OIKOS 113: 91–105, 2006

Seed size and plant strategy across the whole life cycle

Angela T. Moles and Mark Westoby

Moles, A. T. and Westoby, M. 2006. Seed size and plant strategy across the whole life cycle. – Oikos 113: 91–105.

We compiled information from the international literature to quantify the relationships between seed mass and survival through each of the hazards plants face between seed production and maturity. We found that small-seeded species were more abundant in the seed rain than large-seeded species. However, this numerical advantage was lost by seedling emergence. The disadvantage of small-seeded species probably results from size-selective post-dispersal seed predation, or the longer time small-seeded species spend in the soil before germination. Seedlings from large-seeded species have higher survival through a given amount of time as seedlings. However, this advantage seems to be countered by the greater time taken for large-seeded species to reach reproductive maturity: our data suggested no relationship, or perhaps a weak negative relationship, between seed size and survival from seedling emergence through to adulthood. A previous compilation showed that the inverse relationship between seed mass and the number of seeds produced per unit canopy area per year is countered by positive relationships between seed mass, plant size and plant longevity. Taken together, these data show that our old understanding of a species' seed mass as the result of a trade-off between producing a few large offspring, each with high survival probability, versus producing many small offspring each with a lower chance of successfully establishing was incomplete. It seems more likely that seed size evolves as part of a spectrum of life history traits, including plant size, plant longevity, juvenile survival rate and time to reproduction.

A. T. Moles and M. Westoby, Dept of Biological Sciences, Macquarie Univ., NSW 2109, Australia (amoles@bio.mq.edu.au). ATM also at: National Center for Ecological Analysis and Synthesis, 735 State St, Suite 300, Santa Barbara, California, CA 93101, USA.

Ecologists have generally understood a species' seed mass as the result of a tradeoff between producing few, large seeds, each with a high probability of successful establishment, versus producing many small seeds, each with a low probability of establishing. This approach is based on several sound pieces of logic and evidence.

Logically, a plant with a given amount of resource available for seed production will be able to produce more small seeds than larger seeds (Henery and Westoby 2001). There is also strong empirical evidence for a negative relationship across species between seed mass and the number of seeds a plant can produce, both per individual per year (Shipley and Dion 1992, Greene and Johnson 1994, Turnbull et al. 1999, Jakobsson and Eriksson 2000) and per square metre of canopy, or per gram of plant biomass, per year (Aarssen and Jordan 2001, Henery and Westoby 2001).

Many studies have shown that seedlings from large-seeded species have higher rates of survival than seedlings from small-seeded species; both under natural conditions (Bakker 1989, Dalling and Hubbell 2002, Moles and Westoby 2004), and under a wide range of experimentally-imposed hazards including shade (Grime and Jeffrey 1965, Leishman and Westoby 1994a), drought (Leishman and Westoby 1994b, early-stage seedlings only), competition from other seedlings (Turnbull et al. 1999, Leishman 2001), defoliation (Armstrong and Westoby 1993, Harms and Dalling 1997) and

Accepted 2 September 2005

ISSN 0030-1299

competition with established plants, (Gross 1984, Burke and Grime 1996). Furthermore, there are clear mechanisms through which larger seed mass might lead to higher seedling survival and lower seed output. The larger, better provisioned seedlings associated with large seeds (Fenner and Kitajima 2000, Leishman et al. 2000) are expected to be at an advantage in situations where access to water or light increases with distance down or up from the soil surface, or in which seedlings are forced to rely on stored reserves through periods of carbon stress imposed by hazards such as drought, shade, and herbivory (Westoby et al. 1996).

The idea that there is a tradeoff between production of few, large seeds, each with a high probability of successful establishment, and many small seeds, each with a low probability of establishing, has been embedded in several theory lineages, beginning from Smith and Fretwell's (1974) theory. The Smith–Fretwell formulation has been central to most evolutionary theory on the coexistence of multiple seed mass strategies both within- and across species (Geritz 1995, Rees and Westoby 1997, Geritz et al. 1999, Uriarte and Reeve 2003) and to the literature on mother–offspring conflict, for both plants and animals (Haig and Westoby 1988, Godfray and Parker 1991). However, emerging data is shifting our perspective on the ecology of seed size.

First, a compilation of all available data on seedling establishment showed that although large-seeded species do have higher rates of survival during seedling establishment, this advantage is not sufficient to counterbalance the greater number of small seeds that can be produced for a given amount of reproductive effort (Moles and Westoby 2004). Second, although small-seeded species produce more seeds per square metre of canopy per year than do larger-seeded species, large-seeded species have more square metres of canopy (seed mass is positively related to plant size: Levin 1974, Leishman et al. 1995) and more reproductive years with which to produce seeds (Baker 1972, but see Silvertown 1981, Jurado et al. 1991, Leishman et al. 1995, but see Thompson 1984). The upshot is that there is no detectable relationship across species between seed mass and the number of seeds produced per adult plant per lifetime (Moles et al. 2004).

To fully understand the implications of these results, we need to consider them in the context of the entire life history of plants. In this paper, we draw together information on the relationships between seed mass and the probability of individuals surviving each of the hazards encountered between seed production and plant maturity: pre-dispersal seed predation, post-dispersal seed predation, survival in the soil to germination, survival through germination, seedling and sapling survival, and the relationship between seed mass and seed production. We complement these data with new data on the changes in density between seed rain, seedling emergence and adulthood. This allows us to assess where in the life cycle the advantages and disadvantages of large- vs small-seeded species lie.

Methods

Approach

The average number of seeds produced by reproductively mature individuals, multiplied by survival through all of the selective processes between seed production and reproductive maturity, must be approximately equal across species, if populations are self-replacing. This would mean that each individual plant, on average, produces one offspring that survives through to reproductive maturity during its lifetime, irrespective of seed mass. This can be expressed as (Eq. 1):

$$1 = \begin{pmatrix}\text{lifetime}\\ \text{seed output}\end{pmatrix} \times \begin{pmatrix}\text{survival of}\\ \text{pre-disp.}\\ \text{seed pred.}\end{pmatrix}^{t_1} \times \begin{pmatrix}\text{survival of}\\ \text{post-disp.}\\ \text{seed pred.}\end{pmatrix}^{t_2} \times \begin{pmatrix}\text{survival of}\\ \text{storage in}\\ \text{soil.}\end{pmatrix} \times \begin{pmatrix}\text{survival of}\\ \text{germination}\end{pmatrix} \times \begin{pmatrix}\text{seedling}\\ \text{survival}\end{pmatrix}^{t_3} \times \begin{pmatrix}\text{sapling}\\ \text{survival}\end{pmatrix}^{t_4}$$

Terms to the power t_x are used where survivorship is measured on a per-unit-time basis, and t_x is the time over which that survivorship operates. For other terms, survivorship is measured over the whole of the life history stage. Lifetime seed output is a function of canopy area (which is expected to be correlated with the amount of photosynthate available for seed production), plant reproductive lifespan, and seed mass.

Ideally, we would calculate survival through each of these processes, or measure rates of mortality and determine how much time individuals spend passing through each stage. However, it was not possible to compile information on survival through the entire duration of some of these stages (those to the power of t_x in Eq. 1). We might have been able to multiply survival per unit time by the amount of time spent in each stage. However, quantification of the time involved in each case would be nearly impossible. These times are likely to be extremely variable, both within and among species. In addition, cross-species variation in exposure time is likely to vary systematically with seed mass (for example, because small-seeded species are more likely to have persistent seeds than large-seeded species, they are likely to spend more time exposed to mortality as seeds in the soil: Leishman et al. 2000, Thompson et al. 2001). Thus, although Eq. 1 forms the logical basis for this paper, we were forced to take a slightly different approach to synthesising the available data.

