

Seed mass, seedling size and neotropical tree seedling establishment

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Summary

1 We examined among- and within-species effects of seed mass for seedling establishment from seed to 5 years of age in a field experiment at Paracou, French Guiana.

2 Six seeds of each of eight species were weighed and planted into each of 120 plots (1 m²) throughout closed-canopy forest along 12 100-m transects in 1998.

3 We described the microhabitat of each planting site using principal components derived from measurements of light availability, soil moisture, carbon and nitrogen content, and soil phosphorus availability. Although both survival and relative growth rate (RGR) increased with increasing light availability, no other microhabitat variable significantly affected seedling performance. Nor did the magnitude of microhabitat effects on survival or RGR differ among species.

4 Larger-seeded species were more likely to survive from germination to 1 year as well as from 1 to 5 years of age. RGR for seedling height during the first year post-germination was not related to seed mass, but smaller-seeded species did grow slightly faster thereafter. Path analyses revealed that correlations between seed mass and performance were explained in part because larger seeds produced larger initial seedlings, which tended to survive better but grow more slowly.

5 We also analysed within-species effects of seed mass for the larger-seeded *Eperua grandiflora* and *Vouacapoua americana* (both Caesalpiniaceae). Larger seeds produced larger seedlings in both species, but larger seeds survived better only for *Eperua*. Larger seedlings grew more slowly in both species, but did not offset the early (*Eperua*) and later (*Vouacapoua*) positive direct effects of seed mass on RGR that may represent contrasting strategies for reserve deployment.

6 Our results demonstrate that seed size influences performance within and among species in part because of indirect effects of initial seedling size. However, we suggest that traits tightly correlated with seed mass at the species level, such as specific leaf area, leaf longevity and photosynthetic capacity, may also contribute to interspecific performance differences.

Key-words: French Guiana, life-history trade-offs, microhabitat, path analysis, regeneration strategy, relative growth rate, seedling survival, shade tolerance

Journal of Ecology (2005) **93**, 1156–1166

doi: 10.1111/j.1365-2745.2005.01041.x

Introduction

A central tenet of life-history theory proposes a size–number trade-off for offspring (Smith & Fretwell 1974; Godfray & Parker 1991). Indeed, plant life-history theory

has attempted to account for the five-order range of seed size found in many communities (Leishman *et al.* 2000) as a continuum of maternal investment, defined by the extreme cases of many small seeds, each with a low probability of establishment, vs. a few large seeds with high probability of establishment (Venable 1992; Westoby *et al.* 2002). However, recent evidence suggests that this scenario may be too simple. First, smaller-seeded species may not always have a fecundity advantage: although species with larger seeds do tend to produce

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fewer seeds per year (Shipley & Dion 1992; Jakobsson & Eriksson 2000), they may have equal or greater lifetime seed production owing to their greater canopy area and more reproductive years (Moles *et al.* 2004).

Second, larger-seeded species may not always have an establishment advantage. It is true that larger seeds have been observed to better survive stressful environmental conditions including shade (Foster & Janson 1985; Leishman & Westoby 1994b; Osunkoya *et al.* 1994), drought (Baker 1972; Leishman & Westoby 1994a), deep litter (Molofsky & Augspurger 1992; Vazquez-Yanes & Orozco-Segovia 1992) and damage (Harms & Dalling 1997; Green & Juniper 2004a). However, smaller-seeded species tend to have higher potential growth rates and thus may outgrow seedlings from larger seeds, especially when resources are not limiting (Grime & Hunt 1974; Gross 1984; Maranon & Grubb 1993; Swanborough & Westoby 1996; Bloor & Grubb 2003). Thus, a trade-off between survival and growth rate could result in similar establishment probabilities for seedlings from large vs. small seeds (Gross 1984; Kitajima 1994). Furthermore, because the conditions granting a performance advantage to smaller seeds (e.g. high resources, no stresses) differ from those favouring larger seeds (e.g. low resources, high stresses), seedling establishment probabilities among species differing in seed size are predicted to differ along microhabitat gradients (Grubb 1977, 1996; Westoby *et al.* 1996). Spatial heterogeneity in microhabitat occurrence would then promote coexistence among species differing in seed size (Geritz 1995; Chesson 2000; Kneitel & Chase 2004).

Recent attention has focused on the mechanisms that could account for such patterns of differential performance among seeds of varying size, with three potential mechanisms receiving significant attention. First, several authors have investigated the 'reserve effect' hypothesis, which proposes that larger seeds maintain a greater proportion of reserves in storage as the seedling develops (Westoby *et al.* 1996; Green & Juniper 2004a). The reserve effect is based on the observation that larger seeds tend to have hypogeal cotyledons with a primarily storage function and these could maintain seedlings under the carbon deficits imposed by shade or tissue loss and the nutrient deficits of impoverished soils (Kitajima 1994; Ibarra-Manriquez *et al.* 2001). However, Green & Juniper (2004b) found that larger-seeded hypogeal-type species did not invest disproportionately more biomass in resprouting after damage than did smaller-seeded hypogeal species, suggesting that the reserve effect alone cannot explain the influence of seed mass on seedling performance.

