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Evolutionary ecology of seed dormancy and seed size

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SUMMARY

The theoretical ideas underpinning the evolution of seed dormancy and seed mass are briefly reviewed. Comparative tests of these theoretical ideas are then presented; all tests use modern comparative methods to allow accurate, meaningful comparisons across species. The comparative analyses of seed dormancy demonstrate that species that average the environment across time, by having long-lived adults or space as a result of clonal growth, typically have less dormant seeds. Amongst species with seeds unspecialized for spatial dispersal, seed mass is not related to dormancy. However, in species with wind- or animal-dispersed seeds those with heavy seeds typically have less dormancy. This is consistent with heavy seeds having better establishment success and/or suffering higher levels of herbivory. The relationships between seed mass and plant height, lateral spread and adult longevity are explored using the Sheffield dataset. The complex pattern of relationships between these variables is interpreted in terms of dispersal limitation, escape from competition with clonal ramets and differences in establishment conditions. Some of the problems that are frequently encountered in the interpretation of comparative data are briefly discussed.

1. INTRODUCTION

Seeds provide an essential link in population dynamics by allowing the establishment of new individuals, and so the founding of populations. Patterns of seed dispersal, both in time and space, determine who interacts with whom, and hence the strength of interactions both within and between species, which in turn determine observed patterns of species diversity (Law & Watkinson 1989; Tilman & Pacala 1993; Rees *et al.* 1996). Therefore, when considering the evolutionary biology of seed traits it is essential to place this in its ecological context. Likewise when considering the ecology of seed traits one must also recognize their evolutionary significance. For example, theoretical models have demonstrated that seed dormancy can play an important role in allowing coexistence via the so called 'storage effect' (Chesson 1988). This occurs when there is temporal variation in the environment, and the presence of long-lived seeds allows different species to be favoured at different times. Clearly this coexistence mechanism is only likely to be important in those communities where dormancy has evolved, such as in desert annuals (Venable *et al.* 1993) or weeds of arable fields (Rees & Long 1992). However, in other communities, for example those consisting of sand dune annuals, coexistence via a temporal 'storage effect' is unlikely because there are microsites available for colonization in virtually every year, so evolution favours complete germination, with the result that few species have dormant seeds (Kelly 1982; Watkinson & Davy 1985).

Clearly seed traits are embedded in a plant life cycle and so changes in the traits of established plants will have fitness consequences for seed traits and vice versa (Salisbury 1942, 1974; Mazer 1989; Rees 1993, 1994; but see Grime 1979, Grime *et al.* 1987). This means we should expect to find correlations between seed and established plant traits, which is indeed the case (Salisbury 1942; Silvertown 1981; Mazer 1989; Rees 1993), but also that we need to be careful when analysing comparative data because many traits are likely to covary simultaneously, making it important to include several traits and phylogenetic information into analyses. Simply treating species as independent data points in statistical analyses can obscure important ecological and evolutionary relationships (Harvey & Pagel 1991; Garnier 1992; Harvey *et al.* 1995; Rees 1995).

In the rest of the paper I first describe why seed dormancy presents a problem in evolutionary biology, and then review the various theoretical mechanisms that could explain the evolution of dormancy. For each of these mechanisms I outline appropriate comparative tests and present some relevant data analysis. I then briefly describe the theory, such as it is, for the evolution of seed mass, and present some comparative tests. General conclusions from the comparative analyses presented are discussed.

2. WHY HAVE DORMANT SEEDS?

Why is dormancy a problem? The general answer is that we would normally expect individual plants to reproduce as soon as they could. There are two main reasons for this: 1. In an increasing population, early reproduction is favoured because of the multiplicative nature of population growth.

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Table 1. *Theoretical patterns of trait covariation with seed dormancy*

(A ↑ indicates that dormancy is expected to increase with an increase in the trait, a ↓ indicates that dormancy is expected to decrease with an increase in the trait. Note that in several cases the competing theories make similar predictions making it difficult to distinguish between them using comparative tests.)

	traits					
theory	adult longevity	adult lateral spread	adult height	spatial dispersal	seed death rate	seed mass
bet-hedging	↓,↑	↓	↓	↓	↓	↓,↑
sib-competition				↓	↓	
cueing					↓	
chemical packing				↓	↓	

2. Individuals that forgo reproduction may die before they are able to reproduce.

Both processes impose a cost of delayed reproduction (Bulmer 1985). Hence, from an evolutionary perspective, seed dormancy, which is a form of delayed reproduction, presents a problem; and this has led evolutionary biologists to explore the conditions under which the evolution of seed dormancy might be favoured.

