

## SEED SIZE, SEEDLING MORPHOLOGY, AND RESPONSE TO DEEP SHADE AND DAMAGE IN NEOTROPICAL RAIN FOREST TREES<sup>1</sup>

CHRISTOPHER BARALOTO<sup>2,4</sup> AND PIERRE-MICHEL FORGET<sup>3</sup>

<sup>2</sup>Institut National de la Recherche Agronomique, UMR “Écologie des Forêts de Guyane,” Kourou, French Guiana; and

<sup>3</sup>Département Ecologie et Gestion de la Biodiversité, UMR 7179 CNRS-MNHN, Muséum National d’Histoire Naturelle, Brunoy, France

To investigate the existence of coordinated sets of seedling traits adapted to contrasting establishment conditions, we examined evolutionary convergence in seedling traits for 299 French Guianan woody plant species and the stress response in a shadehouse of species representing seed size gradients within five major cotyledon morphology types. The French Guianan woody plant community has larger seeds than other tropical forest communities and the largest proportion of hypogeal cotyledon type (59.2%) reported for tropical forests. Yet the community includes many species with intermediate size seeds that produce seedlings with different cotyledonal morphologies. A split-plot factorial design with two light levels (0.8% and 16.1% PAR) and four damage treatments (control, seed damage, leaf damage, stem damage) was used in the shadehouse experiment. Although larger-seeded species had higher survival and slower growth, these patterns were better explained by cotyledon type than by seed mass. Even larger-seeded species with foliar cotyledons grew faster than species with reserve-type cotyledons, and survival after stem grazing was five times higher in seedlings with hypogeal cotyledons than with epigeal cotyledons. Thus, to predict seedling performance using seed size, seedling morphology must also be considered.

**Key words:** cotyledons; French Guiana; functional morphology; herbivory; life history; phylogeny; regeneration strategy; shade tolerance.

The large range of seed sizes in many terrestrial plant communities has prompted much speculation as to how larger seed size increases fitness (Moles et al., 2005a, b). Several authors have proposed that this gradient may be explained by adaptations for seedling establishment that mitigate survival vs. growth potential (Kitajima, 1994; Rose and Poorter, 2003). Larger-seeded species might survive better because the additional metabolic reserves present in large seeds can buffer carbon losses (Foster and Janson, 1985; Kitajima, 1996; Westoby et al., 1996) associated with low light levels (Bloor and Grubb, 2003; Baraloto et al., 2005a), and herbivore damage on seed reserves or aboveground biomass (Dalling and Harms, 1999; Green and Juniper, 2004). Indeed, larger-seeded woody species possess suites of attributes, such as greater leaf longevity and lower specific leaf area, that confer shade tolerance (Kitajima, 1994; Walters and Reich, 1999). In addition, large seeds tolerate both insect infestation of seed reserves as well as shoot damage (Dalling et al., 1997; Harms and Dalling, 1997; Dalling and Harms, 1999; Hammond et al., 1999; Green and Juniper, 2004).

In contrast, smaller-seeded species have limited reserves and therefore tend to react more negatively to intense postdispersal herbivory (Howe et al., 1985; Molofsky and Fisher, 1993). But smaller-seeded species generally grow faster than larger-seeded species and thus may overcome the initial size advantage associated with larger seed size (Paz and Martinez-Ramos, 2003; Rose and Poorter, 2003; Baraloto et al., 2005a). While this growth advantage appears to be consistent in high and lower (e.g., 2% of full sun) light environments (Kitajima, 1994; Poorter and Rose, 2005), whether it holds in very deep shade (<1% full sun) or in response to seed or seedling damage, remains unclear (Bloor and Grubb, 2003).

The relationships between seed size and seedling performance in contrasting environments may be confounded because larger seeds tend to have hypogeal cotyledons that function as seed reserves, whereas smaller seeds tend to have epigeal foliar cotyledons (Garwood, 1996; Ibarra-Manríquez et al., 2001; Zanne et al., 2005). Thus, larger-seeded species may better resist stem grazing not only because they have more seed reserves, but also because they can resprout from hypogeal cotyledons (e.g., Forget, 1992; Harms and Dalling, 1997; Green and Juniper, 2004). Smaller-seeded species may be less capable of resprouting because they tend to have epigeal cotyledons, but they may respond more quickly to light availability because they have a greater initial allocation to photosynthetic tissue (Kitajima, 1994; Rose and Poorter, 2003). The distributions of tree species differing in cotyledonal morphology suggest that seedlings of different cotyledon types might be adapted to particular environments. For example, species in open areas in Kibale, Uganda tend to have epigeal cotyledons and smaller seeds than those in forest and gap habitats (Zanne et al., 2005). And in Guadeloupe, seedlings with foliar cotyledons are more common in dry forest, whereas those with reserve-type cotyledons are more common in humid forests (Rousteau, 1986). However, the mechanisms responsible for such patterns and the degree to which they are governed

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<sup>4</sup> Author for correspondence (e-mail: baraloto.c@kourou.cirad.fr); phone: 00-594-32-92-91; fax: 00-594-32-43-02; present address: INRA Kourou, BP 709, 97387 Cedex, FRANCE

by seed size are not well understood. Seed mass and cotyledon morphology may be part of coordinated sets of life history traits that include the mode of dispersal mode and the phenology of emergence, which together govern the distribution of new seedlings in space and in time (Moles et al., 2005a).

Tropical forest tree communities encompass the largest range of seed mass among vegetation types reported in the literature (Hammond and Brown, 1995; Metcalfe and Grubb, 1995). Yet for a given amount of seed reserves, it is common to observe species with several different cotyledonal displays or seedling functional morphologies. In the Guiana Shield region of South America, the seed-size gradient includes very large-seeded species with dry seed mass of more than 10 g and constituting more than 10% of species in several tree communities (Hammond and Brown, 1995; Hammond et al., 1996; Baraloto, 2001). In this paper, we investigate the existence of coordinated sets of seedling traits adapted to contrasting seedling establishment conditions. We first examine evolutionary convergence in a syndrome of traits including seed size, cotyledon morphology, dispersal type, and emergence phenology for 299 French Guianan woody plant species. We then describe an experiment examining the responses of woody plant species to stress; the species represent a gradient of seed sizes within each of the five major cotyledon morphology types originally described by Miquel (1987). To separate the confounding effects of cotyledonal morphology associated with seed size, we asked whether the advantages of seed reserves are independent of the way in which those reserves are allocated. In particular, do larger-seeded species have a higher initial survival, and does this advantage increase under deep shade or with increasing damage and tissue loss? Do smaller-seeded species grow faster, and does this advantage change under deep shade or with increasing damage intensity?