An alternative mechanism, referred to by Westoby *et al.* (1996) as the 'metabolic effect', proposes that correlations between seed mass and a suite of other traits are responsible for the observed patterns of performance with seed mass. The slow relative growth rate (RGR) typically associated with larger seed size is taken to indicate inherently lower metabolic rates that permit seedlings to maintain their carbon balance under deep shade or in response to herbivory (see also Green

& Juniper 2004a). Because such a strategy of stress or hazard tolerance is associated with other traits correlated with larger seed mass, such as lower leaf-level assimilation rates, lower specific leaf area, greater leaf longevity and higher leaf toughness (Kitajima 1994; Poorter 1999; Reich *et al.* 1999; Rose & Poorter 2003), this mechanism has been referred to elsewhere as part of a shade-tolerance syndrome (e.g. Poorter & Rose 2005).

A third explanation accounting for patterns of differential performance among seeds of different size is the seedling size effect (Westoby *et al.* 1996; Leishman *et al.* 2000), which proposes that the survival advantage and growth disadvantage of larger seeds occurs because larger seeds produce larger seedlings (Howe & Richter 1982; Gross 1984; Winn 1985; Dalling *et al.* 1997; Dalling & Harms 1999; Green & Juniper 2004a). That is, larger seedlings appear to be less susceptible to size-dependent mortality associated with herbivory (Osunkoya *et al.* 1992; Silman 1996) but grow more slowly because they must allocate more biomass to stem tissue for 'direct support' and thus less to leaves for carbon assimilation (Walters *et al.* 1993; Kitajima 1994; Saverimuttu & Westoby 1996; Poorter & Rose 2005).

Tropical forest tree communities provide an appropriate setting in which to examine the consequences of seed mass for seedling establishment and the underlying mechanisms causing differences in establishment because they encompass the largest range of seed mass among vegetation types reported in the literature (Hammond & Brown 1995; Metcalfe & Grubb 1995). In addition, seed size can differ considerably within species; for example, almost 10% of species exhibit at least two-fold variation in seed size in at least one community (Baraloto 2001).

In this paper we present data from a 5-year field experiment with eight tropical tree species grown from seed, to address both the general hypotheses for coexistence among species differing in seed mass and the mechanistic hypotheses underlying patterns of performance. First, we test for the survival advantage and growth disadvantage of larger seeds predicted by the survival–RGR trade-off hypothesis. Second, we test whether relationships between seed mass and seedling performance (survival, RGR) change along environmental gradients, as predicted by the spatial heterogeneity hypothesis. Finally, we examine the mechanisms underlying correlations between seed mass and seedling performance. In particular, we test the seedling size effect mechanism both among the eight species and within two of the larger-seeded species that each exhibits 10-fold variation in dry seed mass. We discuss the implications for the evolution and maintenance of tree diversity and seed mass variation in tropical forests.

Methods

The experiment was conducted within the Paracou Reserve, near Sinnamary, French Guiana (5°18' N, 52°55' W), a seasonal lowland tropical forest with annual precipitation of 3160 mm ± 161 SE. In 1998, we estab-

lished 120 plots along 12 100-m × 10-m belt transects that were arranged perpendicular to topographic contours to maximize representation of edaphic variability. Plots were established along transects in a random-stratified design; every 10 m along each transect, one square-metre site among the 100 possibilities was chosen using random number tables. No attempt was made either to traverse or to avoid any treefall gaps.

In March 1998, three soil sampling points were established at the points of an equilateral triangle with sides of 50 cm centred within each plot. At each point, litter depth was estimated to the nearest 0.5 cm (Molofsky & Augspurger 1992) and soil surface compaction was estimated using a pocket penetrometer (Forestry Suppliers, Jackson, MS, USA); mean values of the three measures were reported for each plot. One 5-cm-diameter by 10-cm-deep soil core was extracted from beneath the litter layer at each sampling point and then bulked for each plot. Soil moisture content was determined after drying the sample at 60 °C to constant mass. A 50-g subsample of each dried core was transported to the University of Michigan where total carbon, total nitrogen and extractable phosphorus were estimated as described in Baraloto & Goldberg (2004). A principal components analysis (PCA) of variables describing soil properties defined two factors representing 65.1% of the variance: a soil softness factor, with strong contributions from litter depth (correlation = 0.882) and soil surface compaction (−0.847), and a soil richness factor, with strong contributions from soil carbon (0.787), soil nitrogen (0.764), soil phosphate availability (0.727) and soil moisture fraction (0.561). Light availability, estimated as the global site factor (GSF; HemiView software, Delta-T Instruments, UK) using hemispherical photographs at 50 cm height centred within each plot, was orthogonal to other environmental measures, with most sites under closed canopy (Table 1).

Environmental measures were repeated in March 2000 for six points along six of the 12 transects, and these were used to construct PCA axes describing soil conditions, using the same weightings as those in 1998. We observed no significant change between years in environmental characterizations of these sampling points

Table 1 Summary of environmental characteristics of the 120 plots in the experiment. Plots were selected in a random-stratified design, with one randomly chosen plot each 10 m along 1210 × 100-m belt transects. Shown for each variable is the mean and range (values at 5% and 95%), for measurements made at the initiation of the experiment in March 1998

Variable (units)	Mean	5%	95%
Light (% full sun)	1.3	0.5	4.1
Litter depth (cm)	2.2	0.5	4.5
Soil compaction (MPa)	0.11	0.03	0.20
Soil moisture (%)	20.0	13.8	26.6
Soil PO ₄ -P (mg kg ⁻¹)	3.2	0.9	10.4
Soil C (%)	2.61	1.43	5.46
Soil N (%)	0.16	0.10	0.31