It is instructive to begin by looking carefully at the assumptions of models that suggest that there is a cost to remaining dormant. The models assume:

1. Seeds have no information on the quality of the environment.
2. Competition occurs primarily between individuals that are not related rather than between siblings.
3. There is no temporal variation in the quality of the environment.

Allowing seeds to detect the quality of the environment will favour the evolution of dormancy even in a temporally constant environment providing there is spatial variation in establishment conditions (de Jong *et al.* 1987).

If competition occurs primarily between sibs, as a result of dispersal inside multi-seeded fruits, then dormancy may be favoured in a temporally constant environment, even when seeds have no information on the quality of the environment (Ellner 1986). This is a result of a parent-offspring conflict, which the parent wins by using the seed coat to prevent the embryo from germinating. The conflict occurs because parents wish to reduce competition between offspring, whereas the individual offspring whose germination is delayed have lower inclusive fitness than those that germinate. Thus, selection on embryos favours complete germination, whereas selection on the parent favours delayed germination for some of the offspring.

Allowing the environment to vary from one year to the next can also select for the evolution of dormancy even when seeds have no information on the quality of the environment and sib competition is weak. Consider the case where the conditions are suitable for growth and reproduction in some years, but reproduction fails completely in other years. In such an environment an annual plant genotype with no seed dormancy would maximize its arithmetic average population growth rate (λ) but would become extinct the first time that reproduction failed completely. At the other extreme, a genotype that never germinated would also become extinct as a result of seed mortality. Hence, in a variable environment we would expect an intermediate germination strategy to be optimal (Cohen 1966; Bulmer 1984; Ellner 1987).

Theory also predicts that life history attributes that reduce the impact of environmental variation on fitness will show patterns of negative covariation (Venable & Brown 1988; Rees 1993, 1994). For example, species with efficient dispersal in space, either as a result of seed dispersal or vegetative growth, reduce the likelihood that all seeds will be exposed to unfavourable conditions in any one year, and so we would expect a negative relationship between the efficiency of spatial dispersal and dormancy. It has also been suggested that a trade-off between spatial and temporal seed dispersal might arise as a result of physical and biochemical constraints (Lokesha *et al.* 1992). These authors argue that packing seeds with fats allows seed mass to be reduced while maintaining energy content because fats contain more energy per unit mass than proteins or carbohydrates. Hence in wind-dispersed species, where the efficiency of dispersal depends, in part, on seed mass because heavy seeds fall more rapidly than light ones, seeds should contain a higher proportion of fat than protein or carbohydrate. However, the use of fats has several disadvantages: their synthesis is more energy-demanding than the production of proteins or carbohydrates; and lipid autoxidation is thought to cause the disruption of several cell components resulting in loss of viability (Ponquett *et al.* 1992). Therefore, species with wind-dispersed seeds should have a high fat content, and as a result the seeds are short-lived, whereas species that are not wind-dispersed will have a lower fat content and so have greater seed longevity. There is some evidence that wind-dispersed seeds do indeed contain a higher proportion of fat than seeds that are passively dispersed or dispersed by animals (Lokesha *et al.* 1992). Species with large individual seeds are predicted to have reduced dormancy because their seedlings can draw on a larger food reserve, and hence establish in relatively unfavourable environments. In a similar way, species with long-lived adults are buffered from temporal variation in the environment and this also selects for less dormancy (Venable & Brown 1988; Rees 1994). A summary of the various theoretical predictions is given in table 1. Some of these ideas were tested using modern comparative methods, with taxonomy as a surrogate for a phylogeny, by Rees (1993), who found that large-seeded species do have less dormant seeds; species with efficient seed dispersal in space have less seed dormancy; and long-lived species also have less dormancy.

