

Seedling survival and seed size: a synthesis of the literature

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Summary

1 Large-seeded species have long been known to have higher survivorship during establishment than small-seeded species. Here, we assessed the size of this advantage by compiling published data on survival through seedling emergence, seedling establishment and sapling establishment.

2 We found no relationship between seed mass and survival through the transition from viable seed in or on the soil to newly emerged seedlings ($P = 0.47$, $n = 33$ species).

3 Synthesis of data from experimental studies on the advantages of large-seeded species establishing under particular hazards (such as shade, drought or herbivory) confirmed that seedlings of large-seeded species perform better than those of small-seeded species in most situations. However, the magnitude of this advantage was not sufficient to counterbalance the greater number of seeds produced by small-seeded species m^{-2} of canopy outline year^{-1} .

4 Synthesis of data from field studies of populations under natural conditions also showed that large-seeded species have higher survival through early seedling establishment than small-seeded species ($P = 0.006$, $n = 112$ species). However, the magnitude of this advantage would only be sufficient to counterbalance the greater number of seeds produced by small-seeded species m^{-2} of canopy outline year^{-1} if mortality continued at the same rate for some time.

5 The time required for a species with 10-fold larger seeds to recoup the advantage gained by a smaller-seeded species during seed production ranged from 8.8 weeks for the smallest seeded species in the data set, up to an implausible 4.2 years for the largest-seeded species. Thus, while large-seeded species do have a survival advantage over small-seeded species during seedling establishment, the available evidence suggests that advantages must also accrue during other stages in the life cycle. One possibility is that the greater seed production of small-seeded species (m^{-2} of canopy outline year^{-1}) is partly offset by larger canopies and longer reproductive life spans in large-seeded species.

Key-words: life histories, reproductive strategies, sapling survival, seed mass, seedling emergence, seedling establishment

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Introduction

A 10-fold increase in seed mass is associated with a 10-fold decrease in the number of seeds that a plant can produce per unit canopy per year (Aarssen & Jordan 2001; Henery & Westoby 2001). This gives small-seeded species an initial advantage over large-seeded species. However, if both large- and small-seeded strategies are to persist, individuals of both strategies must produce, on average, one surviving offspring during the course of their life. One hypothesis is that large-seeded species make up for their seed production disadvantage

by increased survival during seedling establishment (Westoby *et al.* 2002). This idea has been bolstered by the many field and experimental studies that have shown seedlings from large-seeded species to have higher rates of survival (reviewed in Leishman *et al.* 2000; Westoby *et al.* 2002). However, the magnitude of the advantage of large-seeded species during seedling establishment has not previously been assessed.

Here we compile published data from as many species as possible on survival through three stages: seedling emergence, seedling establishment and sapling establishment, to assess whether the overall advantage of large-seeded species during establishment is sufficient to counterbalance the advantage gained by small-seeded species during seed production.

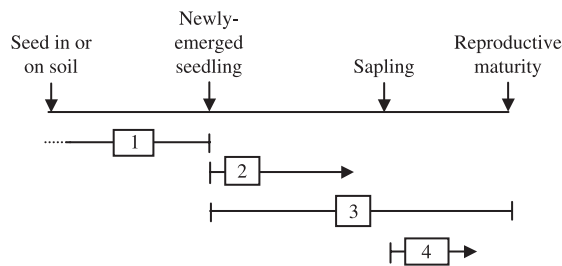


Fig. 1 Schematic diagram showing the relationship between the periods of survival addressed in each section of this study. (1) Survival through the transition from viable seed in or on the soil to newly emerged seedlings. This stage includes mortality occurring during an initial period of storage in soil, germination, and growth of the seedling to the soil surface. (2) Early seedling survival. (3) Survival from seedling emergence to reproductive maturity. (4) Sapling survival. Horizontal arrows indicate that mortality continues for an unknown amount of time. The dashed line at the beginning of stage one reflects the unknown period of mortality during seed storage in the soil before germination and emergence.

First we asked whether large-seeded species might have higher survival from viable seed in the soil to newly emerged seedlings (stage 1, Fig. 1). Most previous evidence suggests that there is no relationship between seed mass and percentage seedling emergence (Jones *et al.* 1994; Eriksson 1997; Chen *et al.* 2002; but see Dalling & Hubbell 2002). However, none of these studies quantified the proportion of viable seeds remaining in the soil. This might lead to systematic bias in estimates of seed to seedling survival, because smaller-seeded species often have greater persistence in the soil (Leishman *et al.* 2000). We provide the first general test for this relationship that accounts for this bias.

Most of the benefit of large-seededness is expected to occur during early seedling establishment (stage 2, Fig. 1). Experiments have shown that seedlings from large seeds are more tolerant of many of the hazards encountered during establishment, including competition from established vegetation, deep shade, defoliation, mineral nutrient shortage, drought and burial under soil or litter (reviewed in Leishman *et al.* 2000; Westoby *et al.* 2002). Seedlings from large seeded species also have higher survival through the establishment phase in some natural situations (Bakker 1989; Streng *et al.* 1989; Eriksson 1997; Dalling & Hubbell 2002; but see Jones *et al.* 1994).

We quantified the magnitude of the advantage of large-seeded species under experimental conditions by calculating the slope relating seed mass to seedling survival under the most severe treatment in each experiment. We also assessed the relationship between seed mass and seedling survival in natural conditions. We began by asking whether there was a relationship between seed mass and the proportion of individuals surviving for 1 week from seedling emergence. All studies monitor seedling survival to at least this age and most species will still be dependent on seed resources at this stage. This comparison therefore provides a fair test for the

presence of a relationship between seed mass and seedling survivorship across different species and studies. However, most seedlings spend more than a week establishing. To quantify the advantage of large-seeded species, we would ideally compile data on survival from seedling emergence to the end of seedling establishment. Unfortunately, because there is no agreed field method for determining when a young plant ceases to be a seedling (Fenner & Kitajima 2000), such data are not available. Instead, we investigated the probable trajectory of seedling survival through time, and asked how many weeks it would take for the higher survival of large-seeded species to counterbalance their disadvantage during seed production.