Table 2 Seed mass for the focal species. Values are the mean dry mass of 50 seeds for *Recordoxylon*, *Dicorynia*, *Sextonia* and *Virola*, the mean dry mass of 50 groups of 20 seeds for *Jacaranda*, and the mean of the 720 seeds used in the experiment estimated from polynomial regressions between fresh and dry seed mass for *Carapa*, *Vouacapoua* and *Eperua*

Species*	Family	Dry seed mass (g) ± SE
<i>Jacaranda copaia</i>	Bignoniaceae	0.038 ± 0.003
<i>Recordoxylon speciosum</i>	Caesalpiniaceae	0.178 ± 0.024
<i>Dicorynia guianensis</i>	Caesalpiniaceae	0.349 ± 0.017
<i>Sextonia rubra</i>	Lauraceae	1.17 ± 0.04
<i>Virola michelii</i>	Myristicaceae	1.25 ± 0.11
<i>Carapa procera</i>	Meliaceae	6.58 ± 0.23
<i>Vouacapoua americana</i>	Caesalpiniaceae	12.39 ± 0.37
<i>Eperua grandiflora</i>	Caesalpiniaceae	27.61 ± 0.86

*Nomenclature follows Boggan *et al.* (1997). Because we did not study any congeneric species, we refer to each species using the genus name in the main text and figures.

(Hotellings $T^2 = 2.19$, $F_{3,68} = 0.71$, $P = 0.551$), although overall soil moisture was slightly higher and litter depth was slightly lower in 2000 than in 1998.

Eight focal species were chosen that represent the range of seed mass in the Paracou tree community (Table 2). Seedlings of all eight species have been observed to survive in shaded conditions with less than 1% photosynthetically active radiation (PAR) (Baraloto & Goldberg 2004). In April 1998, seeds of the focal species were collected from at least five adults per species within the reserve. We measured the wet mass of all seeds planted for the three species exhibiting high variation in seed mass (*Carapa procera*, *Vouacapoua americana* and *Eperua grandiflora*). Wet seed mass was standardized to dry seed mass using polynomial regression equations (for which r^2 varied from 0.87 to 0.94) calculated from at least 30 individuals per species dried to constant mass at 60 °C. For the other five species, the mean dry seed mass of 50 seeds (50 groups of 20 seeds for *Jacaranda copaia*) was determined.

In April 1998, six seeds of each focal species were planted into each of the 120 plots. A 1-m-high wire cage enclosure with 2-cm mesh was installed around each plot, doubled at the base to 20 cm height, to deter mammalian predators from removing seeds. Enclosures were used to avoid the false attribution of mortality to missing seeds that may have been removed by mammalian dispersal agents including *Myoprocta acouchi* and *Dasyprocta leporina*. Toothpicks were placed adjacent to smaller seeds to mark their location, and missing seeds were eliminated from subsequent analyses.

All individuals were censused monthly until 4 months from the first planting date, with seven subsequent censuses up to 5 years after planting. Survival was scored only for seeds that had been observed to germinate at a prior census date. In the case of *Jacaranda*, a species with tegument dormancy, all ungerminated seeds were censused until 8 months from planting, the first date when

germinability tests conducted in growth chambers on a subset of 50 of the remaining seeds resulted in no germination. We did not observe field germination of remaining planted seeds after this time.

Seedling RGR for height growth was calculated to permit comparisons with other published field studies (e.g. Clark & Clark 1992) as

$$\text{RGR} = (\ln(\text{height at date 2}) - \ln(\text{height at date 1})) / \text{time interval.}$$

Although height RGR provides a crude estimate for biomass RGR, height and biomass have been found to be well correlated among these eight species in a complementary shadehouse experiment ($r = 0.94$, $P < 0.001$; C. Baraloto, D. Bonal & D.E. Goldberg, unpublished data).

For seedling RGR, we performed analyses of covariance on RGR from initial size post-germination (4 months since planting) to 1 and 5 years age, for all individuals surviving to each census date. Individuals were assigned the microhabitat conditions (March 1998 measures) of the plot in which they were planted, as well as their estimated seed dry mass (ln-transformed to meet normality assumptions), as continuous independent variables.

For survival data, we performed logistic regressions with the binary dependent variable of survival at the 60-month census date and the microhabitat principal components and seed size as independent variables. The significance of regression coefficients for independent variables and their interactions was tested using Wald's statistic compared against the chi-squared distribution. We also performed regressions following Cox's proportional hazards model to test the effects of species, seed mass and microhabitat on the dependent variable of time surviving, calculated using the last census date at which an individual was observed to be alive (surviving individuals at the 60-month census were thus censored). These results were concordant with those for the logistic regression; here we present the results of logistic regression because they were also used in the path analysis described below.

To examine the relative contributions of direct vs. indirect effects of seed mass to seedling performance, we performed path analyses. Path analysis is useful for separating the effects of correlated independent variables, such as seed mass and initial seedling size, for which a multiple regression analysis may be inappropriate (Li 1981). We constructed a simple path diagram based on our understanding of causal relationships between seed mass, initial seedling size, survival and RGR. Path coefficients were calculated as the standardized partial regression coefficients for simple and multiple regressions: initial seedling height (at 4 months of age) regressed on seed mass, survival regressed on seed mass and initial seedling height, and RGR regressed on seed mass and initial seedling height. To determine whether these relationships changed during the course of the experiment, we calculated these coefficients using datasets at the 12-month and 60-month censuses. To

determine if these relationships were consistent within as well as among species, we also calculated these coefficients for all eight species combined as well as within two species, *Eperua* and *Vouacapoua*, for which seed mass varied more than 10-fold and a sufficient number of seedlings survived to permit comparisons.