We began by quantifying the relationships between the density of yearly cohorts of species at three points in the life cycle: seed rain, newly-emerged seedlings and adult plants. From these data, we were able to quantify the overall change in numbers (and therefore survivorship) occurring as cohorts progressed between stages. This information was used in combination with data on survival through each of the selective processes occurring between life stages. Thus, Eq. 1 was broken into the following stages (Eq. 2):

Survival from seed rain to seedling emergence

$$= \begin{pmatrix}\text{survival of}\\ \text{post-disp.}\\ \text{seed pred.}\end{pmatrix}^{t_1} \times \begin{pmatrix}\text{survival of}\\ \text{storage in}\\ \text{soil.}\end{pmatrix}^{t_2} \times \begin{pmatrix}\text{survival of}\\ \text{germination}\end{pmatrix}$$

$$= \frac{\text{density of yearly cohort of seedlings}}{\text{density of yearly cohort of seed rain}}$$

(Eq. 3):
Survival from seedling emergence to reproductive

$$\text{maturity} = \begin{pmatrix}\text{seedling}\\ \text{survival}\end{pmatrix}^{t_3} \times \begin{pmatrix}\text{sapling}\\ \text{survival}\end{pmatrix}^{t_4}$$

$$= \frac{\text{density of yearly cohort of adults}}{\text{density of yearly cohort of seedlings}}$$

(Eq. 4):
Annual number of seeds dispersed per adult

$$= \begin{pmatrix}\text{annual seed}\\ \text{output per m}^2\\ \text{canopy per adult}\end{pmatrix} \times \begin{pmatrix}\text{adult}\\ \text{canopy}\\ \text{area}\end{pmatrix} \times \begin{pmatrix}\text{survival of}\\ \text{pre-disp.}\\ \text{seed pred.}\end{pmatrix}$$

$$= \frac{\text{density of yearly cohort of seed rain}}{\text{density of yearly cohort of adults}}$$

Thus, we used data on cohort densities at different life stages to estimate the magnitude of survival advantages associated with different seed sizes through small groups of selective processes.

Compilation of density data from the literature

We searched the Biosis database for papers published in journals in English between 1969 and 2002, using the search terms "seedling emergence", "seed rain" and "stem density" or "adult density". We aimed to compile information on the "natural" density of species in the seed rain, as seedlings and as adult plants, in situations where population dynamics were relatively stable (because the theoretical foundations above are based on self-replacing populations). Studies in highly disturbed habitats (such as mines, pastures in recently cleared tropical rainforests and cropping systems), highly successional environments (e.g. sites recently affected by landslides, hurricanes or volcanism, glacier forelands), and sites undergoing rapid changes in species composition (such as grasslands being colonised by woody species and areas experiencing biological invasion) were excluded from this study. Studies using seed supplementation or seedling transplants were also excluded, as were studies that artificially reduced plant mortality (e.g. with herbicides, fencing or supplementary watering).

We aimed to compile information on the average density of seed rain for each species. We excluded studies that quantified the density of seeds dispersed by animals but did not quantify the density of seeds dispersed by other vectors or seeds that fell beneath the parent plant. We excluded seed rain from boundaries between vegetation types, as the density of species at a given distance from seed sources would be expected to be related to dispersal ability of the species, and might therefore be secondarily related to seed mass. Studies quantifying the release of seed from serotinous capsules after fire were also excluded, due to the difficulty of calculating an average annual seed rain density for such species. Studies in which seed rain was estimated through germination were also excluded, as these data are confounded by losses to post-dispersal seed predation, and might also be subject to a seed-mass-related bias resulting from a relationship between seed mass and a tendency for viable seeds to persist in the soil (Venable and Brown 1988, Thompson 2000). We made no attempt to correct for the distance to the nearest seed source when calculating seed rain density. However, we excluded studies where trap locations were located non-randomly with respect to adult trees. Thus, seed rain densities recorded should represent site averages.

Because seedling densities change rapidly with post-emergence mortality, we aimed to compile data on seedling density at emergence. Therefore, we only included studies in which seedling density was recorded at least fortnightly. Studies in which seedling density may have been artificially increased by moving soil to greenhouses to monitor seedling emergence were also excluded. In each case we recorded the total density of seedlings emerging per year.

Studies of established vegetation in which it was not possible to distinguish between densities of juvenile and reproductively mature individuals were necessarily excluded from the compilation of adult densities. In addition, data on adult density and seed rain density were collected only from studies that included more than five species. This restriction was intended to exclude studies in which species were studied only in areas where they occurred at particularly high densities. This restriction was relaxed for seedling emergence data, due to the lower availability of suitable data for this life stage. However, analysis of covariance showed no significant ($P > 0.05$) difference in the slope or elevation of the relationship between seed mass and density of newly-emerged seedlings for species from studies including more than five species, and those from studies including fewer than five species. It therefore seems unlikely that this difference in methodology affected our results.

Compilation of survival data for each life stage

We have compiled data on survival through each life stage in previous papers: pre- and post-dispersal seed predation (Moles et al. 2003a); germination, early seedling survival and sapling survival (Moles and Westoby 2004); lifetime reproductive output and its components (Moles et al. 2004). These compilations gathered together all previous results that could be found for individuals in natural situations. We had not previously compiled data on the relationship between seed mass and survival through time in the soil, so we performed a new compilation.

Compilation of data on seed survival in the soil

We searched the BIOSIS database for papers published in English between 1969 and 2004 that contained the terms seed and burial. To be included, studies had to quantify seed survival (e.g. by using tetrazolium), not just germination. This restriction was imposed to avoid misleading results for species with dormancy mechanisms. Studies had to follow the survival of seeds under relatively natural conditions (excluding greenhouse studies, laboratory studies or studies in which seeds were buried in impermeable containers). Studies on crops, aquatic species and weeds were excluded. This search yielded data for 128 species, from 33 families, from 11 studies. In order to compare data from these different studies, we calculated the proportion of viable seeds after 12 months of burial, assuming an exponential decline in mortality with time.

Calculating the density of yearly cohorts of adult plants

We were able to gather information on the density of seeds falling per square metre, per year, and on the number of seedlings emerging per square metre, per year. However, it was not possible to collate data on the number of adult plants appearing per square metre, per year. Therefore, we collected data on the total number of adult plants encountered in a quadrat at one time. That is, many cohorts of adults were sampled simultaneously (not single cohorts, as for seeds and seedlings). In order to compare the density of individuals fairly across life stages and to calculate the percentage of individuals successfully surviving transitions from one life stage to the next, we needed to determine how many cohorts of adults were present. If a population is approximately at equilibrium, the number of spaces available for colonisation by each year's seed cohort depends on the number of adults dying that year, which is a function of adult density, and the average lifespan of reproductive individuals. Therefore, the expected number of plants reaching adulthood in a single year-cohort was calculated as the number of reproductive plants per m^2/reproductive longevity. Too few data were available to do this for individual species, so the relationship between seed mass and the density of a single cohort of adults was calculated by subtracting the model I regression slope of the relationship between $\log_{10}$ seed mass and $\log_{10}$ reproductive lifespan from the model I regression slope of the relationship between $\log_{10}$ seed mass and $\log_{10}$ adult density (subtracting logged values is the same as dividing untransformed values). Ideally, we would have based this calculation on the species mean reproductive lifespan. Because these data were not available, we used maximum reproductive lifespan data from Moles et al. (2004). Wherever possible, densities of individuals were taken as density of genets. All data on adult densities were compiled from the global literature (methods described above).

The use of maximum rather than mean reproductive longevity will result in underestimation of the density of adult plants in a given cohort. We were unable to calculate formally the likely magnitude of this underestimation, due to lack of data on mean time to first reproduction. However, the slopes of the relationships between seed mass and mean and maximum plant longevity are almost identical (0.60 vs 0.61; Moles et al. 2004), so the degree of underestimation is likely to be independent of seed mass. Further, the relationship between seed mass and mean longevity has an elevation less than one order of magnitude lower than the relationship between seed mass and maximum longevity, compared to approximately eight orders of magnitude variation in adult density for seed masses between 0.1 and 1 mg. Thus, the degree of underestimation of cohort density resulting from our use of maximum reproductive lifespan is likely to be small relative to the variation in density at a given seed mass.

Statistics

Model I vs model II analyses

Model II (also known as standardised major axis or reduced major axis) analyses are appropriate when it is not clear whether y is being predicted from x or vice versa (McArdle 1988, Sokal and Rohlf 1995). Thus, model II slopes were more appropriate for the initial analysis of some of the relationships (e.g. relationships between seed mass and density) presented in this compilation than model I slopes. However, in later parts of this work, we use seed mass to predict survivorship (or density) at different life stages. This is a model I question. We have therefore presented both model I and model II slopes for density relationships. Model II analyses were performed in (S)MATR, a program written by Falster et al. (2003). Confidence intervals were calculated following Pitman (1939). The relationships between seed mass and seed output, plant size, reproductive lifespan, time to reproductive maturity, survival through seed predation, storage in the soil, seedling emergence and establishment and sapling establishment are all presented here with model I slopes (including those analyses performed using random-effects logistic regression). In some cases, this means that slopes are shallower than the model II slopes reported in their original context (because the model II slope = model I slope/correlation r).

