Comparative Ecology of Seed Size and Dispersal [and Discussion]

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Comparative ecology of seed size and dispersal

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SUMMARY

Seed mass is correlated with a number of other plant traits, including dispersal mode, growth form and specific leaf area. Specific leaf area is the main determinant of potential relative growth rate and an indicator of the site quality to which a species is adapted. The relationships with dispersal mode and growth form have consistent form in five datasets from three continents, and each account for about 20–30% of variation in log seed mass. Thus, there is also very substantial variation within growth form and dispersal categories. Much, but not all, of the 20–30% is associated with shifted family composition between growth forms or dispersal modes.

Experiments have shown that seedlings of larger-seeded species are better able to survive hazards including deep shade, drought, physical damage and the presence of competing vegetation. If there is a common mechanism under these different hazards, it seemingly must be a 'reserve effect', whereby during deployment and early growth larger-seeded species hold a bigger percentage of seed reserves uncommitted to seedling structure and available to support respiration or repair damage. A reserve effect has not yet been demonstrated directly. It remains possible that different mechanisms operate under different hazards. Under a reserve effect, advantages of larger seed size should be temporary, and temporary advantage has indeed been observed with regard to seedling survival under dense shade.

Although larger seed mass confers benefits on seedlings, larger seeds must necessarily be produced in smaller numbers per unit of resource allocated. Seed mass is presumed to have evolved as a compromise between these counterposed pressures. Yet there has proved to be surprisingly little difference in average seed mass between very different vegetation regions, at least in temperate climates. Rather, there is startlingly wide variation in seed mass among species growing interspersed with each other. Recent applications of game theory may be capable of accounting for this wide variation between coexisting species, but at present these models are driven by competition among seedling species (as opposed to between seedlings and adults). It remains unclear whether competition among seedlings is a decisive influence on species composition in most of the world's vegetation types.

1. INTRODUCTION

Between about 1965 and 1975, ecology changed research style. People were becoming more acutely aware that patterns as they are found in nature – so-called 'natural experiments' – are hard to interpret because factors are confounded. Even though every effort is made after the fact to account for possible cross-correlations, a natural experiment is not capable of proving which of two confounded influences is a direct cause and which a secondary correlate. In this situation the idea that competitors could be removed, or predators excluded with cages, in a properly replicated and randomized manner in natural environments, caught the imagination of a generation. Manipulative experiments have remained the research style that defined leadership in ecology for the past 25 years up to the present (Roush 1995).

Now during the 1990s, research styles are in transition again. Many hundreds of experiments have accumulated on competition and other interactions. Often they have different outcomes, depending on the species and the situations involved. The problem of scaling-up from experimental results has become acute. Therefore over the next 10–20 years putting species into comparative context will be the key to research ecology. Comparative ecology will be crucial for improved meta-analysis of the large numbers of experiments that have already accumulated, for generalizing from species and situations that have been the subject of experiments, and for intelligent selection of species for further experiments. This paper concentrates on seed mass. Our underlying interest, though, is in understanding the whole attribute-constellation, with a view to plant ecological strategy schemes.

Seed mass varies greatly between plant species (Harper *et al.* 1970; Westoby *et al.* 1992), against a background of comparatively narrow variation within species. Standard deviations for log seed mass between species within a vegetation type are typically about 1.0, in other words, ± one SD spans 100-fold range (unpublished data, seven floras ranging from 0.76 to 1.14). In contrast within-species SDs have medians about 0.3, in other words ± one SD spans about a four-fold range (Michaels *et al.* 1988). Moreover, most of the variation within species occurs among different seeds on the same mother plant (Michaels *et al.* 1988; Obeso

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1993), indicating that it is largely due to vagaries in the developmental process, rather than being heritable.

Ecological research to understand the variation in seed mass (or any other attribute) between species includes four distinct though complementary questions:

1. In what patterns is seed mass correlated with other components of the attribute constellation of plant species?
2. To what extent can larger seed mass be shown experimentally to support better seedling establishment in the face of various hazards?
3. In what way is seed mass correlated with the environmental conditions under which a species' seedlings naturally establish?
4. To what extent does seed mass variation take the form of relatively recent evolutionary divergences, between species within genera, versus the form of older divergences, between say orders or families?

This paper deals with the first three questions in sequence, commenting where possible on the relationship to phylogeny. Seed mass differences are often conservative between genera or families (Hodgson & Mackey 1986; Mazer 1990; Peat & Fitter 1994; Lord *et al.* 1995).