Results

Across all species, high mortality occurred during the first 8 months following planting (Fig. 1). However, 5-year mortality rates differed widely among species (Table 3), with more than 99% of *Jacaranda* seedlings but fewer than 42% of *Eperua* seedlings dying over 5 years (Fig. 1). Overall, larger-seeded species had higher survival rates throughout the experiment (Fig. 2). All species survived better with increasing light availability, but no other microhabitat factor had a significant effect on survival (Table 3). Furthermore, the effect of increasing light availability on survival was not significantly different between species (Table 3).

Although species grew at significantly different rates (Fig. 2), seed mass was a less significant predictor of RGR than it was for survival (Table 3). Among species, initial seedling RGR was not correlated with seed mass, but smaller-seeded species did grow faster from 1 to 5 years of age (Fig. 2). Microhabitat effects on growth were similar to those for survival. All species grew much faster in plots with greater light availability, but no other microhabitat factor influenced RGR, nor did we observe any species \times microhabitat interactions for RGR (Table 3).

We used path analysis to quantify simultaneously the direct and indirect (via initial seedling size) contributions of seed mass to survival and RGR. Path diagrams

Table 3 Summary of the effects of species, seed mass and microhabitat variables (see text for complete descriptions) on seedling performance. Six seeds of each of eight species were planted across 120 planting sites in which environmental conditions were measured in March 1998. Dry seed mass for each seed (ln-transformed) was entered into the models as a covariate. Survival data were analysed using logistic regression for the 3830 seeds that had germinated within 8 months of planting. Shown is Wald's statistic and corresponding probability values, for species effects and interactions with microhabitat descriptors. Seedling relative growth rates (RGR) for height from 4 to 60 months age were analysed using ANCOVA for the 808 seedlings that survived until the final census date. Shown is the F -statistic with corresponding probability values

Factor	d.f.	Survival		RGR	
		Wald	P	F	P
Species	7	94.3	< 0.001	2.12	0.035
Dry seed mass	1	7.46	0.006	4.53	0.034
Light	1	10.3	0.001	7.43	0.007
Soil softness	1	1.22	0.27	0.54	0.46
Soil richness	1	0.45	0.50	0.92	0.34
Species \times Light	7	13.0	0.08	1.03	0.41
Species \times Soil softness	7	4.50	0.72	0.46	0.86
Species \times Soil richness	7	4.85	0.68	0.32	0.95

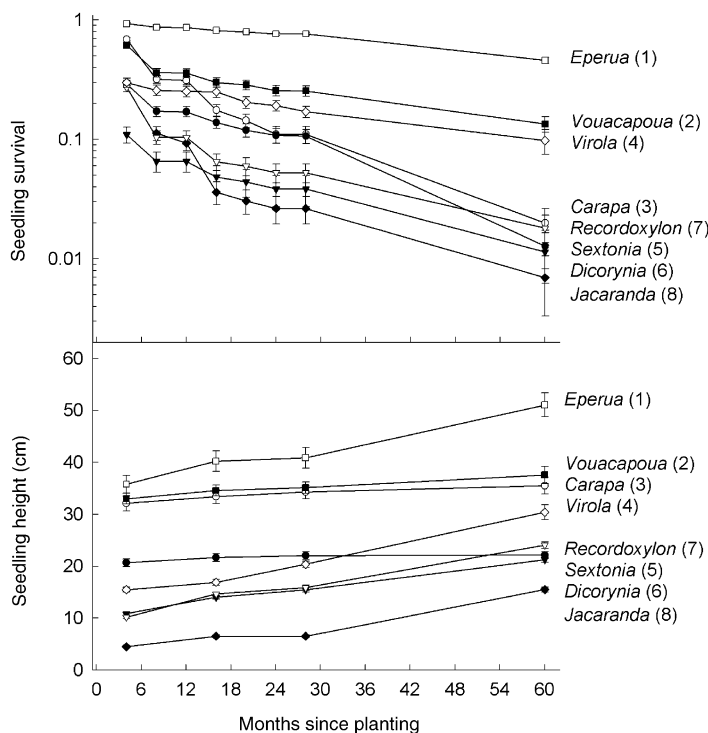


Fig. 1 Changes in survival and seedling height over 5 years for the eight species planted in the field experiment. Data are the means (\pm standard error) of six germinating seeds and the corresponding proportion of surviving seedlings planted into each of 120 plots. Species are identified by genus names adjacent to the axes, with rankings of seed mass indicated in parentheses (see Table 2).

are illustrated in Fig. 3 for all species grouped together, as well as within *Eperua* and *Vouacapoua*. In each diagram, the strength of the path is depicted by the width of each arrow and indicated by the standardized partial regres-

sion coefficient. The total contribution of seed mass to each measure of performance can be estimated as the sum of the direct effect and the product of the two paths describing the indirect effect. For example, across all