We also attempted to quantify the relationship between seed mass and survival from seedling emergence through to reproductive maturity (stage 3, Fig. 1).

The advantage of large-seededness is generally expected to expire after the seed reserves have been deployed (Leishman *et al.* 2000; Dalling & Hubbell 2002; Westoby *et al.* 2002). This expectation is supported by the available empirical data (Walters & Reich 2000; Dalling & Hubbell 2002). However, these data are sparse. Thus our final aim was to provide an additional comparative test of the relationship between seed mass and sapling survival (stage 4, Fig. 1).

In summary, the questions addressed in this study were:

1. Do large-seeded species have higher survival from viable seed in or on the soil to newly emerged seedlings?
2. Do experimental studies of the advantages of large-seededness during seedling establishment under various hazards show a great enough advantage to the large-seeded species to counterbalance their disadvantage during seed production?
3. What is the slope of the relationship between seed mass and early seedling survival under natural conditions, and how long would the initial rate of mortality need to continue to give large-seeded species sufficient survival advantage to counterbalance the seed size/number trade-off?
4. What proportion of plants survive from seedling emergence to reproductive maturity?
5. Is there any relationship between seed mass and sapling survival?

Methods

COMPILATION OF DEMOGRAPHIC DATA FROM THE FIELD LITERATURE

We searched JSTOR (<http://www.jstor.org>), BIOSIS and Current Contents (both from Ovid Technologies Ltd) for papers in English containing the words 'seedling survival' and 'germination'. All publications accessible through these databases in week 38, 2002, were searched. We tried to include only studies of seedlings in natural conditions. Studies were excluded if seedlings were raised in pots, within exclosures, under shelters, with

extra watering, with pesticides, with weeding, or with supplementary fertilization. Studies were also excluded if seedlings were not studied from the day they emerged, or if seedlings were transplanted. Studies that did not report sample size, or included fewer than 10 individuals of a species were also excluded. We excluded studies in which pooled seedling counts might have led to underestimates of seedling mortality. Studies on single species were included if they met other criteria.

We recorded:

1. The proportion of germinable seeds in or on the soil that survived germination and emergence, and reached the earliest category of seedlings recorded by the study. Where possible, we recorded the number of germinable seeds in or on the soil immediately before germination, to minimize the period of pre-germination mortality. However, mortality in soil could not be completely separated from mortality during germination and emergence. Where possible, we also recorded the proportion of viable seeds remaining in the soil at the end of the observation period. When source papers quantified viable seeds remaining in the soil we were able to obtain an unbiased estimate of survival through the seed to seedling transition. Cases where viable seeds were not quantified provided less satisfactory data, but for more species.
2. The probability of newly emerged seedlings surviving to reproductive maturity.
3. The proportion of newly emerged seedlings surviving for 1 week. The following methods were used (listed in decreasing order of preference). (i) The number of seedlings remaining alive at 1 week was read directly from tables or graphs (using Datathief; B. Tummers 1999; <http://www.nikhef.nl/~keeshu/datathief/>). (ii) Equations fitted to entire data sets in source papers were used to calculate the proportion of seedlings alive after 1 week. (iii) At least three data points (preferably close to 1 week, and usually less than 1 year, always including a point at 100% survival for time 0) were read from graphs, tables or text. Exponential, power and linear curves were fitted to these data, and the equation of the line with best-fit was used to calculate the proportion of seedlings alive after 1 week. (iv) If data were only available for time 0 and one later time, we calculated the proportion of seedlings alive after 1 week assuming a constant mortality rate, i.e. exponential decay. Exponential decay was most often the model of best fit where method iii was used.

In some studies, the second observation was more than a month after the initial observation. In these cases, the maximum acceptable interval between observations had to be considered. We aimed to exclude studies where the interval was long enough that mortality was likely to have slowed, or where seedlings might have reached reproductive maturity. In most cases, this meant that data were excluded if the second observation was more than a year after seedling emergence. A lower threshold was applied for annuals and biennials, and second observations up to 15 months after emer-

gence were deemed acceptable in some cases. These decisions were arbitrary, but efforts were made to make decisions as biologically meaningful as possible.

We considered the possibility that systematic bias might arise from a correlation between seed mass and the interval between observations. If ecologists left longer intervals between censuses for large-seeded species than for small-seeded species (perhaps because of lower mortality rates, or a longer time spent as seedlings), and if survivorship curves flattened out over long periods (as observed in some studies, e.g. Chambers 1995; Moles & Westoby 2004; but see Bradstock & O'Connell 1988; Herrera *et al.* 1994), then large-seeded species might artificially appear to have higher 1-week survival. However, we found no evidence for a relationship between seed mass and observation interval ($P = 0.64$, $R^2 = 0.002$, $n = 112$ species). Thus, although we would ideally have used data with equal observation intervals, it seems unlikely that the variable observation intervals gave rise to a systematic bias in this data set.

EXPERIMENTS ON THE ADVANTAGES OF LARGE-SEEDEDNESS

Studies were collected from Westoby *et al.* (2002), plus a Current Contents search for the terms 'seedling survival' and ('seed mass' or 'seed size') in papers published between January 2002 and March 2003. Studies were included only if they included five or more species, with seed masses spanning at least one order of magnitude. We recorded seed mass and seedling survival through the harshest treatment in each study. Where numbers were not reported in text or tables the program 'Datathief' (B. Tummers 1999) was used to read values from graphs. \log_{10} seedling survival was plotted against \log_{10} seed mass, and linear regressions were fitted to the data using Excel 97.

