of *P. copaifera* in Costa Rica, while we found high levels of infestation by two insect species on BCI.

Similarly, experiments are needed to determine the fates of seed reserves retained after the production of functional seedlings and whether under field conditions cotyledons remain capable of producing resprout shoots following herbivory. In the field survey of damage to *P. copaifera* seeds, we found very few viable or germinating seeds and almost one third of those we did find had suffered cotyledon damage similar to our experimental treatments. If *P. copai-*

fera seeds are scatter-hoarded (as are many other large-seeded species on BCI (*e.g.*, Forget 1993, Smythe *et al.* 1982)), then resprouting may be more likely because the cotyledons would be buried and presumably hidden from further attention from seed-predators.

Large seed size is a characteristic of many other species that grow in swamp forests (*e.g.*, *Carapa guianensis* Aublet (Meliaceae), *Pachira aquatica* Aublet (Bombacaceae), and *Mora megistosperma* (Triana) (Fabaceae)). In part, large seed size in this habitat may be necessary to raise the seedling leaves above the water surface, but this may not be the only advantage of large seed size for these species. Seed and seedling size of *P. copaifera* growing in seasonally inundated swamp forest in the Darién Province of Panamá does not appear to be greater than on upland soils on BCI (J. Dalling, *pers. obs.*) and seedlings of *M. megistosperma* retain substantial cotyledon mass for up to 3 y after germination (Janzen 1983; Omar Lopez, *pers. comm.*). Comparative studies of seed predation and resprouting capacity in swamp forests and on upland soils would be necessary to determine the relative importance of the various potential advantages of large seed size to these species.

On BCI, several large-seeded species, differing in life form and shade tolerance, show similar resprouting capacity and/or tolerance to seed feeding insects as *P. copaifera* (Harms & Dalling 1997, *pers. obs.*). We suggest that tolerance of damage *per se*, has received insufficient attention as a determinant of large seed size in moist tropical forests, in comparison with tolerance and avoidance of unfavourable light conditions. As Janzen (1969) suggested, seed and seedling predators may select for smaller seeds, either through predator satiation and escape, or for fewer, larger and/or better protected seeds that better tolerate predators as the opportunity for escape diminishes.

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