Survival probabilities

Data on the relationship between seed mass and survival through pre- and post-dispersal seed predation and sapling survival were presented separately for different habitats and data sources in the original compilations (Moles et al. 2003a, Moles and Westoby 2004). Here, we combine all available information for each life stage from these papers, using random effects logistic regression. These regressions were performed using winBUGS version 1.3 (MRC Biostatistics Unit, Cambridge Univ. 2002). This program uses the Monte Carlo Markov Chain method (Gilks et al. 1996) for estimation. Random effects logistic regression appropriately uses a binomial error structure for data within species (individuals survive or die). An idea of the proportion of variation between species due to factors other than seed mass can be gained by comparing the standard error of the species effect with the range of predicted survival values.

Data on sapling survival are all from Welden et al. (1991). Because sample sizes were not reported in this paper, random-effects logistic regressions could not be performed. Instead, we performed linear regressions on logit-transformed data (results presented in Moles and Westoby 2004). This analysis is functionally similar to logistic regression, but does not include a term for the species effect. Most sapling survival data are expressed in terms of survival between age classes. These data cannot be used at the general, cross-species level, because of the many orders of magnitude variation in size at a given life stage.

In order to avoid computational problems with zero (or 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. Species represented by five or fewer individuals do not appear on graphs, but were included in logistic regressions (in which they receive little weight since species are weighted according to sample size). Seed mass was $\log_{10}$-transformed before all analyses.

Unfortunately, the lack of overlap in species between different life stages and the lack of information about the duration of different sources of mortality prevent us from using key-factor analysis to investigate which processes have the greatest impact on plant fitness.

Phylogeny

Phylogenetic regressions are presented in all but one of the papers from which the data presented in Fig. 1 were taken. In no case were the results of phylogenetic regressions substantially different from cross-species regressions. Thus, for simplicity we consider phylogeny no further in this paper.

A note on data compilation

We compiled most of the data from the global literature. This increases our power to generalise, and makes maximum use of the available information. However, it does mean that data from different studies in different ecosystems are combined, and that different parts of our synthesis include different species. We tried to minimise the effects of different methodologies by imposing strict rules for inclusion in the compilations, and we looked to see whether relationships were acting in similar ways within and across ecosystems. However, it would be fantastic if future work could quantify these relationships in a standard way for all the species in a single ecosystem, to make a more controlled test of the findings of this study.

Results

Density of individuals in the seed rain, as seedlings and as adults

There was a negative relationship between seed mass and density of seeds in the seed rain across 303 species from a range of environments around the world (Fig. 1a; $P < 0.001$; model I slope $= -0.373$; model II slope $= -1.14$; $R^2 = 0.11$; 95% CI: -1.02 to -1.27; Appendix 1). Thus, small-seeded species did have a numerical advantage at this stage in the life cycle.

Surprisingly, there was no detectable relationship between seed mass and the density of seedlings emerging per year, across 102 species from a wide range of ecosystems (Fig. 1e; $P = 0.454$; model I slope $= -0.097$; model II slope not meaningful because of lack of correlation; $R^2 = 0.003$; Appendix 1). Thus, the numeric advantage small-seeded species in the seed

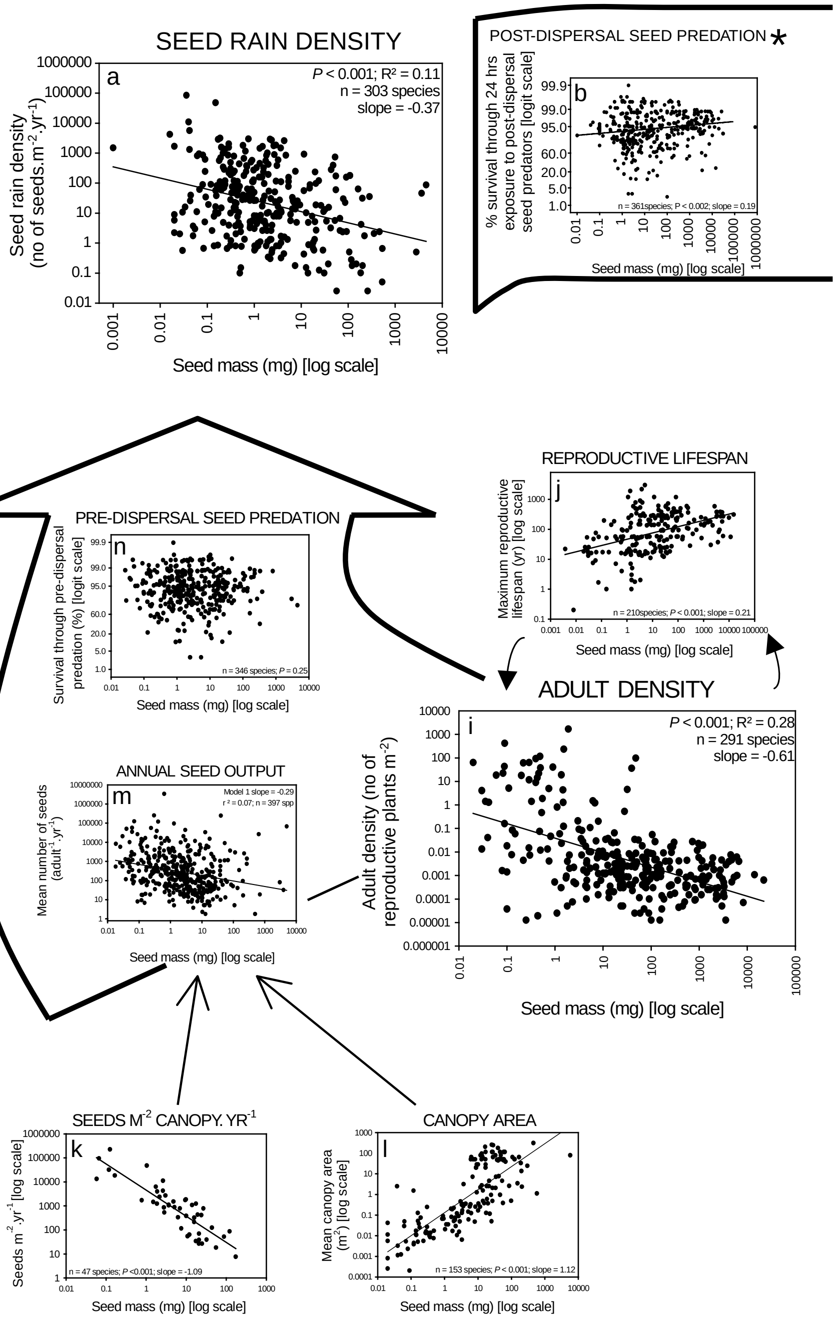
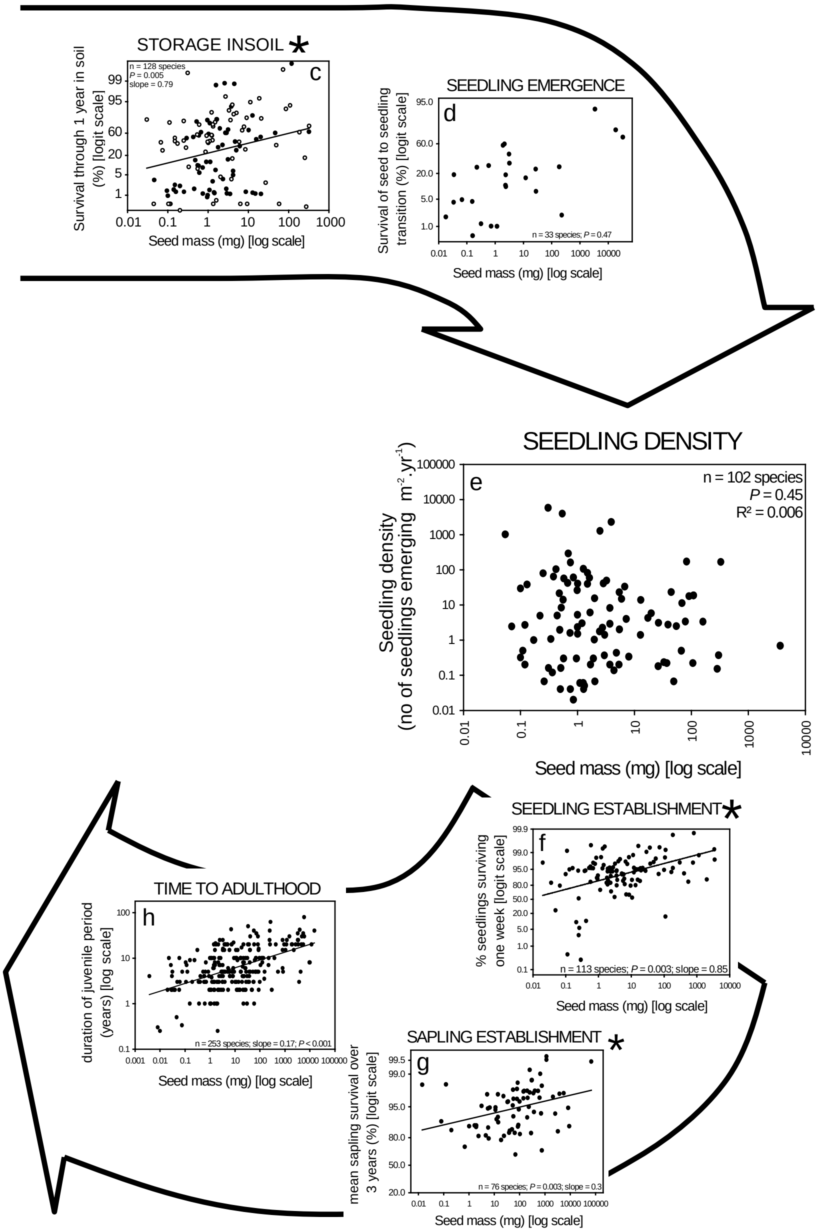