STATISTICS

We used logistic regressions to quantify relationships between seed mass and the proportion of individuals surviving each stage. These regressions assume a binomial data structure within each species (individuals either live or die). Because not all between-species variation in survival is due to seed mass, a term was needed in the model to account for species-to-species variation (McCulloch & Searle 2001). Therefore, we fitted a random effects logistic regression to estimate the relationship between survival and seed mass. We used winBUGS version 1.3 (MRC Biostatistics Unit, Cambridge University, Cambridge, UK, 2002), which uses the Monte Carlo Markov Chain method (Gilks *et al.* 1996) for estimation. In fitting models, we used a burn-in of 1000 updates, followed by 50000 updates. The proportion of variation between species due to factors other than seed mass can be assessed by comparing the standard error of the species random effect (henceforth SESRE) with the range of predicted values (logit-transformed).

In addition to cross-species analyses, we performed phylogenetic regressions (Grafen 1989) on the relationships between \log_{10} seed mass and seed or seedling survival. The phylogenetic trees constructed (Appendices S1 and S2 in Supplementary Material) follow APGII (2003) to order level for angiosperms, and Chaw *et al.* (2000) for gymnosperms. Path segment lengths for phylogenetic trees were calculated by assigning a height to each node that was one less than the number of species below or at that node in the tree (Grafen 1989). It was beyond our ability to devise a phylogenetic random effects logistic regression, so we did linear phylogenetic regression with logit-transformed ($\ln(P/1 - P)$) survival data, using Phylo.glm version 1.03 (Grafen 1989). Linear regression on logit-transformed data is functionally similar to logistic regression. However, the phylogenetic regression did not include a term for a species effect.

In order to avoid computational problems with zero (and 100%) survival values in linear regressions and on the graphs, 0.5 was added to (or subtracted from) the number of surviving individuals recorded for these species. This process was not used on data for logistic regressions, which treat zeros and 100s appropriately. Seed mass was \log_{10} -transformed before all analyses.

Results

SEED TO SEEDLING SURVIVAL

Our searches yielded seed to seedling survival and seed mass data for 178 species from 56 families (data from 82 studies, Appendix S1). The number of seeds remaining viable in the soil seed bank was quantified for 31 species, and not quantified for 145 species. For a further two species, the number of seeds remaining viable in the soil was quantified in one study and not in another. These two species were included in both of the following analyses.

Random effects logistic regression showed a positive relationship between seed mass and the proportion of

individuals surviving emergence for the 147 species (from 65 studies) for which the number of seeds remaining in the soil was not quantified ($P = 0.01$; slope = 0.44 (95% confidence intervals (CI) = 0.18–0.74), SESRE = 1.94; this SESRE is large relative to the range of predicted values (logit-transformed, -2.6 to -1.1) fitted by the random effects logistic regression). Phylogenetic regression, however, showed no significant relationship between seed mass and the proportion of individuals surviving emergence ($P = 0.11$, d.f. = 1,78, $R^2 = 0.03$). The positive relationship in the cross-species regression might reflect lower survival of small-seeded species, or might be an artefact resulting from the greater tendency of small-seeded species to form soil seed banks. To distinguish between these possibilities, we next considered studies in which the proportion of viable seeds remaining in the soil had been quantified.

We found no significant relationship between seed mass and the proportion of individuals surviving the seed to seedling transition across the 33 species (from 18 studies, Appendix S1) for which proportion of viable seeds remaining in the soil was known, in either the logistic regression ($P = 0.47$, slope = -0.17 (95% CI = -0.48 – 0.18), SESRE = 2.57, Fig. 2), or the phylogenetic regression ($P = 0.09$; d.f. = 1,21; $R^2 = 0.13$). The absence of a significant relationship might be partly due to small sample size, but is consistent with previous results (Jones *et al.* 1994; Eriksson 1997; Chen *et al.* 2002).

SYNTHESIS OF EXPERIMENTS ON ADVANTAGES OF LARGE-SEEDEDNESS DURING SEEDLING ESTABLISHMENT

Twenty-five of the 31 studies that matched our search criteria showed that large-seeded species had a significant survival advantage over small-seeded species when establishing under experimentally imposed hazards (Table 1). Almost all exceptions were studies of older seedlings. This is consistent with previous suggestions

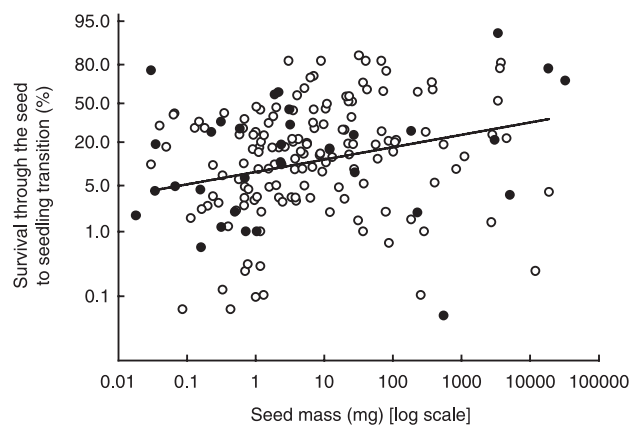


Fig. 2 Proportion of individuals surviving the transition from viable seed in or on the soil to newly emerged seedlings vs. seed mass. Data compiled from the global literature. Filled circles represent species for which the proportion of viable seeds remaining in the seed bank was quantified ($n = 33$, $P = 0.47$); unfilled circles represent species for which the proportion of viable seeds remaining in the soil seed bank was not quantified ($n = 147$, $P = 0.01$; slope = 0.44, solid line). For species represented by unfilled circles, values for the proportion of species surviving the seed to seedling transition should be treated as minimum estimates.