## MATERIALS AND METHODS

**Community trait screening**—Seedling trait associations were analyzed using a seedling morphology database initiated in 1998. The database used herbarium specimens of seedlings grown from seed from adult vouchers collected throughout French Guiana. The database was expanded from 1998–2006 with collections made by the authors primarily at the Paracou experimental site (5°18' N, 52°55' W), a lowland tropical rain forest near Sinnamary, French Guiana, receiving 2875 mm of annual precipitation (mean from 1986–2005, SD = 540 mm; see Gourlet-Fleury et al. [2004] for a complete description of the site). From 1998–2001 during monthly walks along a series of 11 km of trails bordering permanent plots, we collected fresh fruit beneath adult trees that had previously been identified to the species level. Seeds were collected beneath trees of 202 taxa during this period. Taxa were scored for dispersal mode based on fruit size and morphology (Gautier-Hion et al., 1985). Seed size was estimated using relationships with seed length and width, which were obtained from photographs or scaled illustrations; we report these estimates as ordinated classes.

In some cases, fruit or seedlings were not the same species as the nearest tree. Attempts were made to identify these seedlings, but some could not be assigned beyond the family or genus level because adult leaf morphology can differ greatly from that of juveniles. The 202 identified species include more than one third of the arboreal taxa identified at Paracou to date, based on 551 morphotaxa described by Molino and Sabatier (2001), and account for over 80% of the basal area in this forest (Gourlet-Fleury et al., 2004). Vouchers of seedlings surviving in good condition were deposited at CAY (Appendix S1, see Supplemental Data accompanying the online version of the article for accession numbers). An archive of digital photographs of many taxa is available from the authors upon request.

For each taxon collected, 5–20 seeds were planted to determine a suite of traits defining seedling morphology. Seeds were removed from the fruit (if

necessary) and planted on the soil surface in a 1.5-L plastic pot containing a 2 : 1 mixture of ferrallitic clay and white sand. We scored emergence as the median amount of time between sowing and seedling emergence for all seeds that germinated.

Seedling morphology was described when at least three individuals had each developed at least three leaves. Five binary morphological variables were noted to best describe differences among the seedlings during early establishment, the first three of which have been more fully described by Garwood (1996) and result in three-character designations. (1) The form of the cotyledons was scored either as phanerocotylar (sensu Duke, 1965) if the seed coat opened and (for dicots) exposed two cotyledons surrounding the emerging stem or hypocotyls, or as cryptocotylar (sensu Duke, 1965) if the cotyledons remained intact inside the seed coat. (2) The position of the cotyledons was scored either as hypogeal if they remained on the soil surface and the hypocotyl was not above the soil surface or as epigeal if the hypocotyl rose at least 2 cm above the soil surface. (3) The function of the cotyledons was scored either as reserve if the cotyledons were fleshy or as foliar if they appeared to serve primarily as photosynthetic rather than storage organs. Clearly, this binary scoring represents the extremes of a gradient of cotyledon function described by Kitajima (1994, 1996). In many cases, fleshy cotyledons contain some chlorophyll; however, we did not score these as foliar unless they were thin enough to call into question their function as reserves (e.g., *Aspidosperma* spp., Apocynaceae; *Recordoxylon speciosum*, Fabaceae) or unless they had veins (e.g., *Pachira dolichocalyx*, Malvaceae). As a result, our assignments of taxa into the five initial seedling morphology types sometimes differed from those of Miquel (1987) and Garwood (1996).

The stem axis was scored either as orthotropic if during the development of the first leaves the primary meristem elongated vertically with radial symmetry of leaves or as plagiotropic if elongation of the primary axis was horizontal, with bilateral symmetry of leaves. For example, seedlings developing according to the Massart architectural model (Hallé et al., 1978), including *Virola* spp., Myristicaceae, and members of the tribe Moronobidae, Clusiaceae, do eventually develop plagiotropic branches along the secondary axes. However, the primary axis is orthotropic. Conversely, many legumes following the Troll model (Hallé et al., 1978) e.g., *Vouacoupa americana*, Fabaceae, appear to elongate vertically; however, insertion points are not arranged with radial symmetry. Finally the root morphology was evaluated using the presence or absence of a determinate axis or a taproot.

**Analyses**—To determine whether seed mass and/or cotyledon morphology correlate with suites of traits adapted to contrasting establishment conditions, we evaluated their associations with other variables describing initial seedling morphology, dispersal type, and emergence delay. We included all surveyed taxa and thus analyzed seed mass as a discrete variable, as reported in Appendix S1 (see Supplemental Data with online version of this article). Because values for some of these traits may be limited to particular taxonomic groups, we used likelihood ratio tests that correct for phylogenetic relationships among species, using the software Discrete 4.0 (Pagel, 1994). The phylogenetic relationships among the study species were obtained from the angiosperm supertree provided by Davies et al. (2004) using the PhyloCom utility (Webb and Donoghue, 2004). Branch lengths separating dichotomous nodes were set to a default level of 1, with polytomies set to 0.0000001.

To determine whether the results of our study might apply across tropical forest sites, we compared the distribution of taxa among the five cotyledon types of Miquel (1987) between Paracou and nine other sites using data from Garwood (1996) as well as data from recently published studies (Ibarra-Manríquez et al., 2001; Zanne et al., 2005). Where possible, we limited these comparisons to the tree community because all but four of the species sampled in our survey were trees. We tested the null hypothesis that the frequency distribution among these classes at Paracou was similar to that for each of the other sites using chi-square tests between the distribution for Paracou and that for each site. We calculated the expected frequencies using the relative frequencies of the other sites multiplied by the number of tree taxa at Paracou ( $N = 295$ ).

**Manipulative experiment**—**Species**—Twenty focal species were chosen, four in each of the five seedling morphology categories described by Miquel (1987) (Table 1). Within each category, the four species were chosen to represent the entire range of seed sizes in that category. Some categories were naturally restricted to a single order of magnitude (e.g., PER), or to particular taxonomic groups (e.g., CER; primarily within *Virola*, Myristicaceae). Species were also chosen such that seedlings emerged within a 6-wk period beginning

TABLE 1. Morphological traits of the species used in the experiment and the biomass removed in each of the simulated damage treatments. The proportion of original seed mass removed by each treatment is indicated in parentheses.