Our approach through four questions is different, and deliberately so, from that of a number of other contributors to this meeting (e.g. Crawley *et al.*, Franco & Silvertown, Kelly & Woodward, Silvertown & Dodd, all this issue). These authors advocate a single methodology, which they regard as 'correct'. A phylogenetic tree, plus the information on extant species at the tree tips, is used to reconstruct trait changes along branches of the tree. One then tests for correlated evolutionary change – trait A changing in a particular direction along the same branch where trait B changes, more often than expected by chance. This procedure estimates the number of separate divergences for a trait combination. The question addressed is a variant of question 4 above. Our disagreement with these authors is not about the validity of the correlated-change test, but about interpreting its outcome. They regard the test for correlated change as producing the correct answer, whereas tip correlations are flawed because related species may share traits due to 'commom ancestry, not adaptation', leading to 'pseudoreplication' (Silvertown & Dodd, this issue). Regrettably, at this meeting they have continued to represent correlated-change tests as the only path to correct answers, and have not qualified this by warning readers that their claim is controversial (see the 1995 forum in *Journal of Ecology*: Ackerly & Donoghue 1995; Fitter 1995; Harvey *et al.* 1995*a*, *b*; Rees 1995; Westoby *et al.* 1995*a*, *b*, *c*).

In fact, it is meaningless to assert the correctness or otherwise of any statistical test except in relation to a particular question or hypothetical model of the process underlying a pattern (Harvey & Pagel 1991). The generic claim to correctness is actually a claim that only one question or model is worth investigating; similarly with assertions that related species are not independent samples. One cannot say this in the abstract, one might as well say that species are not independent because both have wings on their seeds, or have any other thing in common. Assertions about independence are actually assertions about the model that is being tested.

The test adopted by Silvertown, Kelly and others estimates degrees of freedom correctly as a test of correlated evolutionary change along the same tree branch. But the correlated-change test is simply incorrect for several other models that biologists might be interested in. It is incorrect for the model that change in one trait is a prerequisite for change in another (e.g. Barrett *et al.*, Donoghue & Ackerly, this issue). Tests for this model need to look for changes in A along tree branches that precede changes in B, not along the same branch. The correlated-change test is also incorrect for models that regard stasis or maintenance of a trait as meaningful events, just as meaningful as change. Trait maintenance models should be investigated when traits are suspected to be responsive to selection, or when 'traits' are actually ecological outcomes, such as geographic range (Kelly & Woodward, this issue) or distribution on one soil type rather than another (van Groenendael *et al.*, this issue). Ecological outcome 'traits' (see question 3 above) arguably have to be maintained in each generation by diaspores establishing in some habitats but failing in others. For these models, the correlated-change test incorrectly underestimates the degrees of freedom, by ruling that maintenance of a trait is not evidence for anything, whereas change in a trait is evidence. The correlated-change test is also irrelevant to models about a trait's ecological function in the present day. For the extreme case of a trait that has originated only once, a correlated-change test will find only a single divergence, and therefore will always accept a null hypothesis that nothing meaningful has happened. Plainly it is wrong to conclude that a trait that has originated only once cannot have a meaningful ecological function, so this example illustrates the futility of using a correlated-change test to investigate present-day functionality.

In summary, there are a number of legitimate questions that can be asked (see the four above, also the slightly different list in Westoby *et al.* 1995*b*). Accordingly no single statistical procedure is 'correct' for all purposes, and conversely procedures should not be stigmatized as 'incorrect' without paying careful attention to how the interpretation is phrased. It is interpretations, rather than statistical procedures, that are correct or incorrect.

Perhaps most fundamentally, comparative datasets provide only correlative evidence, and what is more, correlative evidence in which different causes are confounded (Westoby *et al.* 1995*c*). While the correlative evidence deserves investigating for its consistency with a given model of causation, in the final analysis one can not determine causation from cross-correlated patterns, no matter how sophisticated the procedures for correcting one variable for another. Confidence that we have understood causation correctly can only come from a mixture of types of evidence, including experiments on ecological outcomes, and understanding of physiological and de-