Table 1 Table from Westoby *et al.* (2002), updated and with effect sizes added. Studies were included only if they covered at least five species, with seed mass spanning at least one order of magnitude. Relative survival advantage is the slope of a linear regression between $\log_{10}\%$ survival and \log_{10} seed mass in harshest treatment. To counter the seed size/number trade-off, values need to be approximately 1. A value of 0 represents no relationship between seed mass and percentage survival, values less than zero indicate an advantage for smaller-seeded species. *n* is the number of species included in the study. See Appendix S4 for references

Hazard	Larger-seeded species performed better	Relative survival advantage	R^2	<i>n</i>	Study duration	Larger-seeded species did not perform significantly better	Relative survival advantage	R^2	<i>n</i>	Study duration
Competition from established vegetation	Gross 1984 ^a	–	–	–		Thompson & Baster 1992	–0.25	0.05	9	Up to 9 months
	Bakker (1989 ^b)	0.37	0.33	8	13 months					
	Reader 1993 ^{cd}	–	–	–						
	Ryser 1993	0.08	0.25	5	1 growth season					
	Burke & Grime 1996 ^{ce}	–	–	–						
	Eriksson (1997 ^{ce})	–	–	–						
Competition from seedlings	George & Bazzaz (1999); first growth season	0.19	0.77	5	4 months	George & Bazzaz (1999); 1st year ^f	0.58 ^f	0.57 ^f	5	1 year
	Leishman 2001 ^{g,h}	–	–	–						
Deep shade	Turnbull <i>et al.</i> 1999 ⁱ	–	–	–						
	Grime & Jeffrey 1965	0.06	0.87	9	12 weeks	Augsburger 1984	0.11	0.02 (NS)	18	10 weeks
	Leishman & Westoby (1994 ^{ab})	0.05	0.10	23	42 days					
	Osunkoya <i>et al.</i> 1994 ^{ej}	–	–	–						
Defoliation	Saverimuttu & Westoby (1996) ^{ck} ; cotyledon phase	–	–	–		Saverimuttu & Westoby (1996); first-leaf phase ^{ck}	–	–	–	
	Walters & Reich (2000); early phase ^l	0.59	0.7	10	54 days	Walters & Reich (2000); later phase ^m	–0.28	0.23	9	Survey from 60–100 days
	Armstrong & Westoby 1993 ^p	0.06	0.03	44						
Nutrient shortage	Harms & Dalling 1997 ⁿ	0.83	0.53	13						
	Jurado & Westoby 1992 ^{c,k}	–	–	–						
Depth under soil or litter	Milberg <i>et al.</i> 1998 ^{hours}	–	–	–						
	Gulmon 1992 ^{cd}	–	–	–						
	Jurado & Westoby 1992 ^{od}	–	–	–						
	Molofsky & Augspurger 1992 ^{o,d}	–	–	–						
Soil drought	Jurik <i>et al.</i> 1994 ^{cd}	–	–	–						
	Seiwa & Kikuzawa 1996	0.52	0.56	5						
	Leishman & Westoby (1994b), glasshouse	0.63	0.43	23	14 days	Leishman & Westoby (1994b), field	0.01	0.003	18	17 days
	Caddick & Linder 2002 ^{hours}	–	–	–						

a = Significant differences in emergence percentage and growth, but no significant difference in survival.

b = Two species omitted because of small sample size.

c = Survival not reported.

d = Greater emergence.

e = Greater recruitment.

f = The slope of this relationship is greatly influenced by one species with 0% survival. Without this data point the slope is 0.11. The authors of this paper reported this as no relationship, but did not formally analyse the data because of the low sample size.

g = Greater competitive ability.

h = Pooled data only presented.

i = Changes in plant density are shown, but it is not clear how much this is changes in percentage emergence and how much is changes in survival *per se*.

j = Greater growth.

k = Greater seedling longevity.

l = Based on survival to 54 days.

m = Percentage survival from day 60 to day 110, one species omitted as no seedlings remained alive on day 60. Regression not significant.

n = This effect might be largely due to a relationship between seed mass and cotyledon type, epigeal species (small-seeded) would lose their plumular bud in clipping, while large-seeded species with hypogeal cotyledons would not (further discussion in text).

o = Survival data only available for three species, but slope positive.

p = This relationship was reported as only significant in the phylogenetic analyses, not the cross-species. Cross-species slope shown here for consistency.

q = Number of seedlings emerging from under 1 cm of soil as a percentage of number of seedlings emerging from flats with no additional soil layer. This is not the harshest treatment in this study, but was the result analysed by the original authors.

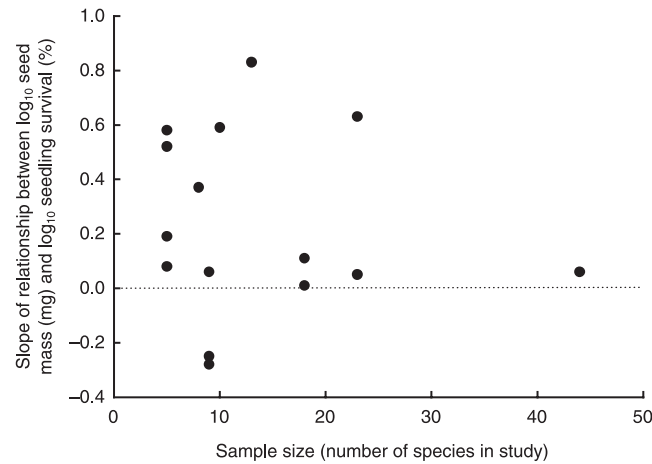


Fig. 3 Funnel graph showing the relationship between the magnitude of the advantage of large-seeded species under experimentally imposed hazards in relation to the number of species included in each study. A slope of one would be required to balance the advantage accrued by small-seeded species as a result of the seed size/number trade-off.

that the advantages of large seededness expire after seed reserves have been deployed (Foster 1986; Westoby *et al.* 1996; Walters & Reich 2000; Dalling & Hubbell 2002).

We were able to calculate the slope of the relationship between \log_{10} seedling survival and \log_{10} seed mass for 10 of the studies that showed an advantage to large-seeded species. The steepest slope was 0.83 (mean = 0.24).