Species	Family	Dry seed mass (g) <sup>a</sup>	Cotyledon type <sup>b</sup>	Biomass removed in treatment		
				Cotyledon (g)	Leaf (g)	Stem (g)
<i>Bagassa guianensis</i>	Moraceae	0.004	PEF	0.001 (0.42)	0.001 (0.48)	0.001 (0.68)
<i>Tabebuia insignis</i>	Bignoniaceae	0.028	PEF	0.010 (0.37)	0.005 (0.17)	0.026 (0.91)
<i>Manilkara bidentata</i>	Sapotaceae	1.1	PEF	0.053 (0.05)	0.046 (0.04)	0.118 (0.11)
<i>Poraqueiba guianensis</i>	Icacinaeae	5.2	PEF	0.19 (0.04)	0.092 (0.02)	0.708 (0.14)
<i>Protium subseriatum</i>	Burseraceae	0.36	CER	0.215 (0.61)	0.087 (0.25)	0.033 (0.09)
<i>Virola surinamensis</i>	Myristicaceae	1.1	CER	1.084 (0.81)	0.084 (0.06)	1.320 (0.99)
<i>Virola michelii</i>	Myristicaceae	1.4	CER	0.904 (0.65)	0.065 (0.05)	1.200 (0.86)
<i>Virola kwatae</i>	Myristicaceae	3.2	CER	1.975 (0.62)	0.14 (0.04)	2.061 (0.65)
<i>Eriotheca surinamensis</i>	Malvaceae	0.15	PER	0.066 (0.43)	0.029 (0.19)	0.028 (0.18)
<i>Dicorynia guianensis</i>	Fabaceae	0.35	PER	0.071 (0.20)	0.036 (0.10)	0.048 (0.14)
<i>Amanoa heteromorphia</i>	Euphorbiaceae	0.75	PER	0.147 (0.20)	0.119 (0.16)	0.387 (0.52)
<i>Hymenaea courbaril</i>	Fabaceae	2.9	PER	0.734 (0.26)	0.294 (0.10)	0.908 (0.32)
<i>Aspidosperma album</i>	Apocynaceae	0.20	PHR	0.122 (0.60)	0.022 (0.11)	0.021 (0.10)
<i>Sextonia rubra</i>	Lauraceae	1.2	PHR	0.493 (0.41)	0.196 (0.16)	0.041 (0.03)
<i>Eperua falcata</i>	Fabaceae	4.2	PHR	1.770 (0.42)	0.396 (0.09)	0.072 (0.02)
<i>Vouacapoua americana</i>	Fabaceae	12.4–22.3	PHR	6.126 (0.33)	0.679 (0.04)	1.219 (0.07)
<i>Protium giganteum</i>	Burseraceae	0.27	CHR	0.245 (0.91)	0.096 (0.36)	0.025 (0.09)
<i>Lecythis persistens</i>	Lecythidaceae	1.4	CHR	0.406 (0.29)	0.273 (0.19)	0.182 (0.13)
<i>Licania heteromorphia</i>	Chrysobalanaceae	2.2	CHR	0.445 (0.20)	0.116 (0.05)	0.211 (0.10)
<i>Carapa procera</i>	Meliaceae	6.6–12.3	CHR	5.150 (0.55)	0.750 (0.08)	1.670 (0.18)

<sup>a</sup> Dry seed mass is the mean mass for 30–50 groups of seeds for small-seeded species (<0.1 g), 30–50 seeds for species of intermediate size (<3 g), and the range of estimated dry mass for larger seeds planted in the experiments, for which wet mass was measured. For these larger-seeded species, the proportion of biomass removed by each treatment was calculated on an individual basis, the mean of which is reported.

<sup>b</sup> Cotyledon type was classified as in Garwood (1996) and described by a three-letter code. The first letter of the code refers to cotyledon form: C (cryptocotylar = inside seed coat) vs. P (phanerocotylar = free). The second letter refers to cotyledon position: E (epigeal = aboveground) vs. H (hypogeal = at or belowground). The third letter refers to cotyledon function: F (foliar = thin and photosynthetic) vs. R (reserve = storage).

in January 2000. *Lecythis persistens* was considered to be cryptocotyledonar for this grouping, even though seedlings of *Lecythis* and *Eschweilera* have been described as lacking true cotyledons (Duke, 1965).

Seeds of the focal taxa were collected beneath at least three adult individuals per species. All species were collected at Paracou, except seeds of *Virola kwatae* were collected from the Montagne Tortue National Forest (5°03' N, 52°15' W). This species was included because it produces the largest seed of the CER species in French Guiana.

Seed mass was measured for each seed before planting, and dry mass was calculated based on equations relating wet and dry seed mass for seeds not used in the experiment ( $r^2 = 0.72$ – $0.96$ ).

**Experimental design**—The experiment, conducted in a shadehouse at the field station at Paracou, used a split-plot design, with two light treatments applied across three main plots and four simulated damage treatments replicated within each main plot. In January–February 2000, seeds were planted into 3-L black polyethylene containers filled with a 2 : 1 soil mixture (to ensure drainage in the pots) of brown clay soil and a white sand. The brown clay soil was collected from 10–30 cm depth, and the white sand was collected from 40–80 cm depth in the white sand forests of Paracou. Soil was sieved to 2 mm to ensure homogeneity but was not sterilized or heated so as to maintain the biological properties of the soil from the field.

The light treatments were designed to simulate contrasting environments encountered by seeds in the forest, including a deep shade treatment (<1% full sun PAR) below the light compensation point of most species (Bloor and Grubb, 2003; Poorter and Rose, 2005) and an open treatment characteristic of a medium-sized canopy gap at Paracou (about 15% of full sun PAR; Baraloto et al., 2005b). Quantum sensors (LI-COR, Lincoln, Nebraska, USA) recording data each minute to a data logger (Campbell Scientific, Logan, Utah, USA) received maximum instantaneous energy levels of  $20.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and  $402.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , on a cloudless day in the “shade” and “sun” treatments, respectively. Daily integrated values were  $0.22 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  and  $4.34 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , respectively. These values correspond to 0.8% and 16.1% of energy transmitted to captors placed in adjacent sites open to full sun, with almost identical results for the maximum instantaneous measure and the daily integrated value.