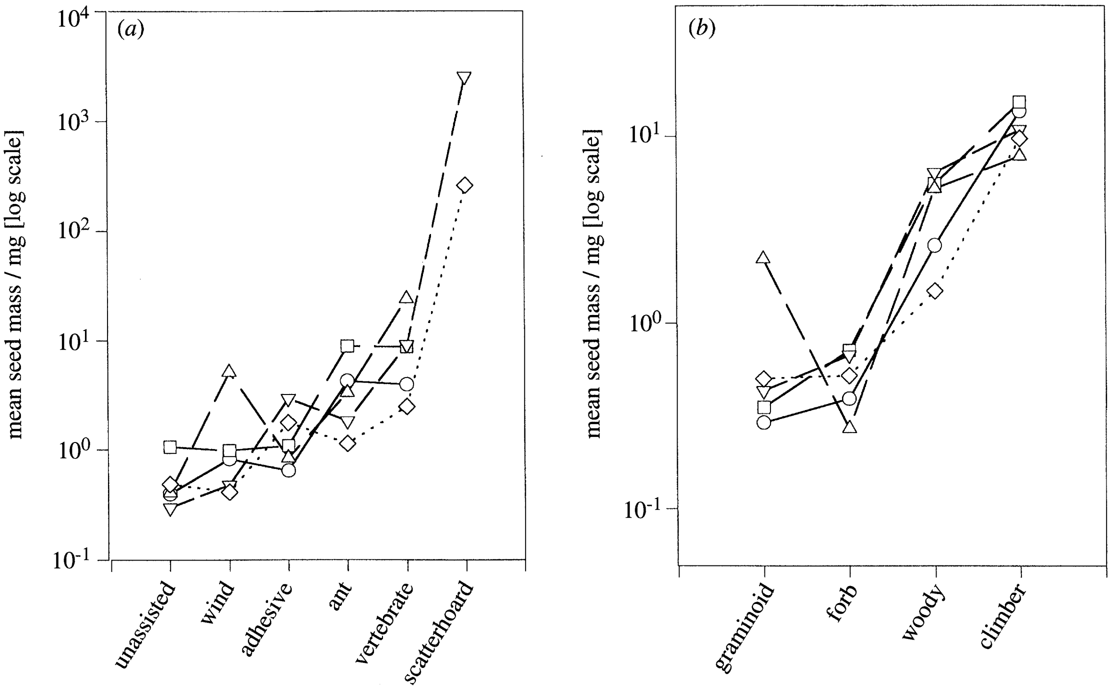

Figure 1. Relationship of seed mass to (*a*) dispersal mode and (*b*) growth form in five temperate floras (open circles: western New South Wales; open squares: central Australia; closed triangles: Sydney; open triangles: Indiana Dunes; open diamonds: Sheffield), after Leishman *et al.* (1995).

velopmental mechanisms, as well as comparative data. This paper brings together different types of evidence about the ecology and evolution of seed mass, and assesses the extent to which these different types of evidence present a consistent picture.

2. SEED MASS IN RELATION TO OTHER ATTRIBUTES OF SPECIES

(*a*) *Dispersal biology*

The relationship between seed mass and dispersal mode is broadly similar in five temperate floras spanning three continents (figure 1*a*). The nature of the relationship is that seeds above 100 mg tend to be adapted for dispersal by vertebrates, seeds below 0.1 mg tend to be unassisted, but between 0.1 and 100 mg all dispersal modes are feasible (Hughes *et al.* 1994). Correspondingly, the relationship has substantial r^2 (0.29), but at the same time fully 71% of variation in log seed mass occurs within dispersal modes. While the differences between floras in the shape of the relationship are significant, they are about ten times smaller than the consistent element of the pattern (flora × dispersal mode interaction $r^2 = 0.03$ *vs* dispersal mode main effect $r^2 = 0.29$; Leishman *et al.* 1995).

Most but not all of the difference in average seed mass between dispersal modes is associated with shifting family representation (85% averaged across six floras; Lord *et al.* 1995). Generally, seed mass is quite phylogenetically conservative, with 55% of log seed mass variation between orders or above, 12% between families within orders, 26% between genera within families and 8% between species within genera (averages across six floras; Lord *et al.* 1995).

(*b*) *Plant height and growth form*

As was the case for dispersal mode, the relationship of seed mass to growth form is reasonably consistent between different floras (figure 1*b*; growth form main effect $r^2 = 0.20$ *vs* growth form × flora interaction $r^2 = 0.02$). Climbers and woody plants have average seed mass about one order of magnitude larger than forbs and graminoids (figure 1*b*).

Growth form and dispersal mode are in turn correlated, so there is some overlap between the proportion of seed mass correlated with growth form and the proportion correlated with dispersal mode, but each is correlated with a substantial portion independently of the other. Taken together, growth form and dispersal mode were capable of predicting between 21 and 47% of log seed mass variation in five different floras (Leishman *et al.* 1995).

Most but not all of the difference in average seed mass between growth forms is associated with shifting family representation (93% averaged across six floras; Lord *et al.* 1995).