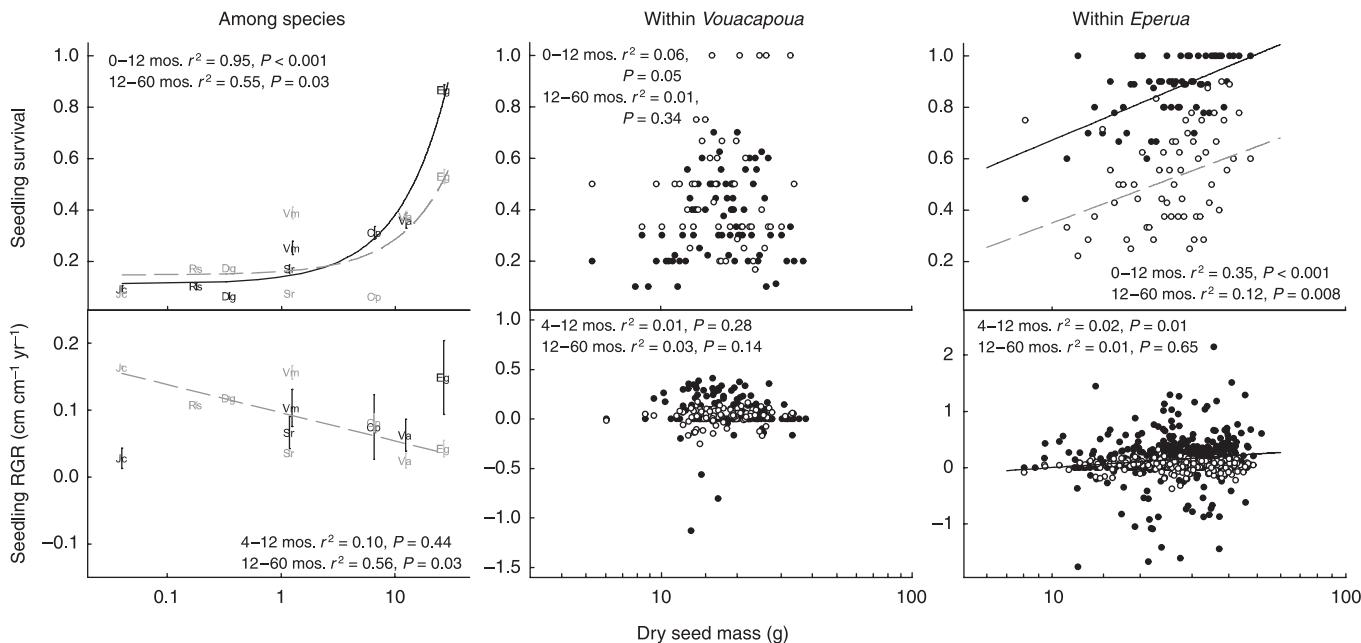


Fig. 2 Among- and within-species effects of seed size on measures of seedling performance. Dry seed mass was estimated from fresh mass using species-specific regressions from 50 seeds dried at the initiation of the experiment. The leftmost panels compare means (\pm standard errors) for eight species identified by specific epithet initials. The centre and right panels present within-species effects for *Vouacapoua* (161 seedlings at 1 year, 84 seedlings at 5 years) and *Eperua* (413, 251). For survival comparisons within species, individuals were orientated by dry seed mass and grouped into bins of 10 for which the mean dry seed mass and proportion surviving were calculated. Correlation coefficients and probability values for linear or loglinear relationships are indicated for each panel at early (solid symbols and curves) and later (grey or open symbols and dashed curves) seedling stages.

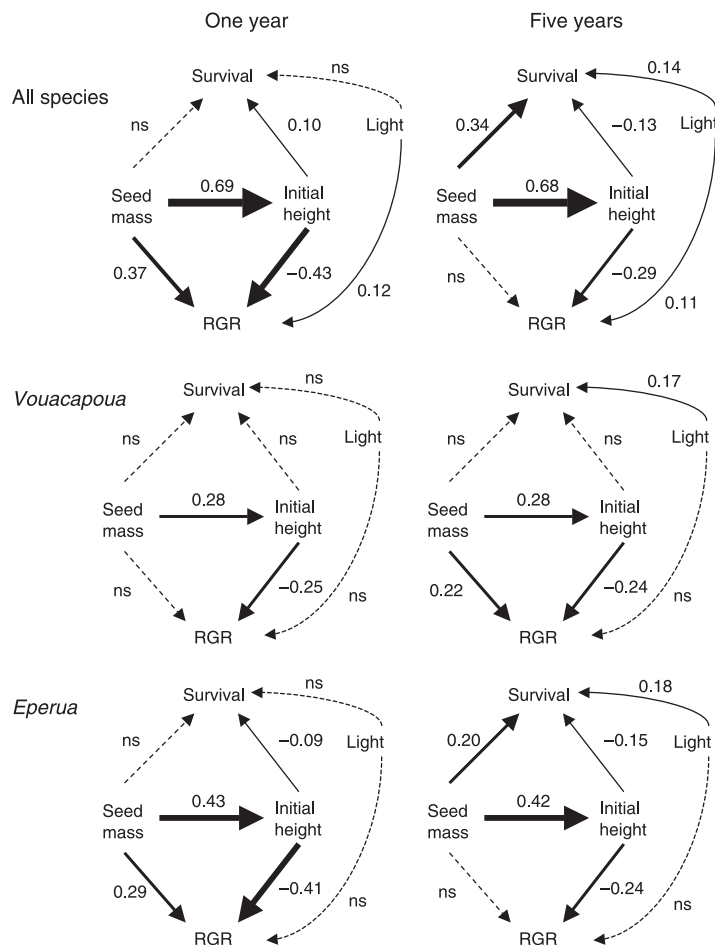


Fig. 3 Path analyses illustrating the direct and indirect effects of seed size, and the effects of plot-level light availability, on seedling performance. In each diagram, the strength of the path is depicted by the width of each arrow and indicated by the standardized partial regression coefficient. The total contribution of seed mass to each measure of performance can be estimated as the sum of the direct effect and the product of the two paths describing the indirect effect. The top panels present analyses for all species combined, whereas the others represent analyses for the single species *Vouacapoua* or *Eperua*. Left- and right-hand panels represent datasets from the 1-year and 5-year census dates. Although it is not noted in the figure, a significant amount of variance in both RGR and survival was not explained by the three variables (light, seed mass or initial seedling height) in all cases.