Fig. 1. Relationships between seed mass and survival through each of the hazards plants are exposed to between seed production and reproductive maturity, and relationships between seed mass and density of individuals at three well-defined life stages: seed rain, newly emerged seedlings and adults. In order, the figures show the relationships between seed mass and: (a) the number of seeds falling in the seed rain per square metre per year; (b) survival through post-dispersal seed predation (from Moles et al. 2003a); (c) survival through one year of storage in soil (black points represent data from Moles et al. 2003b while white points represent data from other published papers); (d) survival through the transition from viable seed in the soil to newly-emerged seedlings (from Moles and Westoby 2004); (e) the number of seedlings emerging per square metre per year; (f) survival through the first week after seedling emergence (from Moles and Westoby 2004); (g) survival through three years of sapling establishment in rainforest understorey (data from Welden et al. 1991); (h) the length of time required for plants to reach reproductive maturity (from Moles et al. 2004); (i) the number of reproductively mature individuals per square metre; (j) the maximum duration of the reproductive lifespan (calculated as the difference between maximum longevity and the minimum duration of the juvenile period for each species; from Moles et al. 2004;

Fig. 1 (*Continued*)



(k) the number of seeds produced per square metre of canopy area, per year (from Henery and Westoby 2001); (l) the mean canopy area of reproductively mature individuals (from Moles et al. 2004; (m) the average number of seeds produced per reproductively mature individual, per year (from Moles et al. 2004); (n) survival through the entire period of exposure to pre-dispersal seed predation (from Moles et al. 2003a). In each figure, each point represents a mean value for one species (means were calculated across data for all habitats or years for which data were available for each species). All data were compiled from the global literature, except those in Fig. 1g (data from tropical rainforest in Panama), and Fig. 1k (data from Sclerophyll shrubland in Sydney, Australia). Relationships between seed mass and survival were quantified with random effects logistic regression. The remaining relationships were analysed using standard model I techniques. The large arrows represent transitions between the three different life stages at which densities were collated, and contain figures depicting survival through each of the major selective processes acting between these life stages. Asterisks on survival figures indicate that the data presented is over a discrete time period rather than the entire duration of exposure.

rain appeared to have been lost by the time seedlings emerged.

There was a negative relationship between seed mass and the density of adult plants across 291 species from a wide range of ecosystems (Fig. 1i; $P < 0.001$; model I slope = -0.619; model II slope = -1.13; $R^2 = 0.28$; 95% CI: -1.069 to -1.301; Appendix 1). This relationship might have resulted partly from the strong positive relationship between seed mass and plant size (Moles et al. 2004), combined with the strong negative relationship between plant size and population density (Enquist et al. 1998, Niklas et al. 2003).

The effect of accounting for the number of coexisting cohorts of adults (Methods) is to decrease the apparent adult density of species with 10 000 mg seeds by approximately 2.5 orders of magnitude, and to decrease the apparent density of species with 0.1 mg seeds by approximately 1.5 orders of magnitude. That is, the negative relationship between seed mass and adult density is steeper when considered on a per cohort basis than when taken across all coexisting individuals.

Within-habitat relationships between seed mass and density

Relationships between seed mass and density might be different within habitats compared to the patterns shown across all habitats pooled. To investigate this possibility, we assigned the species for which we had density data to broad vegetation types (based on Udvardy 1975). Analysis of covariance revealed significant interactions between seed mass and habitat for seed rain density ($P = 0.026$), and for adult density ($P = 0.013$), though not for seedling density ($P = 0.50$; also no significant difference in elevation between habitats, $P = 0.87$).

We performed within-habitat regressions on the relationships between seed mass and species density at each of the life stages (Fig. 2, Table 1). Only three of the eight within-habitat relationships between seed mass and species density in the seed rain were significant ($P < 0.05$; Table 1), and some of these results would be considered non-significant after accounting for the fact that eight regressions were performed in this section. However, two of the habitats in which no significant relationship was found were represented by just seven species, so statistical power to detect non-zero slopes was very low. Further, the trend was toward a negative relationship between seed mass and species density in the seed rain in all habitats represented by more than eight species. Thus, we conclude that there is no evidence that the relationship between seed mass and species density in the seed rain operates in a meaningfully different manner within compared to across habitats, while acknowledging that our statistical power to detect differences was low.

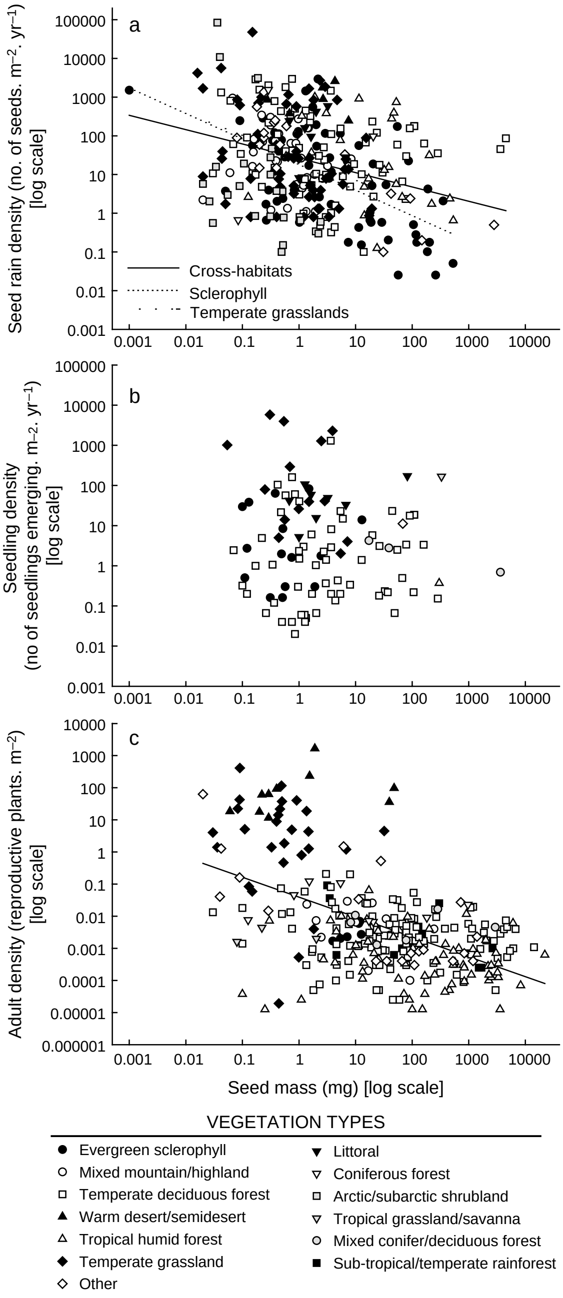


Fig. 2. Within-habitat analyses of the relationships between seed mass and density of individuals in the seed rain, as newly-emerged seedlings, and as adults. Significant cross-habitat and within-habitat slopes are shown for seed rain (a). No significant relationship was found between seed mass and species' density as newly-emerged seedlings, either across- or within-habitats (b). Finally, no significant relationships between seed mass and adult density were found within-habitats. Therefore, only the cross-habitat relationship is shown in (c).