(*c*) *Specific leaf area*

For unclear reasons, species with large seed mass tend to have lower specific leaf area (SLA), leaf area per leaf dry mass (figure 2). Species vary along a spectrum from long-lived, evergreen leaves with low SLA to short-lived leaves with large SLA. Species at the low-SLA end of the spectrum typically have lower N contents per unit mass (though not necessarily per unit area), may allocate substantial mass to tannins, phenols or other defensive compounds, and can achieve only slow relative growth rate (RGR) even under

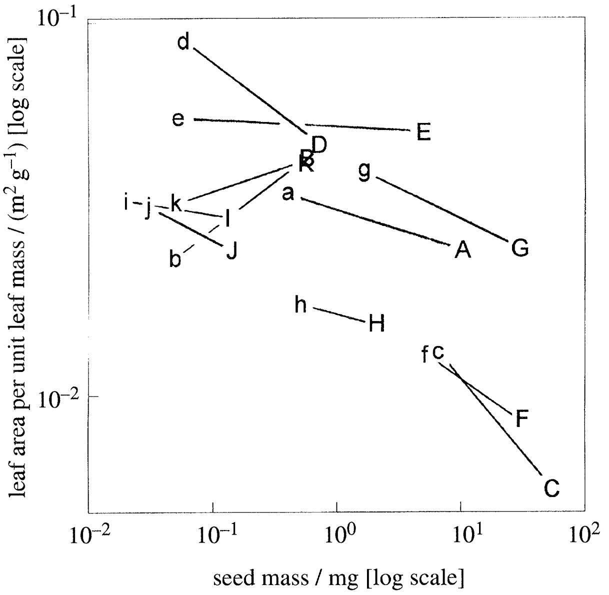

Figure 2. Relationship of SLA measured during seedling growth to seed mass, 11 PICs (data from Saverimuttu & Westoby (1996*b*)).

favourable conditions. Species with high SLA are deploying more light-catching area per unit photosynthate invested, have faster potential RGR (Garnier 1992; Lambers & Poorter 1992; Reich *et al.* 1992, Saverimuttu & Westoby 1996*a*), and the resulting faster turnover of plant parts permits a more flexible response to the spatial patchiness of light and soil resources (Grime 1994).

Low SLA and the associated nexus of attributes has been widely identified as a syndrome of adaptation to unfavourable sites (e.g. Grime 1977; Leps *et al.* 1982; Loehle 1988; Reich *et al.* 1992; Aerts & van der Peijl 1993; Chapin *et al.* 1993; van der Werf *et al.* 1993). Historically, attention first focused on potential RGR of a species (Grime & Hunt 1975), measured on exponentially growing seedlings given plentiful water and nutrients, as the expression of this syndrome. A spectrum of potRGR is central to theories about comparative plant ecology and vegetation dynamics (Grime 1977; Tilman 1990; Keddy & McLellan 1992). It has now become apparent that a trade-off between maximizing light-capturing area and maximizing leaf durability underlies this spectrum. SLA accounts for most potRGR variation between species, though LWR (leaf as proportion of plant mass) sometimes plays a role, especially in comparisons between growth forms.

Species-pairs in figure 2 were chosen to form phylogenetically independent contrasts (PICs). Pairs were contrasted for seed mass, and each pair represented a phylogenetic divergence independent of the other pairs. The SLA–seed mass relationship is present both as a tip correlation considered across all the species, and as a tendency of lines connecting PIC pairs to angle downwards. PICs were mostly within genera or families, so the relationship resides both in differences between superorders, orders and families, and also in differences within genera and families. Some of the effect is associated with species of larger seed mass belonging to taller or more perennial growth forms, but several of the PICs are within growth forms.

Seed mass had previously been found correlated with slower potRGR in most datasets (summaries in Shipley & Peters 1990; Westoby *et al.* 1992; see also Marañón & Grubb 1993; Swanborough & Westoby 1996, using PICs), so the relationship to SLA was predictable, though the basis for it is not yet understood.

3. SEEDLING OUTCOMES ASSOCIATED WITH LARGER SEED SIZE

In experiments where particular environmental hazards are deliberately varied independently of other factors, seedlings from larger-seeded species have often been shown to perform better than those from smaller-seeded species (table 1). These experiments are directed at demonstrating present day functionality. Taken together, they show that larger seed size can be functional in the present day in relation to a wide range of hazards.

Two studies have used species selected to form PICs. Capacity to survive 95% excision of cotyledons was associated with seed mass within genera and families, but between families and orders there was little relationship to seed mass, probably because differences in seedling morphology became more important (Armstrong & Westoby 1993). Cotyledon-stage longevity under dense shade (Saverimuttu & Westoby 1996*b*) was associated with seed mass at all levels, both in PICs within genera and families, and also in older evolutionary divergences across PICs between families and orders.