species larger seeds survived better initially because of a slight indirect effect but survived better later because of a direct effect (and despite a negative indirect effect). Seed mass explained almost half of the variation in initial seedling height across all species, and indirect effects of seed mass on performance mediated by initial seedling height were common both within and among species. However, the magnitude and direction of direct vs. indirect effects varied among vs. within species as well as between the two census datasets. *Vouacapoua* exhibited no direct or indirect influence of seed mass on survival at either census date. By contrast, larger seeds of *Eperua* were less likely to survive initially because they made taller seedlings that appear to have been more vulnerable to stem browsing or branchfall. Both between and within species, seedlings that were larger initially grew more slowly, and this effect persisted through the 5-year census date. Seed mass thus showed a consistent negative indirect effect on RGR that nevertheless did not offset the early (all species, *Eperua*) and later (*Vouacapoua*) positive direct effects of seed mass on RGR.

Discussion

SEED MASS AND MICROHABITATS

One of the most interesting results of this study is that differences between species in the transition between newly germinated and established seedlings in this community were not explained by environmental conditions in the forest understorey. Although both survival and growth were enhanced with increasing light availability, the magnitude of this effect did not differ significantly between species (Table 3). We thus failed to find support for the spatial heterogeneity hypothesis that predicts partitioning of microhabitat gradients among species differing in seed mass (Grubb 1996). There are three possible explanations for this result. First, we may not have adequately described the microhabitat variables to which species respond differentially. Elsewhere it has been suggested that subtle responses of seeds and seedlings to the physical environment are more likely to be detected at the microhabitat spatial scale at which

seedlings actually respond to their environment (Molofsky & Augspurger 1992; Huante *et al.* 1998; Nicotra *et al.* 1999). In this study, we went to great lengths to do just that; we planted seeds across a large random sample of microhabitat conditions, and we quantified the environment in great detail at the microhabitat scale (Table 1). Although microhabitat differences between plots may have changed with seasonal events during the year, the consistency of these measures among the 36 sites characterized both at the start and 2 years into the experiment suggests that our protocol provided an adequate description of plot differences at a particular season for at least the first 2 years of the experiment. Given the large number of replicates used to define gradients of independent variables for regressions, the lack of microhabitat effects is unlikely to be due to a lack of statistical power in the analyses.

An alternative explanation for the lack of species \times environment interactions is that the plots in this study did not encompass the microhabitat types to which species respond differentially. For example, most (112 of 120) of the plots received less than 3% of full sunlight. Our plots did represent most soil types occurring at Paracou, so the only microhabitats absent from our survey were larger canopy openings. Although canopy gaps (where light availability is > 6% of full-sun PAR) represent less than 5% of the ground surface area in many tropical forests (Brokaw 1985; van der Meer & Bongers 1996; C. Baraloto & P. Couteron, unpublished data), it is conceivable that species could partition light gradients that range above that measured in the plots in this study (Rose & Poorter 2003). Nevertheless, the eight species we studied all co-occur in deeply shaded habitats with light levels < 3% of full-sun PAR (Baraloto & Goldberg 2004). Furthermore, in a complementary field experiment in which seedlings of nine species, including six of those studied here, were planted in gap and understorey conditions across four soil types, only three of the 36 possible species pairs were found to switch rankings for survival or RGR between any microhabitat type (Baraloto *et al.* 2005). We thus urge caution concerning the proposed coexistence implications of studies reporting fine-scale differences between tropical tree species in response to gradients of light in the shadehouse (Poorter 1999; Sack & Grubb 2001; Bloor & Grubb 2003) because these results may not be relevant to field situations where other factors, such as herbivores and pathogens, may intervene.

A final possible explanation for the lack of observed microhabitat partitioning is simply that the null hypothesis is true; that is, performance rankings between species differing in seed mass do not change along environmental gradients. We argue that this may indeed be the case, at least across understorey conditions such as those we measured, noting that our results are consistent with those of habitat association field surveys for tropical tree juveniles, in which few or weak relationships between species and environment have been found (Webb & Peart 2000; Baraloto & Goldberg 2004).

SEED MASS AND GROWTH VS. SURVIVAL

Our results do confirm several predictions concerning the influence of seed mass on fitness correlates related to seedling establishment. Seedling survival was positively related to seed mass (Table 3, Fig. 3), as has been found in other tropical tree communities (Osunkoya *et al.* 1992; Boot 1993; Silman 1996). In addition, this study shows the strength of this relationship among the larger-seeded species characteristic of the Guiana Shield forests (Hammond & Brown 1995; Rose 2000; Baraloto 2001). The exception is *Carapa*, which suffered greater seedling mortality than would have been predicted given its larger seed mass (Fig. 1). Given the limited light availability in the plots, this result is not surprising for this species, which appears to be an anomalous large-seeded heliophile (Forget 1997; Baraloto & Goldberg 2004). Seedlings of *Carapa* are often susceptible to an unidentified fungal pathogen (C. Baraloto, personal observation), and such fungi have been found to be especially prevalent in humid understorey conditions of tropical forests (Gilbert *et al.* 2001).