Within each of the two light treatments, a control and three simulated

seedling damage treatments were implemented to represent the most common catastrophes incurred by seedlings following emergence. A cotyledon damage treatment was designed to mimic damage by herbivores that reduces the amount of seed reserves without exhausting them. One half of the cotyledon and/or endosperm volume of the seedling was removed immediately upon emergence without damaging the hypocotyl or cotyledonary petioles. A second damage treatment simulated leaf herbivory and consisted of removal of about one half of the leaf surface area 1 wk after all leaves were fully expanded following emergence. Leaf surface was removed as entire leaves or leaflets randomly selected from the first unit of growth. A third treatment mimicked grazing by understory mammals and consisted of stem cutting 1 wk after all leaves were fully expanded following emergence, at 5 cm from the soil surface, where grazing herbivores such as *Mazama americana* and *Agouti paca* cut the stems (Forget, 1992). For most seedlings with epigeal cotyledons, this treatment resulted in the complete removal of cotyledons, with the simulated grazing site occurring along the hypocotyl. All removed tissue was dried to constant mass at 60°C to report the proportion of initial seedling biomass removed for each species  $\times$  treatment combination (Table 1).

Thirty seedlings of each species  $\times$  light  $\times$  damage combination ( $N = 240$  per species) were arranged in the split-plot design, with 10 seedlings of each damage treatment (subplots) within each of three main plots of paired light treatments, oriented perpendicular to the sun's trajectory across the shadehouse. All pots were watered to field capacity several times each week.

Survival and seedling height were determined 2 and 8 mo following treatment implementation, in March and October 2000. Here we report the proportion of emerging seedlings surviving to 8 mo and of relative growth rate (RGR) for height between 2 and 8 mo age, calculated as  $\text{RGR} = [\ln(\text{height}_8) - \ln(\text{height}_2)] / (0.5 \text{ yr})$ .

We were unable to harvest the experiment as originally planned because an overnight attack by ants (*Atta spp.*) defoliated many seedlings after the October 2000 inventory.

**Analyses**—To test whether species responded differently to treatments, we performed analyses of variance on each dependent variable (survival, RGR) with  $F$ -ratio denominators assigned according to replication within the split-plot design (Sokal and Rohlf, 1995). Survival data were the proportion of

TABLE 2. Observed frequencies (relative percentage) of seedling cotyledon types for random samples of trees alone, except where noted, for Paracou, French Guiana, and nine other tropical forest sites, after Garwood (1996). Differences between each of the distributions and that of Paracou were examined using chi-square goodness-of-fit tests, with the expected frequency for Paracou calculated using the relative proportions in each of the other sites.

Relative frequency of taxa (%)										
Seedling type <sup>a</sup>	French Guiana	Venezuela <sup>b</sup>	Panama <sup>b</sup>	Mexico	Puerto Rico <sup>b</sup>	Uganda <sup>b</sup>	Gabon <sup>b</sup>	Nigeria	Malaysia	Indonesia <sup>b</sup>
PEF	27.5	56.2	42.9	49.5	48.1	72.0	39.0	34.5	34.8	32.7
PER	10.5	19.6	16.1	9.5	18.1	4.0	24.8	43.4	29.0	18.7
CER	2.4	2.6	3.4	2.4	1.3	0	5.2	3.5	7.6	8.0
PHR	27.5	7.2	8.8	7.2	8.8	0	9.0	7.1	10.0	12.0
CHR	32.2	14.4	28.8	31.4	23.8	24.0	21.9	11.5	18.6	28.7
Taxa	295	194	205	210	160	25	210	113	210	150
Chi-square		97.9	47.8	55.5	66.9	40.9	55.9	122.4	57.4	28.7
P		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Reference		Ricardi (1997)	Garwood (1996)	Ibarra-Manríquez et al. (2001)	Duke (1965)	Zanne et al. (2005)	Miquel (1987)	Okali and Onyeachusim (1991)	Ng (1978)	de Vogel (1980)

<sup>a</sup> Cotyledon type was classified as in Garwood (1996) and described by a three-letter code. The first letter of the code refers to cotyledon form: C (cryptocotylar = inside seed coat) vs. P (phanerocotylar = free). The second letter refers to cotyledon position: E (epigeal = aboveground) vs. H (hypogeal = at or belowground). The third letter refers to cotyledon function: F (foliar = thin and photosynthetic) vs. R (reserve = storage).

<sup>b</sup> Data include life forms other than trees.

seedlings surviving within each main plot for each subplot treatment combination (species  $\times$  damage treatment).

To determine whether the influence of seed size differed among seedling types and in response to treatments, we performed ANCOVA analyses to test for differences in slopes in the relationship between seed size and seedling survival or RGR. The mean seedling responses within treatment combinations were used as data points in these analyses. The stem damage treatment was analyzed separately for the two cotyledon types surviving this treatment. Comparisons of means among treatment levels were made using Bonferroni post-hoc tests.

## RESULTS

**Community survey—Comparison with other studied tropical forests**—The data collected for the 299 taxa are given in Appendix S1. We found no difference between the dry seed mass distribution at Paracou ( $N = 273$ ; mean  $\pm 1$  SE =  $2.35 \pm 0.36$  g) and that of trees at Mabura Hill, Guyana (MHER;  $N = 134$ ; mean  $\pm 1$  SE =  $4.78 \pm 0.95$  g) ( $t$ -test on log-transformed values with  $df = 395$ ,  $t = 0.17$ ,  $P = 0.86$ ), whose mean seed size has been shown to be much greater than other lowland tropical forest sites (Hammond and Brown, 1995).

The uniqueness of seedling traits in the Guiana Shield (including both Paracou and MHER) flora is also supported by qualitative traits describing cotyledon morphology. Based on the cotyledon types described by Miquel (1987), the distribution at Paracou was different than that of each of nine other tropical forest sites (chi-square  $P < 0.001$  in all cases; see Table 2). Unlike all other sites, more than half of the species from the Paracou tree sample (59.7%) germinated with hypogeal cotyledons, and less than one third (27.5%) germinated with epigeal photosynthetic cotyledons.

**Correlations among seedling traits**—When accounting for phylogenetic constraints on seedling morphology, we found several patterns of correlated trait evolution. Smaller seeds are strongly associated with epigeal foliar cotyledons, and larger seeds tend to produce seedlings with hypogeal cotyledons (Table 3). Seed size was not correlated with stem axis

orientation, but seedlings with hypogeal emergence tended to have plagiotropic stems. While more than 90% of the taxa surveyed had taproots, the taxa without taproots were associated with smaller seed size but not necessarily epigeal cotyledons.