The exceptions where larger-seeded species did not perform better are of interest. For drought, the exception occurred under very hot field conditions, when survival to emergence was low for all seed sizes. For competition with established vegetation, the exception did not span a very wide range of seed size. For shading, the exceptions occurred after the initial phase of deployment from seed reserves into seedling. This evidence is relevant to mechanisms, which are discussed under the next heading.

4. A COMMON MECHANISM FOR TOLERATING DIFFERENT HAZARDS?

Might the better performance of larger-seeded species, under a range of different hazards (table 1), be mediated through common machinery? There would seem to be three candidates for machinery that might be operating:

1. *Seedling size effect*: because larger seeds give rise to larger seedlings immediately after germination, they may reach deeper into the soil to better water supplies, or higher into the air to a better photosynthetically active radiation (PAR) level.
2. *Reserve effect*: extra metabolic resources in larger seeds may serve to support carbon deficits.
3. *Metabolic effect*: since larger-seeded species tend to have slower potential RGR (for unknown reasons),

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Table 1. *Experiments that manipulated the environment in order to test the proposition that seedlings from species having larger seeds perform better than those from species having smaller seeds, under various hazards*

hazard	larger-seeded species performed better	larger-seeded species did not perform better
competition from established vegetation	Gross & Werner 1982; Gross 1984; McConnaughay & Bazzaz 1987; Bakker 1989; Reader 1993; Burke & Grime 1996	Thompson & Baster 1992
deep shade	Grime & Jeffrey 1965; Leishman & Westoby 1994*a*; Saverimuttu & Westoby 1996*b*; Osunkoya *et al.* 1994	Augspurger 1984[a]; Saverimuttu & Westoby 1996*b*[b]
defoliation	Armstrong & Westoby 1993	
mineral nutrient shortage	Lee & Fenner 1989; Jurado & Westoby 1992	
depth under soil or litter	Gulmon 1992; Peterson & Facelli 1992; Vasquez-Yanes & Orozco-Segovia 1992	
dry environments	Leishman & Westoby 1994*b* (glasshouse)	Leishman & Westoby 1994*b* (field)[c]

[a] PAR at 17.5 μmol m^{-2} s^{-1} was above compensation point. Mortality occurred not at cotyledon stage but mainly between weeks 5–30, was mainly due to disease, and was correlated with lower wood density.

[b] Seedlings grown in full light to first-leaf stage, then transferred to dense shade.

[c] Very severe temperature conditions, low rates of emergence and survival even in the best-watered treatment.

perhaps they have slower respiration rates or otherwise consume metabolic resources more slowly, and it is this rather than seed size that gives them longer survivorship under various hazards.

We have positive evidence that the seedling size effect and the metabolic effect can not be a common machinery, though they might still be relevant in particular situations. The seedling size effect is not capable of accounting for the improved survivorship of seedlings where gradients of resource supply away from the soil surface are not relevant. It cannot account for the longer survival when deprived of any access to mineral nutrients or shaded experimentally below the compensation point, nor for the outcome of the defoliation experiment.

Saverimuttu & Westoby (1996*b*) found evidence against a metabolic rate mechanism. Among seedlings placed in deep shade below the compensation point immediately following germination, at cotyledon stage, larger-seeded species tended to survive longer. But slow dark respiration rates and slow potential RGR in full light were not such good predictors of shade longevity as was seed reserve mass itself. Further, when seedlings were grown in full light through to first-leaf stage, a stage when they had fully embarked on exponential growth and seed reserves had been fully deployed, and only then were transferred to deep shade, longevity in deep shade was not well correlated with seed mass. These seedlings died faster than cotyledon-stage seedlings, the difference being apparent especially for species with larger seed mass. These results indicate that the advantage of larger seeds applies only while the seed reserves are being deployed into the seedling, and does not persist into later seedling life. Augspurger's (1984) finding no relationship between seed mass and survival was also consistent with this conclusion. PAR at 17.5 mol m^{-2} s^{-1} was probably above compensation point, and seedling mortality occurred mainly between weeks 5–30 rather than in earlier weeks, was mainly due to disease and was correlated with lower wood density.