The number of species in these studies was generally small (from 5 to 44). In order to assess the impact of low sample sizes on the results of these regressions, we plotted a funnel graph, showing regression slopes within individual studies in relation to the number of species included. The slope might vary with the type of stress imposed, as well as with its intensity and duration. However, no study showed a slope as steep as the value of 1.0 needed to counterbalance the advantage of small-seeded species during seed production, and the funnel graph weakly converged on a slope much less than 1 (Fig. 3). This strongly suggests that the true slope of the relationship between seed mass and seedling survival is substantially less than 1.0, at least under the circumstances of these experiments.

EARLY SEEDLING SURVIVAL IN NATURAL CONDITIONS

Our searches yielded data on early seedling survival and seed mass for 112 species from 47 families (data from 50 studies, Appendix S1).

There was a strong positive relationship between seed mass and the proportion of seedlings surviving 1 week from emergence (Fig. 4), in both cross-species logistic regression ($P = 0.003$, slope = 0.85 (95% CI = 0.45–1.38), SESRE = 2.01), and phylogenetic regression ($P = 0.004$, d.f. = 1,61, $R^2 = 0.19$, slope = 0.69).

Logistic regression models that included terms for habitat as well as for seed mass and species effects showed a significant ($P = 0.01$) interaction between habitat

and seed mass. Accordingly, data for each habitat were analysed separately (Fig. 4). There was a significant positive relationship across nine species from tropical moist forests ($P = 0.002$, slope = 1.43 (95% CI = 0.47–2.3), SESRE = 3.11), a marginally non-significant positive relationship across 40 species from temperate grasslands ($P = 0.07$, slope = 1.38 (95% CI = 0.03–3.51), SESRE = 2.59), and a significant positive relationship across 63 species from temperate forests or shrublands ($P = 0.02$, slope = 0.46 (95% CI = 0.1–0.86), SESRE = 1.38). It was somewhat surprising that relationships were weaker within habitats than across habitats. Stronger relationships within habitats might have been expected if larger-seeded species were favoured in habitats imposing stronger seedling mortality. It seems most likely that the weaker within-habitat results reflect lower sample sizes. Because the confidence intervals of within-habitat relationships were wide, and because our major question was habitat-independent, we have also presented the pooled regression in Fig. 4.

Individual studies contributed data for between one and 19 species. Survival of species in the same study may not be fully independent, because species were studied under similar environmental conditions. This non-independence could affect our results. For instance, if a study on seedling survival of five large-seeded species was performed during a drought, survival for all five species might be low. If these five species contributed a significant proportion of the large-seeded species in the compilation, the slope of the relationship between seed mass and seedling survival would be artificially shallow. We have not explicitly controlled for this effect. However, inspection of graphs of the major relationships plotted with species coded by study (Appendix S3), suggests this is not a major problem in any of the main relationships investigated here. In addition, relationships between seed mass and seedling survival were similar across species from different habitats. This suggests that the major finding of the present study is not seriously affected by

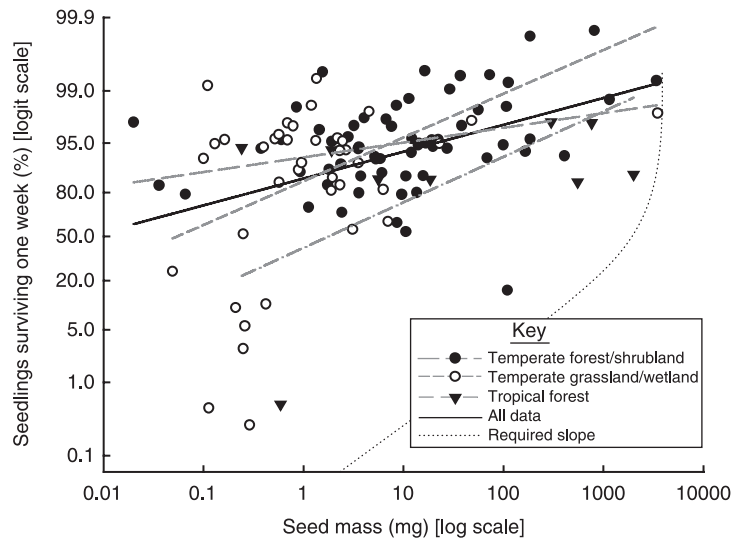


Fig. 4 Percentage of seedlings surviving the first week after germination. Data compiled from the global literature (Appendix S1). Each point represents mean values for one species. Analyses were performed using logistic regression, and were therefore able to deal appropriately with species with 0 and 100% survival (the probability of survival for these species was calculated as $0.5/n$ and $(n - 0.5)/n$, respectively, for presentation on the figures). The solid line was fitted to the whole data set, while the dashed lines represent within-habitat regressions. The dotted curve shows the slope necessary for the advantage of large-seeded species during seedling establishment to counterbalance the advantage gained by small-seeded species as a result of the seed size/number trade-off.