**Shadehouse experiment**—In general, survival increased when light was not limiting and in the absence of seedling damage treatments (Table 4; Fig. 1). Most larger seeds survived better than smaller seeds, but this result was strongly influenced by cotyledon morphology, resulting in a significant seed size  $\times$  cotyledon type interaction term (Table 4). In particular, survival increased with increasing seed size only for seedlings with epigeal cotyledon types (Fig. 1). Seedling type but not seed size affected the response to seedling damage (Table 4). Only species with hypogeal cotyledons survived the stem damage treatment well (Fig. 2). Nonetheless, several seedlings of *V. kwatae* were able to resprout from hypocotyl tissue (Fig. 2). The survival of many *Eriotheca* seedlings was less remarkable, as it resulted from their cotyledons being placed below the 5 cm point at which stems were cut in the treatment. Consequently, they were able to resprout from cut meristems.

The effects of damage, seed mass, and cotyledon type did not change between deep shade and well-lit conditions (nonsignificant interaction terms Table 4; see also Fig. 2). When light was not limiting, survival was higher for almost all species but especially for small-seeded epigeal species such as *B. guianensis* and *T. insignis* as well as the larger-seeded hypogeal *E. falcata* (Fig. 1).

Cotyledon and leaf damage treatments had less severe effects on the growth rate of surviving seedlings than on survival (Table 5). Smaller-seeded species with epigeal foliar cotyledons grew faster than most other species, especially when light was not limiting (Fig. 2). We analyzed the growth response to the stem-cutting treatment only for species with hypogeal cotyledons because they alone retained sufficient sample size. The phanerocotylar species grew slightly faster in response to stem-cutting than did the cryptocotylar species

TABLE 3. Correlations between seed size, seedling morphology, and ecological traits for woody plant species in French Guiana. Correlations were tested using omnibus likelihood ratio (LR) tests for pairs of binary traits (Pagel, 1994) scored in the order presented, with probability values calculated as the proportion of 1000 Monte Carlo simulations with likelihood ratios greater than the observed value.

Traits	Small <sup>a</sup> vs. large seeds			Epigeal vs. hypogeal cotyledons		
	N	LR	P	N	LR	P
Epigeal vs. hypogeal cotyledons	299	17.34	<0.001	—	—	—
Orthotropic vs. plagiotropic stems	299	1.32	0.731	299	7.18	0.004
Absence vs. presence of taproot	299	5.93	0.025	299	3.20	0.195
Animal vs. auto dispersal	249	8.93	0.007	249	12.99	0.002
Delayed <sup>b</sup> vs. immediate germination	192	-0.18	0.988	192	4.07	0.121

<sup>a</sup> Dry seed mass < 0.5 g.

<sup>b</sup> Median germination time > 2 wk.

(effect of type  $F_{1,7} = 11.7$ ,  $P = 0.01$ ; Fig. 2). However, there was no effect of seed size or light treatment on growth rate in response to stem cutting for these species ( $P > 0.05$  for main effects and interactions).

## DISCUSSION

**Intersite comparisons**—The distinct flora of the Guiana Shield relative to other South American moist forests (Ter Steege et al., 2000) appears to be accompanied by community-level differences in seed and seedling traits. The seed size distribution of the Paracou arborescent flora was similar to that of Mabura Hill, Guyana (MHER), which has larger seeds than other neotropical forests, including BCI (Panama) and Manu (Peru) (Hammond and Brown, 1995). However, MHER has more very large-seeded species (especially *Mora* [Leguminosae] and *Chlorocardium* [Lauraceae]) than Paracou, where none of the surveyed taxa had a seed larger than 50 g dry mass (although *Licania macrophylla* [Chrysobalanaceae] [87 g dry mass] occurs in a nearby watershed).

Several mechanisms have been proposed to explain why

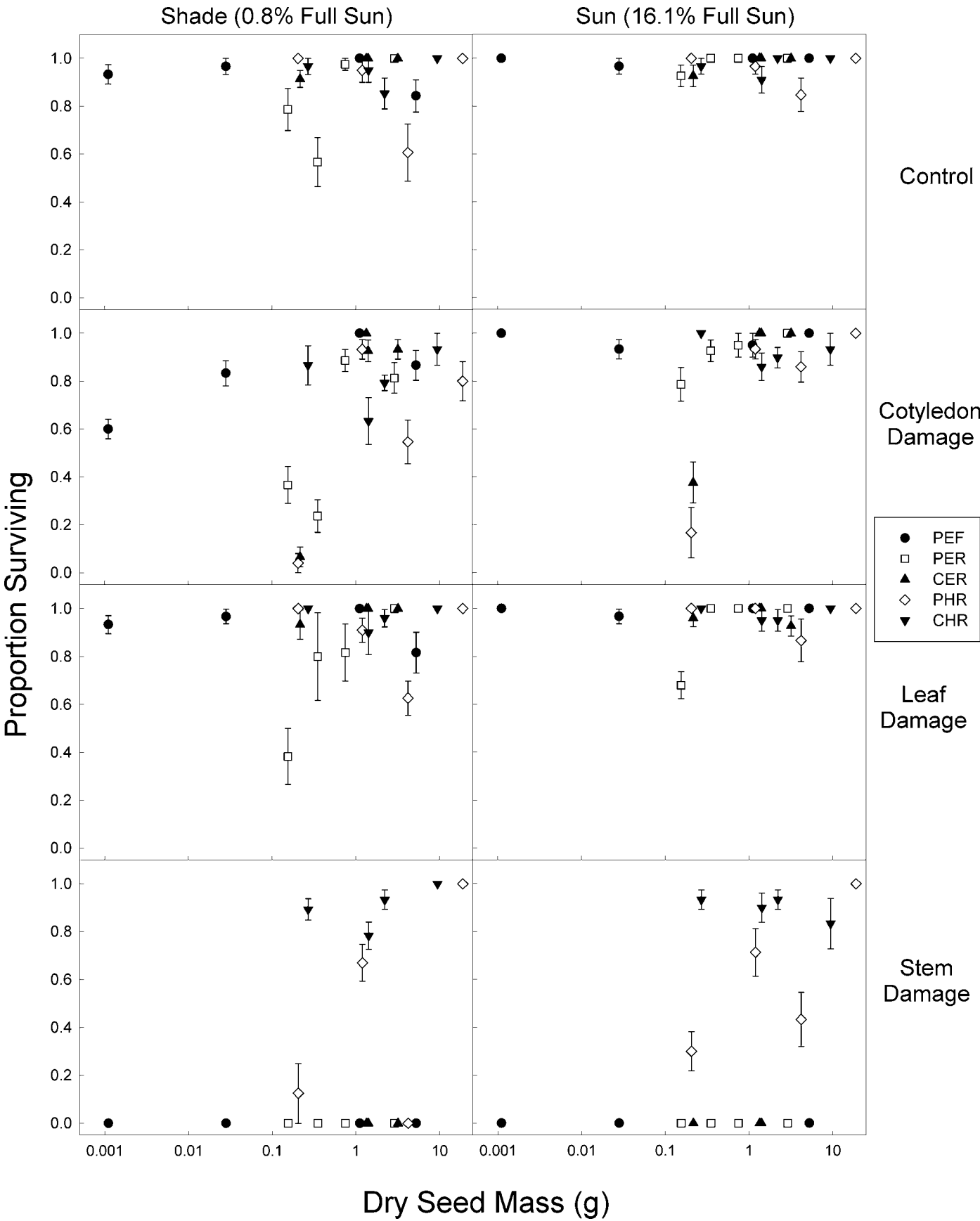
seeds are larger in the Guiana Shield than in other South American moist tropical forests. First, it has been suggested that larger seeds may reflect an adaptation to low mineral nutrient availability in the highly weathered soils characteristic of Guianan forests (Ter Steege et al., 2000). However, nutrient profiles of surface soil layers that are most relevant to seedling establishment are no more deficient at the Paracou site than in other neotropical forests (Baraloto et al., 2005b). Second, larger seeds may reflect an adaptation to dispersal by larger animals, some of which may be extinct (Janzen and Martin, 1981; Hammond and Brown, 1995). Yet many of the very large-seeded species in French Guiana (e.g., *Licania macrophylla*) are dispersed by abiotic mechanisms such as gravity or even water. As a result, smaller-seeds from our sample and the corresponding epigeal seedling types are more likely to be animal dispersed than larger seeds (Table 3). Nonetheless, French Guiana has many species with seeds of more than 10 g that are dispersed by terrestrial rodents (see Appendix S1). A third explanation for larger seeds in the Guianas posits that larger-seeded species are better adapted to later-successional