Not only did larger-seeded species have a survival advantage, but they also maintained a size advantage over smaller-seeded species for 5 years. Larger-seeded species consistently produced taller seedlings across all environments, even though they grew more slowly overall (Fig. 1). Surprisingly, these advantages of larger seed mass did not appear to be offset completely by the predicted RGR disadvantage within the relatively long time period of our study. The largest-seeded *Eperua* and intermediate-sized *Virola* had among the highest RGR initially, and maintained relatively high RGR across the 5-year period (Fig. 2). Extrapolating these data through time, as suggested by Rose & Poorter (2003), the smaller-seeded *Virola*, *Recordoxylon*, *Dicorynia* and *Jacaranda* would require 8–14 years to overcome the initial height advantage of *Carapa* and *Vouacapoua*, and some of the smaller-seeded species would never overtop *Eperua* (Fig. 1). These results are inconsistent with the hypothesized trade-off between survival and RGR that could eventually confer an absolute size advantage on smaller-seeded species (Kitajima 1994; Dalling & Hubbell 2002). One potential explanation for this discrepancy is that the survival–RGR trade-off involving seed mass manifests itself most frequently in microhabitats representing extreme contrasts of light availability (gap vs. understorey; Osunkoya *et al.* 1993; Kitajima 1994). In fact, six of the species studied here do exchange performance rankings for shade survival vs. gap RGR at the later seedling stage (Baraloto *et al.* 2005). Still, the small number of gap sites resulting from our random choice of plot location underlines the relative infrequency with which this contrast manifests itself in this forest, and suggests the potential importance of alternative explanations that might prevent competitive exclusion among the many species surviving and coexisting within the shaded understorey.

SEED MASS, SEEDLING SIZE AND SEEDLING
PERFORMANCE

Our study provides mixed support for the hypothesis that seedling size explains the correlations between seed mass and seedling performance. Although larger seedlings did survive slightly better across all species within the first year, they were more likely to die in the subsequent 4-year period (Fig. 3). Larger seedlings always had higher mortality in *Eperua*, and seedling size had no influence on survival in *Vouacapoua*. By contrast, the proposed survival advantages of larger seedling size are condition-dependent, and our experiment may not have encompassed the conditions under which larger seedlings would be expected to gain advantage. For example, one proposed advantage is that larger seedlings gain access to limited resources with steep vertical gradients such as light or soil moisture (Leishman & Westoby 1994b; Metcalfe & Grubb 1995). Light levels in our experiment were extremely low, and vertical gradients at ground level are likely to be negligible (Leishman & Westoby 1994b), so larger seedlings were not likely to enjoy any increased access to limiting resources. This observation is corroborated by the strong negative effect of seedling size on RGR (Fig. 3), although we note that larger seedlings often have lower RGR because they must invest more biomass in supportive stem tissues (Rose & Poorter 2003).

Another proposed advantage for larger seedlings is that they can emerge above deeper leaf litter (Molofsky & Augspurger 1992). However, the experiment was established at the time of fruiting for the focal species, which corresponds to the annual small rainy season during which leaf litter that accumulates during the dry season has decomposed to shallow (< 2.5 cm) levels (Table 1; see also Baraloto & Goldberg 2004). The surprising negative relationship we found between initial size and survival might be explained because larger seedlings were more apparent to grazing herbivores such as deer (*Mazama* spp.), which were probably able to reach over the exclosures. Alternatively, larger seedlings may be more vulnerable in the shaded understorey because taller seedlings cannot invest as much biomass in leaf area and thus have a higher whole-plant light compensation point (Bloor & Grubb 2003). The increased capacity of larger seeds to resprout (e.g. Harms & Dalling 1997; Green & Juniper 2004a) may explain the direct (and overall) positive influence of seed mass on long-term survival (Fig. 3).

Seedling size was a stronger correlate for RGR than for survival, with larger seedlings growing more slowly across species as well as within both *Eperua* and *Vouacapoua*. Still, a large proportion of variation in both survival and RGR was not explained by the seedling size effect. Some of this variation may have been explained by other seed mass effects. For example, larger seeds may have stored more seed reserves within cotyledons or as non-structural carbohydrates. The larger-seeded species in our study have hypogeal cotyledons and thus are able to resprout in response to leaf or stem

damage common in the forest understorey (Dalling *et al.* 1997; Harms & Dalling 1997; Dalling & Harms 1999). Within several hypogeal-type species, including *Eperua* and *Vouacapoua*, the number of times seedlings can resprout increases with the amount of reserves (Baraloto 2001; Green & Juniper 2004b; P. Jansen, personal communication). *Vouacapoua* may have a delayed deployment of seed reserves that are stored either in cotyledons or non-structural tissue such that larger seeds grow faster in the longer term (Fig. 3). Further research investigating this reserve effect of seed mass on seedling performance will require not only measurements of cotyledon and seedling biomass through time (Green & Juniper 2004a), but also quantification of structural vs. non-structural carbohydrates in stem and root tissue (Myers 2004).