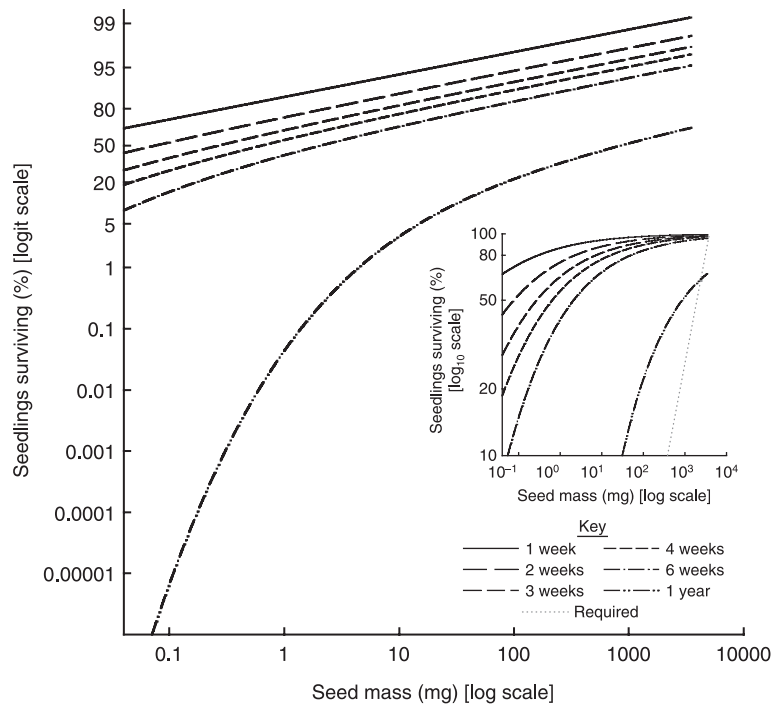


Fig. 5 Seedling survival over 1 week to 1 year (assuming a constant rate of seedling mortality through time). The inset shows the same slopes plotted on a \log_{10} scaled y-axis, as well as the slope necessary for the advantage of large-seeded species during seedling establishment to counterbalance the advantage gained by small-seeded species as a result of the seed size/number trade-off.

this problem, because an outlying study would only affect the results of one within-habitat regression.

The slope of the relationship between seed mass and seedling survival over 1 week was not steep enough to counterbalance the seed size/number trade-off (Fig. 4). However, seedlings must survive much longer than 1 week in natural situations. To assess possible consequences of seed size-related seedling mortality extend-

ing over longer times, we used the result of the logistic regression across all species combined, and forecast the proportion of seedlings surviving to future weeks, assuming mortality continues at the same rate as in the first week (Fig. 5). A constant proportion of seedlings dying each week generates an exponential decline in seedling numbers, and fits seedling survival data well in many natural situations (King 1977; Solbrig *et al.*

1980; Augspurger 1983). After 1 week, the slope fitted by logistic regression predicted that 59.7% of the seedlings of a species with seeds weighing 0.02 mg (the smallest seeds in this data set) would remain alive, compared with 99.2% of the seedlings of a species with seeds of 3489 mg (the largest seeds in this data set). By 6 weeks after emergence 4.5% of the 0.02 mg species' seedlings were predicted to remain alive, compared with 95.3% of the 3489 mg species' seedlings (Fig. 5).

Assuming the proportion of seedlings dying each week remains constant, and using the slope of the relationship between seed mass and seedling survivorship from the pooled data in Fig. 4, we calculated that species with seeds weighing 0.2 mg would require 8.8 weeks to counterbalance the 10-fold greater seed production (m^{-2} canopy year $^{-1}$) of species producing seeds weighing 0.02 mg. This seems quite plausible. However, the slope fitted by the logistic regression is nonlinear, so different times are required in different parts of the seed mass spectrum for counterbalancing to be effective. Species producing seeds weighing 2 mg would need 16.8 weeks to balance the greater seed production of species producing seeds weighing 0.2 mg. The largest seeds in this data set weighed 3489 mg. For this species to recoup the 10-fold greater seed output (m^{-2} canopy year $^{-1}$) of a species producing seeds weighing 349 mg, mortality would need to continue at the rates estimated from Fig. 4 for 4.2 years. By the end of each of these time periods, 10–20% of the seedlings of larger-seeded species, and 1–2% of the seedlings of smaller-seeded species remain alive. This seems plausible. However, it is highly unlikely that seedling mortality continues for 4 years at the same rate as in the first week of seedling establishment in any species. There is some evidence that survival curves flatten out after the initial establishment phase (Chambers 1995; Moles & Westoby 2004; but see Bradstock & O'Connell 1988; Herrera *et al.* 1994). Further, seedling survival may become independent of seed mass later in development (Foster 1986; Westoby *et al.* 1996; Westoby *et al.* 2002, Table 1, but see Sapling Survival, below). Thus, although large-seeded

species do show a clear survival advantage during early seedling establishment, it seems likely that some of the advantage gained by smaller-seeded species during seed production is balanced at other stages in the life cycle.

SEEDLING TO ADULT SURVIVAL

We found published data on the proportion of seedlings surviving to reproductive maturity across only 19 species from 12 families (data from 13 studies, Appendix S1). Further, the survival values recorded for these species (0.5–39.8%) seemed unrealistically high. Unless individuals of species that had 0.5% seedling to adult survival produced fewer than 200 seedlings through their adult lives, there would be an exponential increase in the species' abundance. It is possible that some species have seedling production this low, but 0.5% is not a realistic lower estimate for seedling to adult survival. The unrealistically high survival estimates might arise partly because demographic studies on species with high survival are more feasible than studies on species with low survival, for which thousands of seedlings might need to be tagged at emergence to ensure a few survivors.

There was no relationship between seed mass and the proportion of seedlings surviving to reproductive maturity (Fig. 6), in either cross-species logistic regression ($P = 0.56$, slope = -0.12 (95% CI = -0.53 – 0.26), SESRE = 1.37) or phylogenetic regression ($P = 0.66$, d.f. = 1,14, $R^2 = 0.01$). However, this result should be treated with caution as data were only available for 19 species, were probably not representative, and may not be fully independent (see above).