TABLE 4. Summary of an ANCOVA analysis for seedling survival to 8 months of age, testing interactions between seed size (seed) and seedling cotyledon type (cot), and factorial treatments of light and seedling damage. Data were the mean survival rates in each treatment for each of 20 species, angularly transformed to meet assumptions of normality.

Source	df	Mean Squared		
		Error	F	P
Dry seed mass (seed)	1	0.45	5.65	0.02
Light	1	0.62	7.76	0.007
Damage treatment	3	3.64	45.9	<0.001
Cotyledon type	4	0.65	8.16	<0.001
Seed × light	1	0.001	0.01	0.93
Seed × damage	3	0.15	1.95	0.13
Seed × cot	4	0.21	2.66	0.04
Light × damage	3	0.03	0.38	0.77
Light × cot	4	0.03	0.46	0.77
Damage × cot	12	0.26	3.29	<0.001
Seed × light × damage	3	0.004	0.05	0.98
Seed × damage × cot	12	0.098	1.24	0.27
Seed × light × cot	4	0.028	0.35	0.84
Light × damage × cot	12	0.026	0.33	0.98
Seed × light × damage × cot	12	0.03	0.37	0.97
Error	80	0.08	—	—

TABLE 5. Summary of an ANCOVA analysis for seedling relative growth rate for height, testing interactions between seed size (seed) and seedling cotyledon type (cot), and factorial treatments of light and seedling damage. The stem damage treatment was not included in the analysis because of reduced sample size due to high mortality. Data were the mean relative growth rates in each treatment for surviving individuals of each of 20 species. Significant mortality in several treatment combinations resulted in an unbalanced design, so sums of squares were weighted in the analysis.

Source	df	Mean Squared Error		
		F	P	
Dry seed mass (seed)	1	0.009	3.58	0.06
Light	1	0.004	1.45	0.23
Damage	3	0.008	3.0	0.06
Cotyledon type	4	0.02	7.96	<0.001
Seed × light	1	0.005	1.95	0.17
Seed × damage	2	0.002	0.68	0.51
Seed × cot	4	0.003	1.05	0.39
Light × damage	2	0.002	0.61	0.55
Light × cot	4	0.010	3.81	0.008
Damage × cot	8	0.002	0.72	0.67
Seed × light × damage	2	0.001	0.07	0.93
Seed × damage × cot	8	0.001	0.56	0.80
Seed × light × cot	4	0.007	2.93	0.03
Light × damage × cot	8	0.001	0.47	0.88
Seed × light × damage × cot	8	0.001	0.24	0.98
Error	59	0.003	—	—