3. DATA AND COMPARATIVE METHODS – SEED DORMANCY

Two data sets were used in the analyses, the first was collected by Harold Roberts (Roberts 1964, 1979; Roberts & Boddrell 1983), the second is the Sheffield database (Grime *et al.* 1988, Hodgson *et al.* 1995). Roberts's data allow a quantitative estimate of seed dormancy (see below), whereas in the Sheffield database species are categorized on a three-point scale: type 1 transient, seeds rarely persisting for more than one year; type 2 short-term persistent, seeds persisting for more than one year but usually less than five; and type 3, long-term persistent seed persisting for at least five years, and often much longer (Hodgson *et al.* 1995).

In Roberts's experiments freshly collected seeds were mixed with the upper 7.5 cm of steam-sterilized sandy clay loam confined in open-ended 23-cm diameter cylinders sunk in the ground outdoors and netted to exclude birds. There were two replicate cylinders per species, each containing usually 1000 seeds. On three occasions each year the soil layer containing the seeds was mixed to its full depth to simulate cultivation. All seedlings were recorded and removed soon after they appeared. Recording continued usually for 5 years; the soil dug up and the number of viable seeds remaining determined. For most species, separate experiments were begun in each of three different years using freshly-collected seeds. Between 1953 and 1986 data were obtained for 171 species. A species list for the annual and perennial forbs is given in Rees & Long (1993).

Hence, for each species we have a pattern of seedling emergence times describing the number of recruits in each year of the experiment. The main variable analysed was the number of seedlings that emerge during the first year divided by the total number of seedlings that emerge during the 5 years of the experiment, this quantity was termed p1. Note that because seed mortality is completely unobserved this quantity cannot be simply interpreted as a probability of germination (see Rees & Long (1993) for a discussion of this point). However, species with high germination rates would be expected to have high p1 values.

Species with high seed mortality will automatically have higher p1 values than species with low seed mortality, simply because those seedlings that emerge in year 1 will be a greater proportion of those that ever emerge. However, analyses using the proportion of all seeds sown that emerge in year 1, called s1, gave similar results. s1 will be sensitive to differences in initial seed viability but relatively insensitive to differences in seed mortality during the experiment. Hence, the results presented largely reflect differences in seed germination probability.

The information on p1 was integrated into a database that contained life history information on each of the species. The variables used and the data sources were:

1. Adult longevity was determined using a simple scoring system, annual = 1, biennial = 2, monocarpic = 3, perennial = 5. Species in composite categories were given a weighted score; the first term given a weight of 1, the second 0.5 (e.g. annual/perennial = (1+0.5*5)/(1+0.5)). (Data sources: Grime *et al.* 1988; Clapham *et al.* 1989; Hodgson *et al.* 1995.)
2. Adult lateral spread and adult height were coded into categories following Hodgson *et al.* (1995). Where possible the species were coded using the information in Hodgson *et al.* (1995), species not in this database were classified using information from Clapham *et al.* (1989) and Stace (1991).
3. Seed masses (mg) were obtained from Grime *et al.* (1988) and also the ecological flora database (Fitter & Peat 1994). Seed masses were log transformed prior to analysis.
4. Spatial seed dispersal was assessed using the data in Hodgson *et al.* (1995).

The relationships between these traits, p1 and the Sheffield three-point seed bank score were explored using independent contrasts, calculated using the CAIC package (see Purvis & Rambaut (1995) for details). The phylogeny used in the calculation of the contrasts was phylogeny B of Chase *et al.* (1993). A detailed discussion of the rational underlying this method of analysis is given in Harvey & Pagel (1991).

4. RESULTS – SEED DORMANCY

(*a*) *Relationships between established plant traits*

Considering the species in Roberts's dataset first we find that the relationship between adult longevity and lateral spread was positive and statistically significant ($r^2 = 0.79$, $p < 0.0001$, $n = 41$). Surprisingly there was no significant relationship between lateral spread and plant height ($r^2 = 0.005$, $p > 0.05$, $n = 41$) or between longevity and height ($r^2 = 0.003$, $p > 0.05$, $n = 41$). Multiple regression analyses modelling variation in the contrast for one variable as a linear function of the other two gave similar results. Analyses using species as independent data points also gave qualitatively similar results; there were no significant relationships between height and either lateral spread or longevity, however the relationship between lateral spread and longevity was highly significant ($r^2 = 0.53$, p < 0.0001, $n = 169$).