SAPLING SURVIVAL

Because of subjectivity in determining when a 'seedling' becomes a 'sapling', it was not possible to synthesize data from different studies to quantify survival through the seedling to sapling transition. However, we were able to combine data on sapling survival on Barro Colorado Island in Panama from Welden *et al.* (1991) with seed

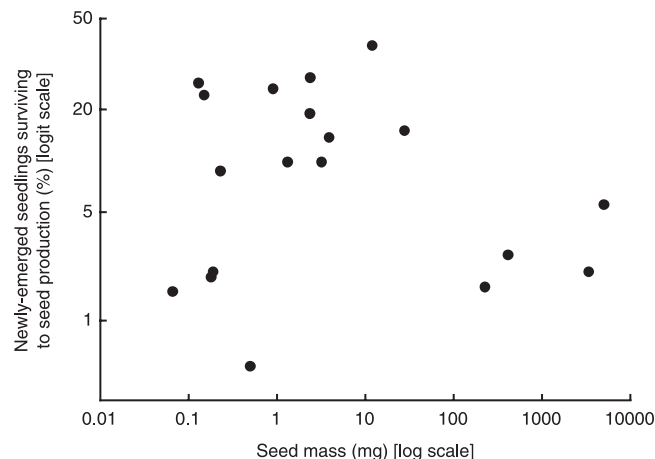


Fig. 6 The relationship between seed mass and the proportion of seedlings surviving through to seed production. Each point represents one species.

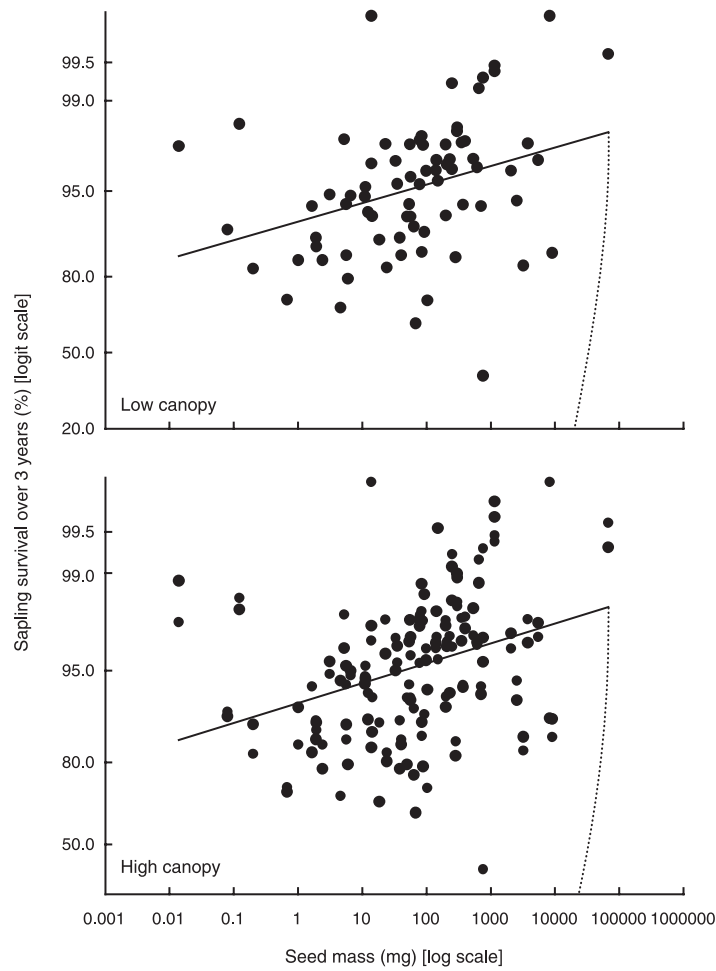


Fig. 7 Percentage of saplings surviving 3 years in a neotropical rain forest on Barro Colorado Island, Panama, in (a) a low-canopy site and (b) a site where the canopy was high above the saplings. Data from Welden *et al.* (1991). Each point represents one species. The dotted lines represent the slope that would be required to counterbalance the seed size/number trade-off. $n = 76$ species in each habitat.

mass data from other published sources (Appendix S2), to investigate the relationship between seed mass and sapling survival in high (≥ 10 m) and low (< 10 m) canopy environments across 76 species from 30 families. These data did not include sample sizes, so were analysed using linear regression on logit-transformed data rather than the logistic regression with random effects used for similar relationships elsewhere in this paper.

There was a strong positive relationship between seed mass and sapling survival in the low canopy environment (Fig. 7a) in both cross-species regression ($P = 0.004$, d.f. = 75, $R^2 = 0.11$, slope = 0.34) and phylogenetic regression ($P = 0.01$, d.f. = 1,37, $R^2 = 0.16$, slope = 0.35). There was also a strong positive relationship between seed mass and sapling survival in the high canopy environment (Fig. 7b), in both cross-species regression ($P < 0.006$, d.f. = 75, $R^2 = 0.10$, slope = 0.31) and phylogenetic regression ($P = 0.015$, d.f. = 1,37, $R^2 = 0.15$, slope = 0.30). The slopes of these relationships did not appear steep enough to counter the seed size/number trade-off alone (Fig. 7), but might contribute to the establishment advantage of larger-seeded species.

The positive relationship between seed mass and sapling survival found at Barro Colorado contrasts with the results of most previous studies, and seems unlikely to be a general phenomenon. Therefore, formal analyses of how long this mortality rate would need to persist to balance the seed size/number trade-off seemed inappropriate.

Discussion

SAPLING SURVIVAL

The positive relationship between seed mass and sapling survival through 3 years in Panama was unexpected. Previous work had led us to expect that the mortality rates of large-seeded species would become indistinguishable from those of small-seeded species once seed reserves were fully deployed (Foster 1986; Westoby *et al.* 1996; Walters & Reich 2000; Dalling & Hubbell 2002; Westoby *et al.* 2002). It is possible that resources from the large seeds of these rainforest species were still being deployed at sapling stage. However, it seems more likely that the positive relationship resulted from

a secondary correlation between seed mass and some other trait that affects sapling survival.