Table 1. Within-habitat relationships between seed mass and density as seeds, seedlings and adults. All slopes reported were calculated using model I techniques. n is the number of species in each habitat. Regressions were only performed in habitats that were represented by at least five species.

Habitat	Seed rain				Adults				Seedlings		
	P	R^2	slope	n	P	R^2	slope	n	P	R^2	n
Evergreen sclerophyllous shrubland/forest	<0.001	0.35	−0.66	59	0.06	0.63	0.97	6	0.97	0.00	15
Mixed mountain and highland	0.31	0.03	−0.26	32	0.20	0.14	−0.42	13			0
Sub-tropical and temperate rainforest				0	0.08	0.27	−0.42	12			0
Temperate broadleaf forest	0.13	0.03	−0.18	72	0.08	0.03	−0.12	119	0.57	0.01	59
Warm deserts/semi-deserts	0.28	0.22	0.41	7	0.36	0.11	0.21	10			0
Tropical humid forests	0.16	0.09	−0.37	23	0.39	0.01	−0.08	66			1
Temperate grasslands/herbfields	0.01	0.13	−0.58	57	0.50	0.02	−0.33	27	0.19	0.14	14
Coastal/littoral	0.99	0.00	−0.01	7				0	0.18	0.28	8
Temperate coniferous forest				3	0.67	0.02	−0.06	10			0
Tropical grasslands/savanna				0				3			1
Tundra/high latitude heath	0.02	0.21	−1.11	24				0			0
Mixed deciduous/conifer forest				0	0.91	0.00	−0.03	6			3

There was no significant relationship between seed mass and species density as newly-emerged seedlings within any of the habitats investigated here. Thus, the within-habitat patterns were similar to the cross-habitat pattern (Fig. 2b).

None of the within-habitat relationships between seed mass and the density of adult plants were significant ($P > 0.05$ in all cases; Table 1, Fig. 2c). The cross-habitat slope seemed to be largely driven by a cloud of small-seeded, high-density species from temperate grasslands (Fig. 2c). However, the negative relationship between seed mass and adult density cannot be entirely attributed to species from temperate grasslands, as the relationship remained significant ($P < 0.001$) when these species were excluded from the analysis. A significant relationship between adult density and seed mass across species from habitats classified as "other" probably also contributes to the overall negative relationship, and is likely to be similarly influenced by juxtaposition of species from different habitats. Thus, within-habitat relationships between seed mass and adult density were not consistent with the cross-habitat result, and the cross-habitat result seems likely to be partly an artefact caused by combination of non-significant relationships between seed mass and adult density from different habitats.

Density shifts and survival through various hazards

In the following sections, we attempt to quantify shifts in density of cohorts between the three life stages, seed rain, seedlings and adults. In each section, we first assess the relative importance of each of the causes of mortality identified in Eq. 2 to 4 that contribute to the shifts in density between the respective life stages. We then assess the density shifts directly.

Causes of mortality 1: the seed rain to seedling transition

The main causes of mortality between seed rain and seedling stages are post-dispersal seed predation, viability loss during seed storage in soil, and mortality during seedling emergence (Eq. 2, Fig. 1a–e).

Post-dispersal seed predation

A combination of field and literature post-dispersal seed predation data (from Moles et al. 2003a) was analysed. We found a significant positive relationship between seed mass and survival through 24 hours exposure to post-dispersal seed predators (Fig. 1b; $P = 0.002$; slope $= 0.19$ [95% CI $= 0.07$ to 0.31]; standard error of the species random effect $= 1.87$ [see methods for a guide to interpreting these values]; $n = 361$ species).

Although the slope of this relationship is quite modest when survival through post-dispersal seed predation is taken on a per 24-h basis (as in Fig. 1b), the seeds of most species will be exposed to post-dispersal seed predators for much more than one day. As the relative advantage of large-seeded species increases with increasing duration of exposure, the difference in survival through the entire duration of exposure to post-dispersal seed predation might have a substantial effect on the relative advantage of large- and small-seeded species.

Storage in soil

We gathered data on the relationship between seed mass and the survival of seeds in the soil through compilation of data from the international literature (Methods). Linear regression (model I) showed that $\log_{10}$-transformed seed mass was positively related to logit-transformed survival through one year in the soil (Fig. 1c; $P = 0.005$; slope $= 0.79$ [95% CI $= 0.25$ to 1.34]). Approximately half of the data included in this analysis came from Moles et al.'s study in the Australian arid zone (Moles et al. 2003b). We were concerned that Moles et al.'s data might be non-representative (Moles et al. 2003b), so we also performed an analysis on all data except those from the Moles et al. study. In this analysis, we found no significant relationship between $\log_{10}$-tranformed seed mass and logit-transformed survival through one year in the soil (Fig. 1c, white points; $P = 0.208$; slope $= 0.46$ [95% CI $= -0.26$ to 1.18], $n = 61$ species).

Even if there is no relationship between seed mass and survival through a given amount of time in the soil, the tendency of small-seeded species to produce seeds that spend long periods of time in the soil before germinating (Thompson and Grime 1979, Thompson 1987, Leck 1989, Thompson et al. 1993, 2001, Price and Joyner 1997, Bekker et al. 1998, Hodkinson et al. 1998, Funes et al. 1999, Moles et al. 2000) would mean that small-seeded species were exposed to the action of burrowing seed predators and fungal pathogens for much longer than large-seeded species. Small-seeded species are therefore expected to have lower survival through their time in the soil than are large-seeded species.

Seedling emergence
There was no evidence for a relationship between seed mass and survival through the transition from viable seed in the soil to newly-emerged seedlings under natural conditions (Fig. 1d; $n = 33$ species; $P = 0.47$; data from Moles and Westoby 2004).

Several studies have shown that seedlings from small seeds are inferior to seedlings from large seeds in their ability to emerge from burial under soil or litter (Maun and Lapierre 1986, Gulmon 1992, Jurado and Westoby 1992, Jurik et al. 1994). Thus, if there were no relationship between seed mass and survival through the transition from viable seed in the soil to newly-emerged seedlings under natural conditions, this might suggest that small-seeded species were avoiding germinating from depth (probably through dormancy mechanisms or by germinating immediately, Milberg et al. 2000).

Density shifts across the seed rain to seedling transition
The proportion of seeds in the seed rain that survived through to seedling emergence was estimated using the formula: seeds surviving from seed rain to seedling emergence = seedling density/seed rain density (Eq. 2). On average, approximately 8% of 0.1 mg seeds survived to seedling emergence, compared to almost 100% of seeds >1000 mg. That is, the net result of selection occurring through post-dispersal seed predation, storage in the soil and seedling emergence was that small-seeded species had much lower survival from seed rain to newly-emerged seedlings than did large-seeded species. The greater survival of large-seeded species calculated from the change in density between seed rain and newly-emerged seedlings is consistent with the advantage of large-seeded species through post-dispersal seed predation and possibly through storage in the soil.

Causes of mortality 2: the seedling to adult transition

The selective processes acting between seedling and adult stages are mortality during seedling establishment and mortality during the sapling stage (Eq. 3, Fig. 1e–i). There is no clear demarcation between these two stages, but the literatures tend to be separate. Mortality acts for differing amounts of time on species with different sized seeds, on account of the relationship between seed mass and the time taken for plants to reach reproductive maturity.

Seedling survival
There was a strong positive relationship between seed mass and the percentage of seedlings surviving through the first week of establishment across 113 species from around the world (Fig. 1f; $P = 0.003$; slope $= 0.85$ [95% CI $= 0.45$ to 1.38]; standard error of the species random effect $= 2.01$; data from Moles and Westoby 2004). Thus, seedlings from large-seeded species had higher survival rates than seedlings from small-seeded species. However, the magnitude of this advantage would only be sufficient to counterbalance the greater number of seeds that small-seeded species produce m^{-2} of canopy outline $year^{-1}$ if mortality continued at the same rate as in the first week after emergence for an implausibly large number of weeks (up to 4.2 years for the largest-seeded species in the dataset, Moles and Westoby 2004).