In the Sheffield dataset we find similar results: the relationship between adult longevity and lateral spread is positive and statistically significant ($r^2 = 0.46$, $p < 0.0001$, $n = 113$). The relationship between height and adult longevity is not statistically significant ($r^2 = 0.03$, $p > 0.05$, $n = 113$), however in contrast to Roberts's dataset there was a positive, statistically significant relationship between height and lateral spread ($r^2 = 0.15$, $p < 0.001$, $n = 113$). These results are mirrored in analyses that use species as independent data points; the relationship between adult longevity and lateral spread was positive and highly significant ($r^2 = 0.48$,

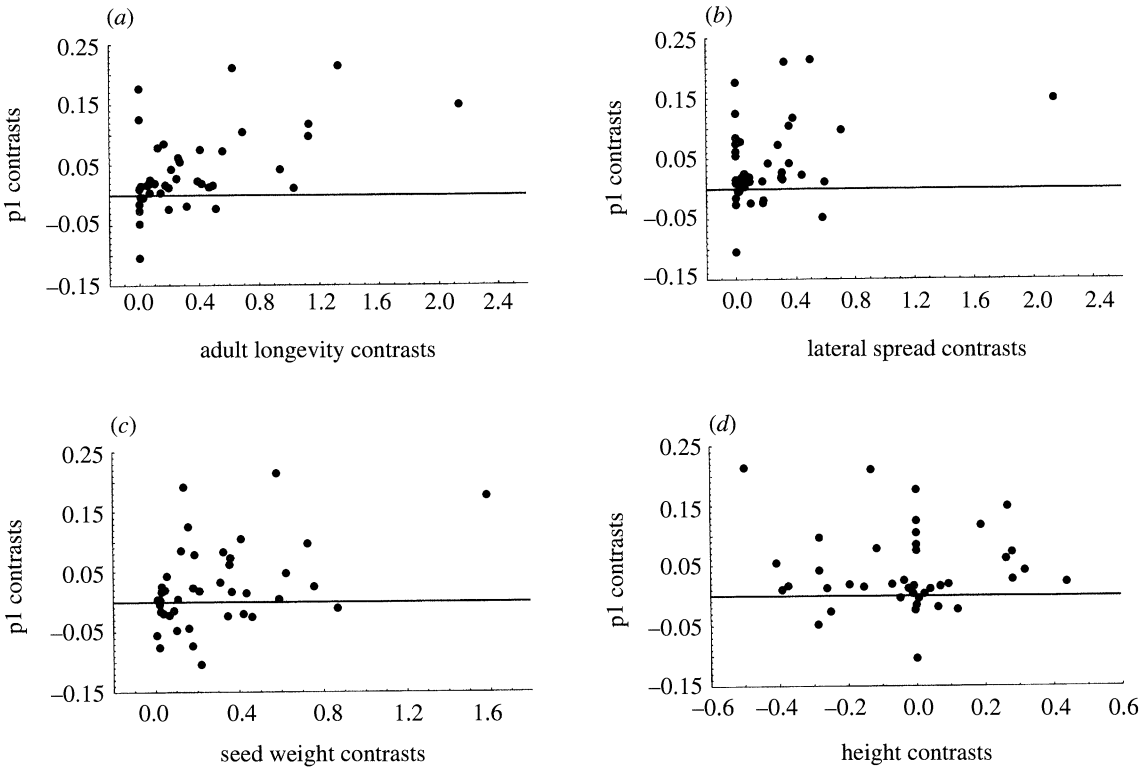

Figure 1. Independent contrast analyses of p1, the proportion of all seedling observed that emerge in year 1. Relationships between p1 and (*a*) adult longevity, (*b*) lateral spread, (*c*) seed weight and (*d*) height. See text for details.

$p < 0.0001$, $n = 513$), the relationship between plant height and adult longevity was not significant ($r^2 = 0.01$, $p > 0.05$, $n = 513$), however there was a positive, statistically significant relationship between height and lateral spread ($r^2 = 0.10$, $p < 0.0001$, $n = 513$).

(*b*) *Relationships between p1, seed bank scores and other traits*

In the p1 analyses plant height was never significant in any regression model. However, there were highly significant positive relationships between lateral spread, seed mass, adult longevity and p1 (p1 *vs* lateral spread $r^2 = 0.27$, $p < 0.001$, $n = 41$; p1 *vs* seed mass $r^2 = 0.30$, $p < 0.001$, $n = 41$; p1 *vs* longevity $r^2 = 0.49$, $p < 0.001$, $n = 41$; see figure 1). In a multiple regression model for p1 with all four variables, only seed mass and adult longevity were statistically significant (seed mass $p < 0.001$, longevity $p < 0.001$, $r^2 = 0.65$, $n = 41$).