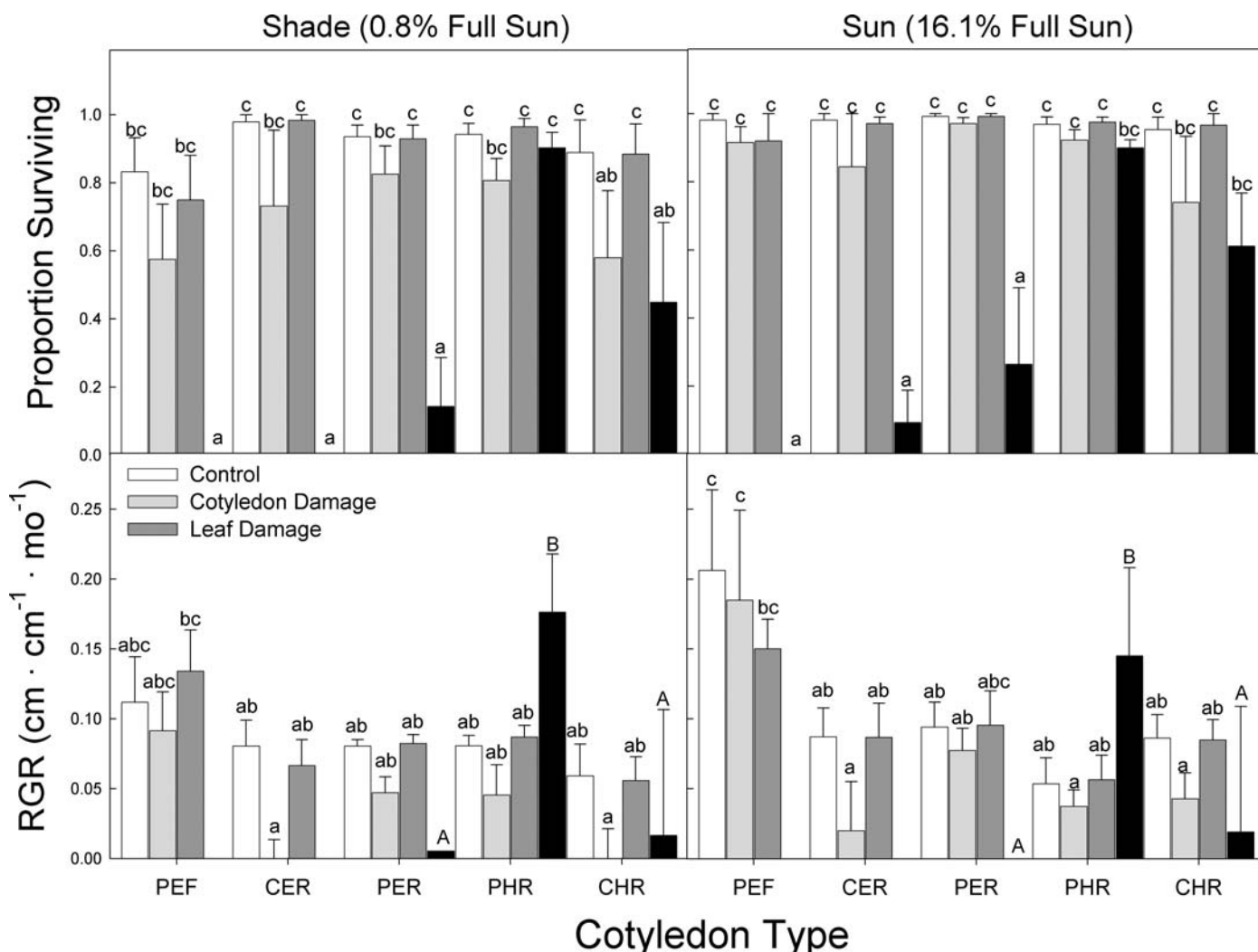
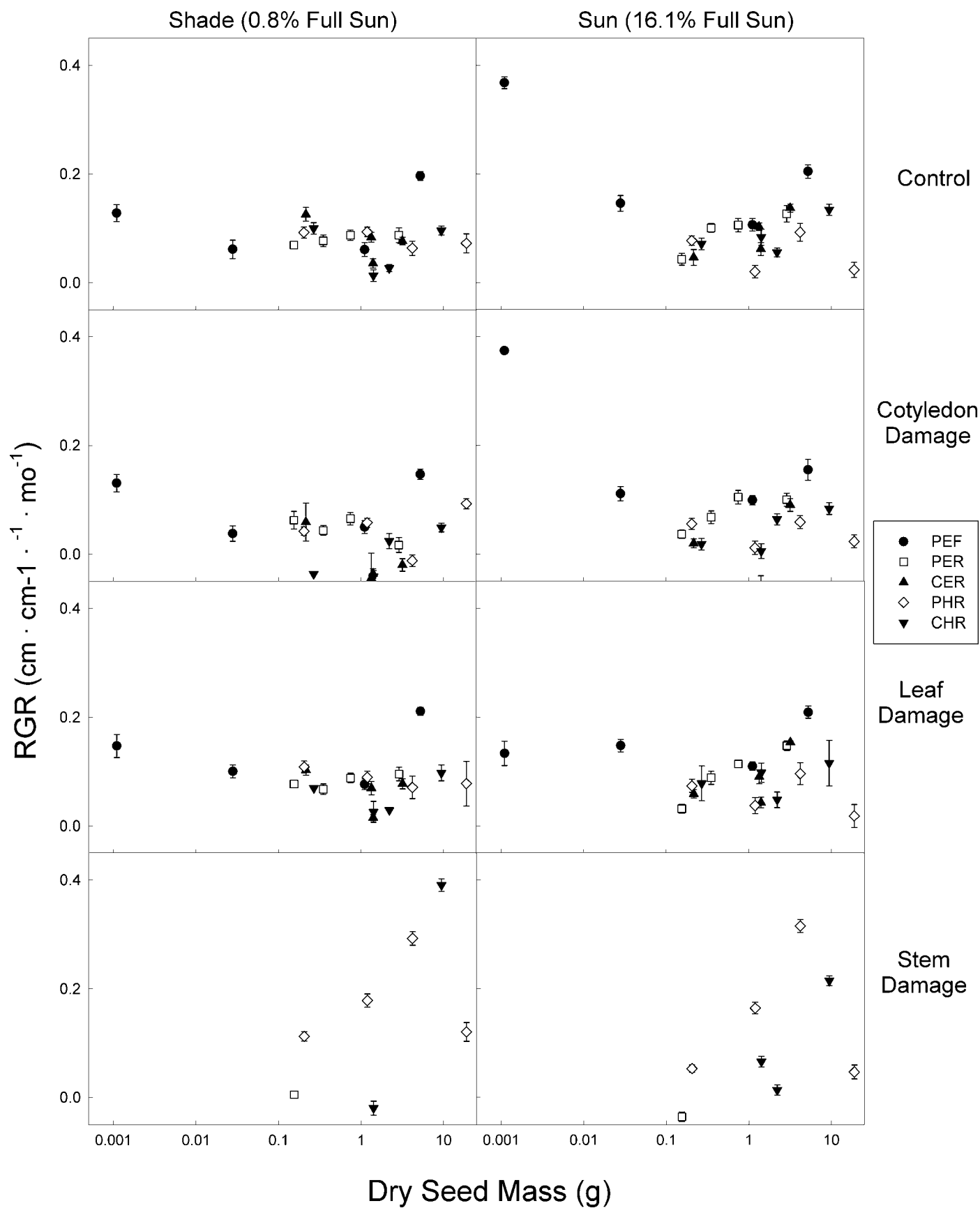


Fig. 2. Seedling survival and growth in a shadehouse experiment as related to damage treatment and cotyledon type. Bars are the mean performance of seedlings of four species within each of the five cotyledon types described in the text. Standard deviations of the mean represent variation among species within each treatment  $\times$  cotyledon type combination. Bars with similar noncapitalized letters indicate groups that are not significantly different based on post-hoc comparisons using Bonferroni tests across all light  $\times$  treatment  $\times$  cotyledon type combinations. Capital letters in the relative growth rate (RGR) panels indicate differences among the hypogeal cotyledon types.

forests that are hypothesized to characterize the Guiana Shield. It is unlikely, however, that large seed size at Paracou is related to forest age or successional status, as was suggested for MHER (Hammond and Brown, 1995); Paracou is thought to be part of a relatively young (<3000 yr) coastal lowland forest (Charles-Dominique et al., 2000). Interestingly, germination of many of the larger-seeded French Guianan species with hypogeal cotyledons is delayed by more than 2 wk, a trait that has been suggested to reflect adaptations to disturbance

(Garwood, 1983). In fact, we found no correlation between seed mass (or cotyledon type) and germination delay (Table 3). The large seed size (and accompanying hypogeal cotyledons) in French Guiana may instead simply reflect the historic dominance of families such as the Chrysobalanaceae and Lecythidaceae, both characterized by large seeds, in the Guiana shield relative to sites in Amazonia and Central America (Terborgh and Andresen, 1998; Ter Steege et al., 2000; Ibarra-Manríquez et al., 2001).