Three points may be made in summary of present knowledge about the mechanism or mechanisms by which larger seed size permits better seedling performance in the face of different hazards. First, if there is a single underlying mechanism, it must be the reserve effect, as there is clear evidence against a size effect or a metabolic effect, at least for some types of hazard. But why should larger seeds have more resources available to them *relative to the size of the seedling to be supported*? The reserve effect would seem to require that in larger-seeded species, a greater proportion of the seed's stored resources are in some sense uncommitted during deployment, capable of being used to support respiration under carbon deficit. However, this proposition that during deployment from seed into seedling, larger-seeded species hold a greater proportion of seed reserves in forms where they can be retrieved to support respiration, has yet to be tested directly.

Second, if the reserve effect is a single unifying mechanism, larger seed size might initially arise due to selection by one type of hazard, but would subsequently be ecologically functional in relation to another type – indeed, in relation to *all* other types of hazard. This illustrates the general principle that forces favouring the initial emergence of a trait are not necessarily the same as those maintaining it. Conversely, experiments about present-day functionality are not eligible evidence for researchers seeking to infer the origins of traits, unless they are willing to make an argument that past ecological circumstances have much in common with those of the present day.

Third, if the mechanism is via a reserve effect, the benefits conveyed by large-seededness are temporary. At some point between cotyledon stage and true-leaf stage, reserves are irreversibly deployed into the body of the seedling and large-seeded species have no further advantage. An important implication is that large-seededness would only be expected to convey benefits in relation to hazards that are temporary, where there is at least some probability that conditions will improve after a while.

5. PATTERNS OF SEED MASS IN RELATION TO ENVIRONMENTAL FACTORS

The only clearly established pattern in the field is a tendency for species maintaining populations where establishment in the shade is required to have larger seeds (table 2). Any relationship to drought risk is much more marginal. Mazer (1989) did not find it. Baker (1972) is often cited as having found it, but his California data actually show little trend across moisture classes 1–5, with any tendency to smaller seeds present only in intermittently or permanently flooded sites of moisture class 6 (Westoby *et al.* 1992).

The absence of any pattern in relation to soil nutrients is consistent with the idea that advantages ought to apply only where the hazard may be temporary. Similarly, it seems reasonable to regard shading as a hazard that is potentially temporary. While an increase in longevity below the compensation point from (say) 15 to 30 days only provides a small absolute probability that a tree will fall and a light gap open up while the seedling is still alive, the probability is nevertheless doubled. With regard to drought, plainly dry soil is capable of being a temporary rather than a continuing problem for a seedling. It is not clear, though, whether environments with lower annual rainfall pose a greater hazard of drought during establishment. Seedlings will germinate only at particular times of year, sometimes only after soil-saturating initial rainfall. Possibly in the period of 1–2 weeks between germination and independence from seed reserves, seedlings in high rainfall zones are just as much at risk from drought as seedlings in arid zones.

6. STATE OF EVIDENCE ON BENEFITS OF LARGER SEED MASS IN RELATION TO DIFFERENT HAZARDS

In summary, experiments show that larger seed mass can be functional in relation to a wide range of environmental hazards, but only in relation to establishment in the shade does there appear to be any strong or consistent distribution pattern in the field. (Though patterns in the field have hardly been investigated in relation to seedling physical damage risk and soil nutrients, and the evidence remains indecisive in regard to drought risk.) Even in relation to shading, the mechanism is not understood in depth. For most benefits, the benefit and the larger seed mass are modulated together to some extent within genera and families, but in addition much of the correlation is underpinned by older evolutionary divergences, between families, orders or superorders.

7. THE WIDE SPREAD OF COEXISTING SEED SIZES IMPLIES THEY ARE DETERMINED GAME-THEORETICALLY RATHER THAN BY SIMPLE OPTIMIZATION IN RELATION TO ENVIRONMENT

Seed mass is thought to be shaped as a size-number compromise (Harper *et al.* 1970; Harper 1977; Willson 1983; Westoby *et al.* 1992). This idea is made graphical in the Smith & Fretwell (1974) model. The Smith-Fretwell function describes a diminishing returns relationship between seed reserve mass and a seedling's chances of establishing and eventually reproducing. The prediction follows that there should be a single best (fastest) λ seed size. If species have different seed sizes (as indeed they do), this should express the fact that they are evolving under different Smith-Fretwell functions.

Since the 1970s, most research on seed mass has been directed at understanding how larger versus smaller seeds perform under various hazards. The implied agenda has been to look for differences in the Smith-Fretwell functions. This implied agenda now needs to be reconsidered. It has become apparent that there is a wide range of seed mass strategies occurring interspersed within most vegetation types, compared to surprisingly small differences in the mean between environments. Across five datasets, variation within accounted for 96% of total variance, differences between for only 4% (Leishman *et al.* 1995). Given that the datasets ranged from arid woodlands, through coastal rainforest and sclerophyll rainforest, to cool temperate closed grasslands, it is hard to reconcile this with the idea that the prevalence of different physical circumstances during seedling establishment is the main force favouring one seed size versus another.