Analysing only those species that have no mechanisms for spatial seed dispersal (i.e. those with no morphological features to aid dispersal, classified by Hodgson *et al.* (1995) as unspecialized, plus those dispersed by ants) we find that neither seed mass nor lateral spread entered the analysis significantly, either when alone or with the height and/or adult longevity ($p < 0.05$ in all cases). In contrast adult longevity was significant, both when entered alone, and also with the other variables (longevity alone – $r^2 = 0.36$, $p < 0.001$, $n = 29$; longevity with seed mass, height and lateral spread – $r^2 = 0.50$, $p < 0.001$, $n = 29$). When considering species with efficient mechanisms for spatial dispersal (i.e. those with wind- or animal-dispersed seeds) there were no significant relationships between p1 and seed mass or plant height, however there were positive statistically significant relationships between p1 and lateral spread and between p1 and adult longevity (lateral spread $r^2 = 0.49$, $p < 0.01$, $n = 16$; adult longevity $r^2 = 0.63$, $p < 0.001$, $n = 16$). In the full model with adult longevity, lateral spread, seed mass and height, only adult longevity was significant ($r^2 = 0.65$, $p < 0.05$, $n = 16$).

Analyses of the complete Sheffield dataset demonstrate that lateral spread, seed mass and adult longevity were all negatively related to seed bank score; there was no significant effect of plant height. This indicated that large-seeded plants, long-lived plants and those with wide lateral spread are less likely to have long-lived seed banks, in agreement with the analysis of Roberts's dataset. However, in contrast to Roberts's dataset, in the full model adult longevity was not statistically significant; only seed mass and lateral spread entered the full model significantly (see table 2).

The dataset was then divided into three dispersal categories; unspecialized, wind-dispersed and animal-dispersed, using the data in Hodgson *et al.* (1995). In the set of species with seeds unspecialized for spatial dispersal there were negative relationships between lateral spread and seed bank scores, and also between adult longevity and seed bank scores, however there was no relationship with seed mass or height (see table 2). Species with wind- or animal-dispersed seeds show similar relationships between seed bank scores and lateral spread, longevity and seed mass when these variables are used as the only explanatory variable in an analysis. However, in the full model wind dispersed

Table 2. *Regression models for seed bank score contrasts*

(In the single effect models only a single term was included in each model, in the full model all four terms were included simultaneously. The table entries give the sign of the relationship, significance levels (*ns* = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$), and for the single effects models the coefficient of determination. The coefficient of determination for the full model and the number of contrasts in each of the analyses are given in the right hand column. All regressions were forced through the origin.)

	Single variable model				Full model				
	adult height	lateral spread	seed mass	adult longevity	adult height	lateral spread	seed mass	adult longevity	
full data set	n.s. $r^2 = 0.002$	−*** $r^2 = 0.16$	−*** $r^2 = 0.20$	−*** $r^2 = 0.15$	n.s.	−**	−***	n.s.	$r^2 = 0.35$ $n = 106$
unspecialized	n.s. $r^2 = 0.08$	−* $r^2 = 0.14$	n.s. $r^2 = 0.003$	−** $r^2 = 0.20$	n.s.	n.s.	n.s.	n.s.	$r^2 = 0.23$ $n = 40$
wind-dispersed	n.s. $r^2 = 0.006$	−*** $r^2 = 0.33$	−** $r^2 = 0.21$	−** $r^2 = 0.22$	+*	−***	−**	n.s.	$r^2 = 0.60$ $n = 30$
animal-dispersed	n.s. $r^2 = 0.01$	− $r^2 = 0.08$	−*** $r^2 = 0.60$	−* $r^2 = 0.09$	n.s.	n.s.	−***	n.s.	$r^2 = 0.65$ $n = 47$

seeds show a negative relationship between lateral spread, adult longevity and seed bank scores, and there is a marginally significant positive relationship between seed bank scores and plant height (see table 2). Whereas in those species dispersed by animals only seed mass was significant in the full model.