An alternative explanation for the observed direct correlations between seed mass and seedling performance is that performance is influenced by a suite of traits that are tightly correlated with seed mass (Poorter & Rose 2005). Shadehouse studies of the same species we studied here revealed that the smaller-seeded species tend to invest more in leaf allocation (i.e. they have higher leaf mass fractions) and have thinner leaves with increased surface area per unit of biomass invested in leaf tissue (i.e. they have higher specific leaf area), both of which contribute to a higher leaf area ratio (C. Baraloto, D. Bonal & D.E. Goldberg, unpublished data). Further observations across a wider light gradient will be necessary to investigate the contribution of relationships between seed mass and other traits conferring shade tolerance, to any trade-offs between survival and growth.

SEED MASS, LIFE-HISTORY TRADE-OFFS AND
TROPICAL TREE COMMUNITY STRUCTURE

Moles & Westoby (2004) propose that the fitness consequences of larger seed mass are best examined across the entire plant life cycle, including seed production, pre-dispersal predation, dispersal, post-dispersal predation, seedling emergence and establishment, growth to reproductive maturity and survival at reproductive age. Accordingly, the extent to which interspecific differences in seed mass permit potentially competing tropical tree species to coexist may best be analysed by placing the seedling establishment phase examined in this study within the context of the entire life cycle.

Although the seed mass – seed number trade-off may not result in an advantage to smaller-seeded species over their lifetimes (Moles *et al.* 2004), it appears to be a general phenomenon by which smaller-seeded species enjoy a numerical advantage in any given year (Henery & Westoby 2001). Still, the most recent meta-analysis included only one tropical tree (Moles *et al.* 2004), so further research on more tropical tree species from different forests will be required to confirm this pattern. The yearly numerical advantage of smaller-seeded species may manifest itself as a better rate of colonization across the forest landscape (Westoby *et al.* 1996; Nathan &

Muller-Landau 2000). Seed trap studies in several tropical forests show that smaller-seeded taxa reach a greater proportion of traps (Silman 1996; P.-M. Forget, unpublished data), but this may be due to some confounding of seed size with dispersal ability rather than fecundity *per se*; smaller-seeded species tend to have long-tailed seed dispersal shadows (Augspurger & Franson 1988; Hammond & Brown 1995).

Our study suggests that the larger-seeded species begin to compensate for any colonization disadvantage when they arrive in the same site as a smaller seed. Across most of the plots we established, larger-seeded species outperformed their smaller-seeded neighbours and would be predicted to exhibit better establishment when arriving at the same site at the same time. However, as Moles & Westoby (2004) point out, such an advantage would need to continue at the same rate for periods of weeks to years (depending on the seed mass difference) to counterbalance the numerical advantages of small seeds. In our study, for example, the first-year survival advantage of *Eperua* would need to continue for 8–14 more years to compensate for the estimated 100–1000-fold greater annual seed output of smaller-seeded *Dicorynia*, *Recordoxylon* and *Jacaranda*. In fact, this survival advantage was observed to diminish during the 5-year observation period (Fig. 1). Thus, although the larger-seeded species in our study show the clear early survival advantage found in many plant communities (Leishman *et al.* 2000), some additional advantage of larger seeds must occur to offset the annual numerical advantage of small seeds.

In fact, many studies, including this one, may actually underestimate the natural survival advantage of larger-seeded species because they score removed seeds as dead, or exclude potential seed removers as we did here. In tropical forests, many larger seeds that are removed are then cached by terrestrial rodents in adjacent sites, and this burial may help them to avoid surface predation by bruchid beetles (Forget 1991, 1997; Theimer 2003). Although a similar type of removal and dispersal may occur for smaller-seeded species via insect vectors (e.g. Hughes & Westoby 1992), the degree to which this removal influences the seed-mass–establishment relationship defined when these seeds are assumed to be dead (e.g. Moles *et al.* 2003) is an important subject that requires further observation.

The life cycle of long-lived perennials such as tropical trees does not end with seedling establishment, and the longer-term effects we uncovered here suggest that species differing in seed mass are likely to exhibit differential transitions in subsequent stages. We suggest that these stages merit further investigation. For example, Moles & Westoby (2004) present evidence from a single tropical tree community suggesting that the positive relationship between seed mass and survival is maintained at the sapling stage within the 3-year period originally reported by Welden *et al.* (1991). By contrast, a longer-term study (12 years) for 23 species at the Paracou site, including the eight studied here, reveals no relationship

between seed mass and sapling survival ($F_{1,22} = 0.003$, $P = 0.98$; C. Baraloto, unpublished data). Clearly, a complete understanding of the relationship between seed mass, seedling establishment and microhabitat specialization will require further examination of performance differences across life-history stages that are mediated either by seed mass itself or other traits with which it is highly correlated.

Acknowledgements

We thank CIRAD-Forêt and Silvolab-Guyane for permission to conduct research in the Paracou reserve. C.B. was supported during the establishment of the experiment with grants from the University of Michigan, and regional grants from ECOFOR and the CPER in French Guiana, and acknowledges the Department of Botany at the University of Florida where he was in residence during the completion of this manuscript. We are grateful to L. Curran, L. Haddon, M. Hutchings, J. Vandermeer, A. Winn, J. Wright, D. Zak, two anonymous referees, and especially to Lourens Poorter, for their useful comments on earlier drafts.

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Received 7 December 2004

revision accepted 9 May 2005

Handling Editor: Michael Hutchings