Fig. 1. Seedling survival as related to seed mass, cotyledon type, and light and damage treatments in the shadehouse experiment. Data are the proportion of seeds surviving to 8 months of age in each of four damage treatments including a control (Control), removal of one half of cotyledon mass (cotyledon damage), removal of one half of initial seedling leaf area (leaf damage), and stem cutting at 5 cm from soil surface (stem damage). Standard errors of the mean were calculated by pooling seedlings within each of the three main plots in the split-plot experimental design. Species sharing cotyledonal morphology are indicated with the same symbols; the legend refers to cotyledon type as described in the text (see Table 1 for full descriptions of species).



**Seed size and seedling morphology**—Seedlings with hypogeal cotyledons are consistently associated with larger seed size, not only at Paracou but in other neotropical and paleotropical forests (Garwood, 1996; Silman, 1996; Ibarra-Manríquez et al., 2001; Zanne et al., 2005). This pattern may partly reflect the constraints imposed on cotyledon functional morphology by seed size; the largest seeds cannot be physically supported in an epigeal position. Indeed, all but one surveyed taxon (*Poraqueiba guianensis*, Icacinaceae) at Paracou with dry seed mass greater than 5 g have hypogeal cotyledons. Correlations among seed mass, seedling type, and other seedling traits suggest the evolution of a coordinated set of traits for seedling establishment, defined by a gradient from smaller-seeded species with epigeal foliar cotyledons, orthotropic stems, and dichotomous root systems at one extreme, to larger-seeded species with hypogeal reserve cotyledons, plagiotropic stems, and taproots at the other extreme. Nonetheless, within the intermediate seed size class of 0.5–1 g dry mass, cotyledon types are equally represented, suggesting the potential for complementary axes of trait divergence that may reflect adaptations to limiting resources or herbivore pressure. We examined the differential responses to such treatments in the manipulative experiment.

**Seed size, seedling morphology, and seedling performance**—A major contribution of this study is the clear demonstration that correlations between seed size and seedling performance depend strongly on seedling functional morphology. Large-seeded species are predicted to be better adapted to the catastrophic events encountered by seedlings because they can compensate for damage using seed reserves (Foster, 1986; Westoby et al., 1996). However, in our study the effects of seed size on seedling performance differed among seedling cotyledonal types. When cotyledon type was not considered, larger-seeded species survived better, especially in response to damage (Fig. 1) and grew more slowly, especially when light was limiting (Fig. 3). The increased survival of larger-seeded species depends greatly on cotyledons (hypogeal) that tolerate deep shade and tissue removal. Hypogeal species better survived stem cutting because meristematic tissue was not completely removed by this treatment as was the case for seedlings with epigeal cotyledons. This suggests that in the forest, hypogeal species will have a survival advantage in the presence of grazing herbivores. Exceptions, and the possibility for more complex tradeoffs, may occur if some smaller-seeded species also invest in anti-herbivore chemical defenses (Rosenthal and Kotanen, 1994; Fine et al., 2006).

Although larger-seeded species with hypogeal cotyledons did tend to grow more slowly, they were also able to respond rapidly to stem cutting (Fig. 3). When light is not limiting, these species may use seed reserves to invest in root development or to store nutrients (Raaijmakers and Lambers, 1996) or nonstructural carbohydrates (Myers and Kitajima, 2007). Morphological plasticity in response to light conditions has often been attributed to smaller-seeded species and may

give them an advantage in dynamic light environments (Poorter and Rose, 2005). Our results suggest that large seed size is part of a suite of traits that enable the seedling to tolerate low resource availability (Baraloto et al., 2005a; Poorter and Rose, 2005); plasticity in root allocation in response to light availability may enable the seedling to save resources for future growth (Grime, 1979).

Although our experiment included a large number of species, the results may have been influenced by the choice of focal species for at least two reasons. First, we attempted to represent the entire seed size range of each cotyledon type, yet some of these types have little overlap (Table 3; see also Appendix S1). Many effects of seed size were driven by species representing the extremes, where the number of cotyledon types represented is reduced. Further research investigating more species at the intermediate seed size classes, where all types are represented, will be necessary to tease apart these effects. Second, within at least one seedling type (cryptic epigeal reserve), we were limited in species choice to a contrast that was not phylogenetically independent, with three congeners represented (Table 1). However, the community survey revealed that this seedling type is very rare at Paracou as well as in other tropical forests (Table 2). As more species are surveyed, we may find other examples of this seedling type in other families, but to date it appears restricted within the Myristicaceae and the Burseraceae (see Appendix S1).

**Implications for differential seedling establishment**—Further research on field performance of species differing in seed mass and seedling morphology will be necessary to understand the consequences of the fitness differences observed here. For example, in a complementary field survey for the 10 species with hypogeal seedling morphology studied here, more than half of all seedlings in the shaded understory exhibited evidence of grazing, with no differences among species differing in seed mass (C. Baraloto, unpublished data). It is likely that species and environment interact with the incidence of damage as well as the response of seedlings to damage events. For example, several studies have indicated that larger-seeded species suffer higher seed predation and/or seedling browsing rates in gap conditions than in adjacent understory sites (Schupp, 1988; Schupp and Frost, 1989; Molofsky and Fisher, 1993; Hammond et al., 1999). Presumably, this is due in part to the higher activity of rodents and deer in gaps than in understory environments (Emmons, 1982; but see Beck et al., 2004). However, the degree to which such patterns are related to species traits such as seed size, and other environmental descriptors such as topography or forest type, remains to be explored.

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Fig. 3. Seedling relative growth rate (RGR) as related to seed mass, cotyledon type, and light and damage treatments in the shadehouse experiment. Data are the RGR for height of all seedlings surviving to 8 months of age in each of four damage treatments as described in the text. Standard errors of the mean were calculated by pooling seedlings within each of the three main plots in the split-plot experimental design. Species sharing cotyledonal morphology are indicated with the same symbols; the legend refers to cotyledon type as described in the text (see Table 1 for full descriptions of species). Note that for several species no seedling survived some treatments.

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