SEEDLING SURVIVAL UNDER EXPERIMENTAL CONDITIONS

Although seedlings from larger-seeded species tended to survive better under experimentally imposed hazards, their advantage did not seem sufficient to counterbalance the advantage of smaller-seeded species during seed production. However, the magnitude of the large-seeded species' advantage could have been underestimated in these studies for at least three reasons. First, most experiments have exposed seedlings to only one hazard at a time, while in natural situations many hazards will act simultaneously. Secondly, ecologists performing experiments may have chosen hazard intensities lower than those experienced by natural seedling populations, in order to have a reasonable number of live seedlings remaining at the end of the experiment. Thirdly, most experiments use relatively few seedlings of each species, because of constraints on time and space. The maximum observable advantage of large-seeded species relative to small-seeded species depends on the sample size. For example, in a study where seed masses ranged over four orders of magnitude, at least 10^4 seedlings of the smallest-seeded species would be required to detect a 10-fold increase in seedling survival for every 10-fold increase in seed mass.

The slope of the relationship between seed mass and seedling survival under experimental conditions might be sufficient to counterbalance the advantage of the small-seeded species if survival differences continued at similar levels for longer times. However, in most of these experiments, survival was quantified over a time likely to have encompassed most of the period over which large-seededness is expected to benefit seedlings. In two of three cases in Table 1 where seedling establishment was monitored in later-stage seedlings, the early advantage of the large-seeded species disappeared (Saverimuttu & Westoby 1996; George & Bazzaz 1999; Walters & Reich 2000). Therefore, although the slope of the relationship between seed mass and survival through the entire seedling establishment period might be somewhat steeper than has been found by this compilation, it seems unlikely that the advantage of large-seeded species persists for sufficient time to balance the greater number of seeds m^{-2} of canopy $year^{-1}$ produced by small-seeded species.

SEEDLING SURVIVAL UNDER NATURAL CONDITIONS

The most important finding in this work was that although large-seeded species have higher survival through the first week after emergence in natural conditions, mortality would need to continue at the same rate for a number of weeks if it were to counterbalance the advantage accrued by the small-seeded species as a result of the seed size/number trade-off. The number of

weeks required would be unrealistic, at least across the upper part of the range of seed masses included in this study. Thus, the magnitude of the advantage of large-seeded species during seedling establishment is not, in itself, sufficient to counterbalance the advantage of small-seeded species during seed production.

Why might this be the case? Here, we consider two possibilities: (i) the inversely proportional relationship between seed mass and the number of seeds produced $m^{-2} year^{-1}$ does not hold for all vegetation types; and (ii) the remainder of the advantage of small-seeded species is made up by the large-seeded species at another life-history stage.

Logically, the number of seeds a plant can make should be a function of the amount of resources devoted to reproduction, divided by the mass of individual seeds plus accessories (Henery & Westoby 2001). Allocation to accessories varies widely, but on average increases approximately isometrically with seed mass (Henery & Westoby 2001; Moles & Westoby 2003). The amount of photosynthate available for reproduction is expected to be related to the amount of canopy area available for photosynthesis (with some variation due to differences in the proportion of photosynthate allocated to reproduction; Weiner 1988; Greene & Johnson 1994). Thus, seed mass is expected to be inversely proportional to the number of seeds produced for a given plant size. This expectation has been strongly supported by empirical data from many different ecosystems (Shipley & Dion 1992; Greene & Johnson 1994; Turnbull *et al.* 1999; Jakobsson & Eriksson 2000; Aarssen & Jordan 2001; Henery & Westoby 2001). Further, those studies quantifying the relationship between seed mass and seed production per unit canopy have found relationships with slopes not significantly different from -1 (Aarssen & Jordan 2001; Henery & Westoby 2001). There may be differences in the strength and the elevation of this relationship in different environments, and across different species. However, the logic of the prediction combined with field evidence suggests that the seed size/number trade-off is a global phenomenon.

The advantage of small-seeded species might be made up partly during seedling establishment and partly at other stages in the life cycle. Previous investigations have shown no relationship between seed mass and survival of pre-dispersal seed predation across 174 species from around the world and a weak positive relationship between seed mass and survival of post-dispersal seed predation across 280 species from around the world (Moles & Westoby 2003). However, the advantage of large-seeded species during post-dispersal seed predation does not seem great enough or consistent enough across ecosystems to counterbalance the seed size/number trade-off. The advantage of large-seeded species does not seem to lie in survival in the soil either: the relationship between seed mass and survival in the soil is negative in many places (Leishman *et al.* 2000). Results from the present work indicate that there is no relationship between seed mass and survival from

viable seed in or on the soil to seedling emergence (Fig. 2). Thus, it seems unlikely that much of the advantage of large-seeded species is gained between seed dispersal and seedling emergence. The evidence reviewed in the present paper suggests that this advantage is also unlikely to be found in later stages of recruitment (sapling or juvenile survival). However, it is possible that some of the advantage of large-seeded species occurs during seed production. Seed mass is positively correlated with both plant size and plant longevity (Leishman & Westoby 1994; Leishman *et al.* 1995; Rees 1996; Ehrlen & Lehtila 2002). Therefore, although large-seeded species produce far fewer seeds m^{-2} canopy year⁻¹, they tend to have more square metres of canopy per individual and more reproductive years. The slope of this relationship between seed mass and lifetime seed output will be quantified in a separate paper.

Conclusion

It seems most likely that the advantage of small-seeded species due to the seed size/number trade-off is balanced by a combination of: (i) the advantages of large-seeded species during seedling establishment; and (ii) the greater canopy area and longevity of large-seeded species. Our previous concept of seed mass as a straight trade-off between producing a large number of small seeds, each with low establishment ability, and producing fewer, larger seeds, each with a higher chance of successful establishment (Westoby *et al.* 2002), will need to be reassessed in light of these results.

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC884/JEC884sm.htm>

Appendix S1 Phylogenetic tree and data used to investigate relationships between seed mass and survival of the seed to seedling transition, the seedling to adult transition, and early seedling survival.

Appendix S2 Phylogenetic tree and data used to investigate the relationship between seed mass and sapling survival.

Appendix S3 Relationships between seed mass and survival plotted with species coded by study.

Appendix S4 References for Table 1.

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