Recently, game-theoretic methods have been applied to seed mass (Geritz 1995; Rees & Westoby 1996), superceding the tacit assumption that the competitive context can be subsumed into the shape of the Smith-Fretwell function. As we should have expected, the game-theoretic approach makes a fundamental difference. Suppose we assume that seeds fall at random into patches just big enough to accommodate a single adult plant. Competition determines that within a patch, a larger seed will be successful at

Table 2. *Publications reporting whether species whose seeds establish under particular environmental conditions tend to have larger seed mass*

	yes	uncertain	no
shaded	Salisbury 1942; Foster & Janson 1985; Mazer 1989; Hammond & Brown 1995	Metcalfe & Grubb 1995	
low soil nutrients			Westoby *et al.* 1990; Hammond & Brown 1995
droughted		Salisbury 1942; Baker 1972	Mazer 1989

the expense of smaller seeds. Then, no single seed mass strategy constitutes an evolutionary stable strategy (ESS). A strategy-set consisting of a single, medium seed size, as might be predicted from Smith-Fretwell, can be invaded by larger seeds because they win competition in those patches where they occur. Smaller seeds can invade, because they are produced in greater numbers and there will be some patches that are reached by them but not by any larger seeds. The upper bound to the strategy-set is where the seeds produced are so few that $\lambda \leqslant 1$. The lower bound is at the seed mass that maximizes λ after density-independent mortality during dispersal and germination, but before competition. A broad mix of seed-size strategies is expected between those bounds. This result echoes conclusions from models formulated as lotteries (Ågren & Fagerstrom 1984) and as a colonization-competition trade-off (Tilman 1994), though those models were not explicitly about seed mass.

So a game-theoretic approach is capable of predicting a wide mix of seed-mass strategies coexisting, and this actually occurs for reasons otherwise unexplained. But the game-theoretic models only apply literally where species composition is determined to a substantial extent by competition between seedlings. This might be plausible for vegetation of annuals, fire-prone vegetation, arid-zone vegetation where seedling establishment occurs in bursts after major rain, and forest vegetation with gap dynamics, but most plant ecologists would not yet be ready to believe that it applies universally in all vegetation types.

8. OUTSTANDING MATTERS THAT ARE NOT YET CLEAR

The present state of knowledge includes both some matters that seem reasonably settled and consistent, and other matters that are by no means clear. The most important unclear questions are:

1. What is the mechanism by which larger seeds support seedlings better under different hazards – is it the case that larger seeds make a less complete commitment of their reserves during seedling deployment, holding more available to support the seedling during temporary carbon deficits? Does the mechanism imply that the benefit of larger seed mass will be generic, applying under a wide range of different possible hazards? And, might it be possible to find an indicator of this incomplete commitment that would serve as a better predictor than seed mass itself?
2. What is the reason for the correlation of larger seed mass with lower SLA and its associated nexus of attributes related to vegetative growth? Some of the raw correlation is associated with taller growth forms, but the correlation is also present within growth forms.
3. What might account for the very broad spread of seed mass within vegetation types, compared to the minor differences in mean seed mass between very different vegetation types? Four hypotheses seem possible candidates: (i) species germinate under different circumstances, and therefore face a sufficiently broad variety of establishment hazards within each vegetation type – a sufficient diversity of Smith-Fretwell functions – to account for the spread of seed mass; (ii) many species in any vegetation type might occur as sink populations with internal $\lambda < 1$, but supported by dispersal from source populations in other habitats; (iii) Game-theoretic for seed mass as in the models of Geritz (1995) and Rees & Westoby (1996) – this implies that species composition is substantially determined by competition among seedlings; (iv) game-theoretic for some other attribute, with seed mass secondarily correlated with this other attribute.

9. SOME MATTERS THAT SEEM SUFFICIENTLY CLEAR

As well as pointing out matters that remain unresolved and where further research is needed, it bears emphasizing that we have also substantial knowledge about seed mass, reasonably firmly established:

1. Larger seed mass does convey benefits in seedling establishment, under a wide variety of circumstances.
2. Seed mass is correlated with several other plant attributes, those of greatest importance in defining the ecology of a species being height or growth form, dispersal mode and SLA or potential RGR. These relationships have substantial r^2, and their patterns appear consistent in floras from very different environments and having different phylogenetic backgrounds. Attributes of the regenerative phase of life histories are not in general well correlated with attributes of vegetative growth (Grime *et al.* 1988; Shipley *et al.* 1989; Leishman & Westoby 1992). But seed mass is connected both to dispersal biology and to growth form and SLA, and occupies a pivotal position in the constellation of attributes that determines under what environmental opportunities a species is most competitive.