Sapling survival
Because of the subjectivity involved in defining the term "sapling", it was not possible to synthesise data from different demographic studies to look at the relationship between seed mass and sapling survival (It is not possible to use size-based definitions of "sapling" to fairly compare species with different growth forms). However, data on sapling survival were available for saplings establishing in rainforest understorey on Barro Colorado Island in Panama (Welden et al. 1991). These data were matched with seed mass data from other published sources. Data for high (≥ 10 m) and low (<10 m) canopy environments have been combined here, to give a mean sapling survival for 76 species from 33 families. We found a significant, positive relationship between $\log_{10}$ seed mass and logit-transformed sapling survival through three years ($P = 0.003$; $R^2 = 0.11$; slope $= 0.3$; Fig. 1g).

The positive relationship between sapling survival and seed mass was unexpected: most previous evidence has shown the advantages of large-seededness to be transient (Westoby et al. 2002). It seems most likely that the relationship observed here results via some third variable, such as relative growth rate or shade tolerance.

Time to reproductive maturity

There was a strong positive relationship between seed mass and the time taken for individuals to reach reproductive maturity across 253 species from around the world ($P < 0.001$; model I slope $= 0.17$; $R^2 = 0.26$, Fig. 1h, Moles et al. 2004). Thus, although larger seeded species had lower instantaneous mortality rates for both seedling and sapling stages, they were exposed to that mortality risk for a longer period than the earlier-maturing small-seeded species.

The positive relationship between seed mass and time to maturity (Fig. 1h) is probably partly due to the positive relationship between plant size and seed mass. That is, large seeds are produced on large plants, and it generally takes longer to produce a large plant than a small one (Moles et al. 2004).

To illustrate the potential effect of time to maturity on survival to adulthood, we consider two species, one with large seeds, one with small seeds (Fig. 3). Experimental and field data suggest that large-seeded species have a lower rate of initial mortality, but lose this advantage once the seed reserves have been deployed (evidence reviewed in Moles and Westoby 2004). Thus, the large-seeded species is expected to have lower initial rates of decline, but to have mortality parallelling that of the small-seeded species in later stages of establishment. The early advantage of the large-seeded species would carry through to adulthood, if both species reached maturity at the same time (for instance, time A in Fig. 3). However, the number of individuals surviving to adulthood is a function of both the rate of mortality and the time taken to reach maturity. If the large-seeded species took longer to mature (for instance, if it took until time B in Fig. 3 to mature while the small-seeded species matured at time A), the small-seeded species would have the same survival through to adulthood as the large-seeded species, despite its higher initial rate of mortality.

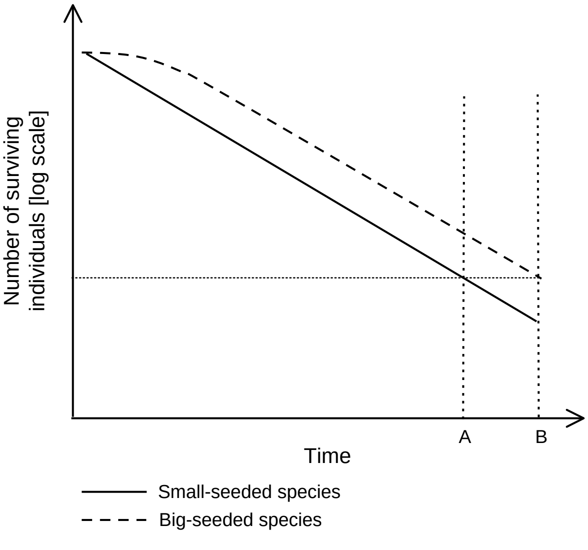


Fig. 3. Schematic showing how differences in time to adulthood could affect the proportion of individuals surviving to adulthood. The dashed curve represents survival of a large-seeded species, while the solid line represents survival of a small-seeded species. The dotted vertical lines (A and B) represent different times to adulthood. If it took until time B for the large-seeded species to reach maturity, and the small-seeded species reached maturity at time A, then the small-seeded species would have the same survival through to adulthood as the large-seeded species, despite its higher initial rate of mortality.

Density shifts across the seedling to adult transition

Because of the difference between cross-habitat and within-habitat relationships between seed mass and adult density (which prevent us from calculating a generalisable slope for this relationship) it was not possible to formally quantify the relationship between seed mass and survival from seedling emergence to reproductive maturity. However, the data suggested that the slope of the relationship between seed mass and the total (cross-cohort) density of adults was either non-significant (within-habitats; Fig. 2c, Table 1), or negative (cross-habitats; Fig. 1i; although it seems most likely that this negative relationship was an artefact caused by pooling data from different habitats). The relationship between seed mass and reproductive life-span was certainly positive across habitats (Fig. 1j), and is highly unlikely to be negative within any habitat (the relationship between seed mass and maximum longevity was similar across vs within habitats; Moles et al. 2004). Thus the relationship between seed mass and the density of a single cohort of adults is either non-significant or (more likely) negative-and is almost certainly not positive.

Taking the negative or non-significant relationship between seed mass and the density of a yearly cohort of adults together with the non-significant relationship between seed mass and the density of yearly cohorts of newly-emerged seedlings strongly suggests that survival from newly-emerged seedling to reproductive maturity was either independent of seed mass, or greater for small-seeded species. This conclusion is contrary to the prediction of most of the seed ecology literature (Leishman et al. 2000), but is consistent with the idea that the positive relationship between seed mass and seedling (and sapling) survival per unit time (Fig. 1f, 1g) is offset by the greater time taken for the seedlings of large-seeded species to reach reproductive maturity (Fig. 1h, Fig. 3).

Our inability to obtain a firm estimate of the slope of the relationship between seed mass and the density of yearly cohorts of adult plants is the weakest (and most frustrating) aspect of this compilation. We have tried to do the most reasonable analyses of the data available from the published literature. Future estimates of this relationship from newly collected field data will be extremely valuable, as they will allow a more rigorous quantification of the survival from seed production to adulthood.

Causes of mortality 3: seed production and survival to seed dispersal

An individual's annual seed production is a function of the number of seeds that can be made per square metre of canopy per year, and its canopy area. The major cause of mortality between seed production and dispersal is pre-dispersal seed predation (Eq. 4, Fig. 1i–a).

Seed production

It is well established that small-seeded species produce more seeds per square metre of canopy outline per year than large-seeded species. The model I slope of this relationship across 47 species in sclerophyll shrubland in Sydney was -1.09 (Fig. 1k: data from Henery and Westoby 2001). However, species with large seeds tend to have larger canopy areas than species with small seeds (Fig. 1l; $n = 153$ species; model I slope $= 1.12$; $P < 0.001$; data from Moles et al. 2004). Thus, although large-seeded species produced fewer seeds both per square metre of canopy and per individual than small-seeded species, the slope of the relationship between seed mass and the total number of seeds produced per adult plant per year was much shallower than -1 (Fig. 1m; $n = 397$ species; model I slope $= -0.29$; $R^2 = 0.07$; $P < 0.001$). In fact, it is surprising that there was a negative relationship at all, given that the slope of the relationship between seed mass and seed production per square metre of canopy per year (-1.09) was almost exactly the inverse of the slope of the relationship between seed mass and canopy area (1.12).

Pre-dispersal seed predation

Logistic regression on combined field and literature pre-dispersal seed predation data from Moles et al. (2003a) showed no significant relationship between seed mass and survival through the entire duration of pre-dispersal seed predation ($P = 0.25$; slope $= -0.72$ [95% CI $= -1.72$ to 0.46]; standard error of the species random effect $= 9.85$; $n = 346$ species; Fig. 1n). Thus, pre-dispersal seed predation will act to reduce the elevation of the relationship between seed mass and the number of seeds produced per year, but there is no evidence it will change its slope.

The relationship between adult density and seed rain density

In theory, the density of seeds falling in the seed rain should simply be the product of annual seed output per reproductively mature individual and the density of reproductively mature individuals, minus losses to pre-dispersal seed predation. Combining the moderate negative relationship between seed mass and annual seed output per individual (Fig. 1m) with the likely moderate negative relationship between seed mass and adult density would generate a slope of approximately the same magnitude as that observed between seed mass and seed rain density (Fig. 1a). However, we are unable to quantify this slope, because we cannot calculate a general slope for the relationship between seed mass and adult density.