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Discussion

H. Poorter (*Department of Plant Ecology and Evolution Biology, P.O. Box 800.84, 3508 TB Utrecht, The Netherlands*) This morning some people conveyed the message that, in their view, comparative plant ecology could not be done without PICs. In your presentation you showed trends within PICs as well as between all species investigated. Could you comment on how important and how necessary you think PICs are if correlations between traits are of interest.

M. Westoby. First I would like to emphasize that PICs cannot solve the problems of deciding whether a trait has a particular function in the present day. A trait can perfectly well be functional, but have arisen on one or a few separate occasions, so that a contrasts analysis can never have enough degrees of freedom to show a relationship. Conversely, a trait can be repeatedly correlated with an ecological outcome across many PICs, but nevertheless not be the true cause. An example in our paper is the relationship of seed mass to cotyledon-stage seedling shade survival. This occurs repeatedly within PICs, but nevertheless we currently think the true cause of longer shade survival is slower commitment of the seed reserves, rather than larger seed reserves absolutely. Understanding of function comes about through combining comparative information with understanding and with experiments on field outcomes.

On the other hand when the issue is how evolution happened up the phylogenetic tree, then naturally 'tree-thinking' is obligatory. PICs are one form of tree-thinking, though not the only one. A significance test using PICs addresses a model of correlated evolution, that when one trait has changed along any given branch length of the evolutionary tree, a second trait has changed in concert. Other models of the evolutionary history, for example one trait having been a prerequisite for another, demand other significance tests.

In my opinion, phylogeny will have a bright future in functional ecology. This will not be for the usual reason given, that phylogeny applies a supposed correction for lack of independence in the evidence. That supposed correction is spurious, as I have explained. Rather, the bright future will be in selecting species to study according to phylogenetic designs. My group's work up to the present has selected species to form PICs, but these are relatively primitive designs, and we hope to do better in the future. The objective of selecting species according to phylogenetic designs would be to extrapolate understanding of function more powerfully. Physiologists and experimentalists necessarily are restricted in how many species they can study. But we know that ecology and therefore function are often conservative down lineages, so by hanging our knowledge about function on the phylogenetic tree, we can hope to arrive more quickly at an overview of function across the whole of the seed plants.

In summary, then, phylogenetic information has a considerable role in ecology, whether as PICs or as other designs. But much more care is needed in the interpretation of phylogenetic analyses. Especially, it needs to be more widely understood that PIC analyses do not settle questions about present-day function, one way or the other, and therefore they most definitely are not obligatory for functional ecologists. Phylogeny is stimulating as a fashion but stultifying as a dress code.

Daniel J. Schoen (*Department of Biology, McGill University, Montreal, Quebec, Canada H3A 1B1*) What do the game-theoretical models for seed size predict about the shape of the distribution of seed sizes produced by an individual plant? It would seem that if you apply your logic and experimental findings to the question, one might expect that seed size distributions ought to be skewed; in other words, it may be beneficial for an individual plant to first invest in 'stay-at-home' (or heavy) seeds before it becomes profitable to invest in 'dispersal' (or lighter) seeds. Does this seem to be the case?

M. Westoby. A very interesting point. The theoretical situation is fluid at present, but in my view the fact that the between-species distribution of seed mass is broad and approximately lognormal, is quite a significant line of evidence supporting the game-theoretical models.

Geritz (1995) presents his game-theoretic model as predicting a wide spread of seed mass within species, but in fact it simply predicts a wide spread of seed mass strategies, and says nothing about how those strategies are inherited. There are several reasons to expect that each new strategy invading the strategy mix would usually take the form of a new species invading, rather than the form of a seed polymorphism emerging within a species already present.

The spacing between seed mass strategies, in the ESS strategy mix, will be driven by the workings of competition (Rees & Westoby 1996). What seed size advantage will be required for one strategy to consistently defeat another? Probably competitive advantage depends on the ratio between seed mass strategies – say, a twofold mass difference means the larger seed wins 90% of the time – rather than on the arithmetic difference. This would spread out the coexisting strategies on a log scale rather than an arithmetic scale, consistent with the roughly lognormal distribution of seed mass strategies that is actually observed.