Density shifts across the seed rain to adult transition

The relationship between seed mass and cohort density (Fig. 1a, 1e, 1i, 1j) shifted elevation between the seed rain, seedling and adult stages. These elevation shifts showed that mortality between dispersal in the seed rain and seedling emergence was much less severe than mortality between seedling emergence and reproductive maturity, especially for large-seeded species.

Seed rain density and cross-cohort adult density did not differ significantly in their relationship to seed mass within any habitat (analysis of covariance for different slopes, $P > 0.05$). The density of a year-cohort reaching adulthood (total adult density divided by reproductive lifespan) would have a steeper relationship to seed mass. Below, we attempt to assess the likely slope of this relationship.

Lifespan only increased by approximately one order of magnitude as seed mass increased from 0.1 mg to 10 000 mg. If the within-habitat relationships between seed mass and adult density were truly flat (as opposed to being so variable that their confidence intervals overlapped a slope of zero), then species with seeds of 0.1 mg would have cohort densities approximately one order of magnitude higher than species with 10 000 mg seeds. That is, the relationship between the density of year-cohorts reaching adulthood and seed mass would have a slope of approximately -0.3. This slope would be shallower than the slope of the relationship between seed mass and the density of a yearly cohort of seed rain (-0.37); suggesting that large-seeded species have slightly higher survival from seed dispersal to reproductive maturity (the slope would be approximately 0.07).

If populations were just replacing themselves, the slope of the relationship between seed mass and offspring survival to reproductive maturity would be the inverse of the slope of the relationship between seed mass and annual per-capita seed production. The model I slope of the relationship between annual seed production and seed mass across 397 species from around the world was -0.29 (Fig. 1m). This suggests a positive relationship between seed mass and seed survival to reproductive maturity with a slope in the vicinity of 0.3 might be expected.

Discussion

Our previous understanding that a species' seed mass represents a compromise between producing few large seeds each with high establishment probability, and producing many small seeds each with a low probability of successful establishment clearly needs to be reassessed. Although large-seeded species do make fewer seeds per square metre of canopy outline per year (Fig. 1k), they also tend to have larger canopies and longer reproductive lifespans than do small-seeded species (Fig. 1j, 1l). Similarly, although there is a positive relationship between seed mass and seedling survival through a given amount of time (Fig. 1f), this is countered by the positive relationship between seed mass and the time taken for newly emerged seedlings to reach reproductive maturity (Fig. 1h, 3). Overall, this synthesis showed that large-seeded species had higher survival through post-dispersal seed predation, through a given time as seedlings and saplings, and probably through storage in the soil (though there is some doubt about the generality of the relationship for sapling survival). These advantages were balanced by the greater annual seed production per adult plant of small-seeded species, and their shorter time to reproductive maturity.

Perhaps the most important element missing from the traditional understanding of seed mass is consideration of the time over which mortality acts. The importance of the time period through which plants are exposed to each source of mortality is immediately apparent from the transition matrices commonly used in the demographic literature, and the effect of time to reproduction on population growth rates has received considerable attention in plant demography (Cole 1954, Harper 1977). However, time of exposure to various hazards (including seed predation, time spent in the soil before germination, and the time taken for newly-emerged seedlings to reach reproductive maturity) seems usually to have been overlooked in the comparative ecology literature (including by ourselves). Failure to consider the amount of time taken for newly-emerged seedlings to reach reproductive maturity is particularly important, as this has led us (wrongly) to interpret higher rates of seedling survival per time as being synonymous with higher survival to reproductive maturity. This oversight has allowed the Smith–Fretwell (1974) model, the foundation for most evolutionary theory on the ecology of seed size, to pass for almost three decades without an appropriate test of its assumptions.

Smith and Fretwell (1974) reasoned that offspring fitness should increase (though with diminishing returns) with increasing maternal investment in each offspring, and that the optimal seed mass would occur at the point where the expected offspring success per maternal investment was highest. Their assumption that increasing investment in offspring improves their survival seems intuitively reasonable. Many studies showing that seedling survival through a given amount of time is positively correlated with seed mass have been seen as supporting Smith–Fretwell (Leishman et al. 2000, Westoby et al. 2002). However, the requirement of the Smith–Fretwell model is for a positive relationship between seed mass and survival through to reproductive maturity, not just per unit time. The tacit assumption that survival per unit time would be correlated with survival to maturity, other things being equal, turns out to be wrong at the cross-species level because other things are not equal, and especially, because large-seeded species need more time to reach adulthood. While the present study failed to make a firm estimate of the relationship between seed mass and survival from seed production to reproductive maturity, it does (to the best of our knowledge) represent the first attempt to do so at a comparative scale. Improved quantification is an important goal for the future.

Both the logic and the evidence (though this evidence is weak) suggest that the relationship between seed mass and survival from seed dispersal to reproductive maturity is most likely to be a moderate positive relationship. Taking this conclusion together with the likely negative or zero slope of the relationship between seed mass and survival from seedling emergence to reproductive maturity, and the observation that the numerical advantage of small-seeded species in the seed rain had been lost by the stage of seedling emergence suggests that much of the advantage of large-seeded species occurs between seed production and seedling emergence. This finding is in contrast to the previous expectation of most seed ecologists, and is certainly worthy of further investigation.

The advantage large-seeded species enjoy between seed dispersal and seedling emergence probably results from their higher survival through post-dispersal seed predation and through the entire period of burial in the soil. The other major advantages of large-seeded species lie in the positive associations between seed mass, canopy area and reproductive longevity, and in their higher rates of seedling survival. These advantages are offset mainly by the tradeoff between seed size and the number of seeds that can be made for a given amount of energy, and the greater time taken for large-seeded species to reach adulthood. Thus, the indirect effects of correlations between seed mass and plant size, plant longevity and time to maturity have at least as much influence on the overall advantage of a given seed mass strategy as the direct effects of seed size on seedling survival and seed production.

In conclusion, seed size cannot be adequately understood at the cross-species level as a simple tradeoff between producing many offspring each with low establishment probability, and producing few, better provisioned offspring, each with higher establishment probability. Instead, it seems that seed mass is best understood as part of a suite of interrelated plant traits, including seedling survival rate, canopy area, reproductive longevity and time to maturity. This understanding of seed ecology is consistent with a theory lineage developed by Charnov (1993) for understanding life history strategies in mammals. We hope to present a full discussion of the application of Charnov's theory to plant life histories in a future paper. In the meantime, our (admittedly imperfect) data suggest that studies quantifying the time taken for seedlings to reach maturity, and studies quantifying survival from seedling emergence to adulthood will contribute much more to our understanding of seed ecology than will further studies of the relationship between seed mass and rates of seedling survival.

Acknowledgements – Special thanks to Anna-Maria Llorens and Ulysse Bove for help with the preparation of Fig. 1, to Peter Vesk, Ian Wright and Christopher Baraloto for commenting on drafts of the manuscript and to Daniel Falster, Huw Morgan and Glenda Wardle for helpful discussion of results. Supported by an Australian Postgraduate Award to ATM and by Australian Research Council funding to MW.

Supplementary material

Appendix 1. A list of species and data included in compilations of density data, showing density at seed rain, seedling and adult stages, seed mass and data sources. This Appendix can be found at: www.oikos.ekol.lu.se as 014194.

References

Aarssen, L. W. and Jordan, C. Y. 2001. Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. – Ecoscience 8: 471–477.

Armstrong, D. and Westoby, M. 1993. Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. – Ecology 74: 1092–1100.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. – Ecology 53: 997–1010.

Bakker, J. P. 1989. Nature management by grazing and cutting: on the ecological significance of grazing and cutting regimes applied to restore former species-rich grassland communities in the Netherlands. – Kluwer Academic Publishers.

Bekker, R. M., Bakker, J. P., Grandin, U. et al. 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. – Funct. Ecol. 12: 834–842.

Burke, M. J. W. and Grime, J. P. 1996. An experimental study of plant community invasibility. – Ecology 77: 776–790.

Charnov, E. L. 1993. Life history invariants: some explorations of symmetry in evolutionary ecology. – Oxford Univ. Press.

Cole, L. C. 1954. The population consequences of life history phenomena. – Q. Rev. Biol. 29: 103–137.

Dalling, J. W. and Hubbell, S. P. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. – J. Ecol. 90: 557–568.

Enquist, B. J., Brown, J. H. and West, G. B. 1998. Allometric scaling of plant energetics and population density. – Nature 395: 163–165.

Falster, D. S., Warton, D. I. and Wright, I. J. 2003. (S)MATR: standardised major axis tests and routines. Version 1.0.

Fenner, M. and Kitajima, K. 2000. Ecology of seedling regeneration. – In: Fenner, M. (ed.), Seeds: the ecology of regeneration in plant communities. CABI Publishing, pp. 331–359.

Funes, G., Basconcelo, S., Diaz, S. et al. 1999. Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. – Seed Sci. Res. 9: 341–345.

Geritz, S. A. H. 1995. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. – Am. Nat. 146: 685–707.

Geritz, S. A. H., van der Meijden, E. and Metz, J. A. J. 1999. Evolutionary dynamics of seed size and seedling competitive ability. – Theor. Popul. Biol. 55: 324–343.

Gilks, W. R., Richardson, S. and Spiegelhalter, D. J. 1996. Markov chain Monte Carlo in practice. – Chapman and Hall.

Godfray, H. C. J. and Parker, G. A. 1991. Clutch size, fecundity and parent–offspring conflict. – Philos. Trans. R. Soc. B 332: 67–79.

Greene, D. F. and Johnson, E. A. 1994. Estimating the mean annual seed production of trees. – Ecology 75: 642–647.

Grime, J. P. and Jeffrey, D. W. 1965. Seedling establishment in vertical gradients of sunlight. – J. Ecol. 53: 621–642.

Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. – J. Ecol. 72: 369–387.

Gulmon, S. L. 1992. Patterns of seed germination in Californian serpentine grassland species. – Oecologia 89: 27–31.

Haig, D. and Westoby, M. 1988. Inclusive fitness, seed resources, and maternal care. – In: Lovett Doust, J. and Lovett Doust, L. (eds), Plant reproduction ecology patterns and strategies. Oxford Univ. Press, pp. 60–79.

Harms, K. E. and Dalling, J. W. 1997. Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. – J. Trop. Ecol. 13: 617–621.

Harper, J. L. 1977. Population biology of plants. – Academic Press.

Henery, M. L. and Westoby, M. 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. – Oikos 92: 479–490.

Hodkinson, D. J., Askew, A. P., Thompson, K. et al. 1998. Ecological correlates of seed size in the British flora. – Funct. Ecol. 12: 762–766.

Jakobsson, A. and Eriksson, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. – Oikos 88: 494–502.

Jurado, E. and Westoby, M. 1992. Seedling growth in relation to seed size among species of arid Australia. – J. Ecol. 80: 407.

Jurado, E., Westoby, M. and Nelson, D. 1991. Diaspore weight, dispersal, growth form and perenniality of central Australian plants. – J. Ecol. 79: 811–830.

Jurik, T. W., Wang, S. C. and Vandervalk, A. G. 1994. Effects of sediment load on seedling emergence from wetland seed banks. – Wetlands 14: 159–165.

Leck, M. A. 1989. Wetland seed banks. – In: Leck, M. A., Parker, V. T. and Simpson, R. L. (eds), Ecology of soil seed banks. Academic press, pp. 283–305.

Leishman, M. R. 2001. Does the seed size/number tradeoff model determine plant community structure? An assessment of the model mechanisms and their generality. – Oikos 93: 294–302.

Leishman, M. R. and Westoby, M. 1994a. The role of large seed size in shaded conditions-experimental evidence. – Funct. Ecol. 8: 205–214.

Leishman, M. R. and Westoby, M. 1994b. The role of seed size in seedling establishment in dry soil conditions-experimental evidence from semi-arid species. – J. Ecol. 82: 249–258.

Leishman, M. R., Westoby, M. and Jurado, E. 1995. Correlates of seed size variation – a comparison among five temperate floras. – J. Ecol. 83: 517–529.

Leishman, M. R., Wright, I. J., Moles, A. T. et al. 2000. The evolutionary ecology of seed size. – In: Fenner, M. (ed.), Seeds – the ecology of regeneration in plant communities. CAB International, pp. 31–57.

Levin, D. A. 1974. The oil content of seeds: an ecological perspective. – Am. Nat. 108: 193–206.

Maun, M. A. and Lapierre, J. 1986. Effects of burial by sand on seed germination and seedling emergence of four dune species. – Am. J. Bot. 73: 450–455.

McArdle, B. H. 1988. The structural relationship-regression in biology. – Can. J. Zool. 66: 2329–2339.

Milberg, P., Andersson, L. and Thompson, K. 2000. Large-seeded species are less dependent on light for germination than small-seeded ones. – Seed Sci. Res. 10: 99–104.

Moles, A. T. and Westoby, M. 2004. Seedling survival and seed size: a synthesis of the literature. – J. Ecol. 92: 372–383.

Moles, A. T., Hodson, D. W. and Webb, C. J. 2000. Do seed size and shape predict persistence in soil in New Zealand? – Oikos 89: 541–545.

Moles, A. T., Warton, D. I. and Westoby, M. 2003a. Do large-seeded species suffer higher levels of pre- or post-dispersal seed predation than small-seeded species? – Ecology 84: 3148–3161.

Moles, A. T., Warton, D. I. and Westoby, M. 2003b. Seed size and survival in the soil in arid Australia. – Austral Ecol. 28: 575–585.

Moles, A. T., Falster, D. S., Leishman, M. R. et al. 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. – J. Ecol. 92: 384–396.

Niklas, K. J., Midgley, J. J. and Enquist, B. J. 2003. A general model for mass-growth-density relations across tree-dominated communities. – Evol. Ecol. Res. 5: 459–468.

Pitman, E. T. G. 1939. A note on normal correlation. – Biometrika 31: 9–12.

Price, M. V. and Joyner, J. W. 1997. What resources are available to desert granivores: seed rain or soil seed bank? – Ecology 78: 764–773.

Rees, M. and Westoby, M. 1997. Game theoretical evolution of seed mass in multi-species ecological models. – Oikos 78: 116–126.

Shipley, B. and Dion, J. 1992. The allometry of seed production in herbaceous angiosperms. – Am. Nat. 139: 467–483.

Silvertown, J. W. 1981. Seed size, lifespan & germination date as co-adapted features of plant life history. – Am. Nat. 118: 860–864.

Smith, C. C. and Fretwell, S. D. 1974. The optimal balance between size and number of offspring. – Am. Nat. 108: 499–506.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry: The principles and practice of statistics in biological research. – W. H. Freeman and Company.

Thompson, K. 1984. Why biennials are not as few as they ought to be. – Am. Nat. 123: 854–861.

Thompson, K. 1987. Seeds and seed banks. – New Phytol. 106 (Suppl.): 23–34.

Thompson, K. 2000. The functional ecology of soil seed banks. – In: Fenner, M. (ed.), Seeds: the ecology of regeneration in plant communities. CABI Publishing, pp. 215–236.

Thompson, K. and Grime, J. P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. – J. Ecol. 67: 893–921.

Thompson, K., Band, S. R. and Hodgson, J. G. 1993. Seed size and shape predict persistence in the soil. – Funct. Ecol. 7: 236–241.

Thompson, K., Jalili, A., Hodgson, J. G. et al. 2001. Seed size, shape and persistence in the soil in an Iranian flora. – Seed Sci. Res. 11: 345–355.

Turnbull, L. A., Rees, M. and Crawley, M. J. 1999. Seed mass and the competition/colonization tradeoff: a sowing experiment. – J. Ecol. 87: 899–912.

Udvardy, M. D. F. 1975. A classification of the biogeographic provinces of the World. – Int. Union Conserv. Nat. Nat. Resour.

Uriarte, M. and Reeve, H. K. 2003. Matchmaking and species marriage: a game-theory model of community assembly. – Proc. Natl Acad. Sci. USA 100: 1787–1792.

Venable, D. L. and Brown, J. S. 1988. The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risks in variable environments. – Am. Nat. 131: 360–384.

Welden, C. W., Hewett, S. W., Hubbell, S. P. et al. 1991. Sapling survival, growth and recruitment: relationship to canopy height in a neotropical rainforest. – Ecology 72: 35–50.

Westoby, M., Leishman, M. and Lord, J. 1996. Comparative ecology of seed size and dispersal. – Philos. Trans. R. Soc. B 351: 1309–1318.

Westoby, M., Falster, D. S., Moles, A. T. et al. 2002. Plant ecological strategies: some leading dimensions of variation between species. – Annu. Rev. Ecol. Syst. 33: 125–159.

Subject Editor: Ove Eriksson