5. EVOLUTION OF SEED MASS

Salisbury (1942) argued that seed mass reflected the establishment conditions that seedlings experienced. More precisely he argued 'that the large seed, with its copious provision of food, will be especially advantageous in closed communities where the colonising individual must be capable of growing above the surrounding vegetation, or at least into a level of moderate illumination, before it can receive a sufficient intensity of light to manufacture its own food at a rate comparable to that of its neighbours.' Tilman developed these ideas within the context of his size-structured model of competition called Allocate, and came to similar conclusions to Salisbury (Tilman 1988); namely that increased seed mass would be favoured in habitats where competition for light is important. Tilman also noted that increased seed mass would be favoured in habitats with resource-poor soils if resource availability increased with depth. In Tilman's model all species have identical adult traits (i.e. allocation patterns to roots, shoots and photosynthetic tissues) and exclusion of small seeded species occurs as a result of competition between juveniles. These ideas lead to two predictions: (1) tall species should have larger seeds than short species; (2) perennials should have larger seeds than annuals. These predictions assume that as plants get taller competition for light becomes more important, and that perennials typically occur in closed habitats where competition for light is more intense.

The standard treatment of the evolution of offspring size assumes a simple relationship between investment per offspring and offspring success (Smith & Fretwell 1974; Lloyd 1987), and uses this assumed relationship to derive the ESS (Evolutionarily Stable Strategy) or optimality solutions. However, by assuming the existence of a particular relationship between investment in each offspring and its subsequent success we rule out the possibility that frequency-dependent processes affect fitness (Lloyd 1987). This severely restricts the range of ecological processes that could determine the relative fitness of different sized offspring. For example, if we assume seed mass determines competitive ability, which in turn affects fitness, then to evaluate fitness we would need to know the distribution of seed masses that an individual competes against (Parker & Begon 1986): a 2 mg seed might be a good competitor against 1 mg seeds but a poor one against 3 mg seeds. This means that the curves used in the standard Smith-Fretwell analysis are not fixed but depend on the frequency distribution of seed sizes in a population or community. Therefore to study traits that affect competitive ability we require a game theory approach that allows the analysis of frequency-dependent coevolutionary games (e.g. Brown & Vincent 1987; Vincent *et al.* 1993).

The standard analysis, with its fixed relationship between resources invested and fitness, predicts a single evolutionary optimum investment per offspring (Smith & Fretwell 1974; Lloyd 1987). However, even within guilds within communities there is often a wide range of seed masses, for example in the four species guild of sand dune annuals studied by Rees *et al.* (1996) there was a 27-fold variation in seed mass. Hence, we need to reconcile the existence of broad variation in seed mass within guilds and communities with the theoretical prediction of a single evolutionary optimal seed mass. One obvious explanation for the wide range of seed masses observed is that establishment conditions vary enormously within communities (see below).

Recent theoretical work has extended the classical frequency independent models to include frequency dependence (Geritz 1995; Rees & Westoby 1996). These models assume seed mass determines the number of progeny produced per unit reproductive effort (i.e. there is a size number trade-off), and competitive ability. The outcome of competition is assumed to be determined by seed mass. Competition between individuals derived from seeds of different masses is assumed to be asymmetric with individuals from larger seeds having a greater negative effect on individuals derived from small seeds than vice versa. In Geritz's models a single seed mass is never evolutionarily stable, whereas in the models of Rees & Westoby a single seed mass can be evolutionarily stable but generally the ESS is made up of several species/strategies each with a different seed mass (Geritz 1995; Rees & Westoby 1996). Hence, in plant communities we should expect to see a range of seed masses, and this is indeed the case (Salisbury 1942). It is important to note that one of the key assumptions of Geritz's model, that results in many seed masses being present in the ESS, is that different species/strategies generate small-scale spatial variation in establishment conditions. Large-seeded species/strategies exclude small-seeded ones from microsites as a result of shading or nutrient uptake, however, large-seeded species/strategies produce fewer seeds and so have a disadvantage in colonization. Hence, the new models can be thought of as spatial extensions of Salisbury's original idea with the presence or absence of different species/strategies generating the variation in establishment conditions. An important corollary of the coexistence of many seed masses within the models is that a component of seed size variation may not be correlated with other life history traits (Rees & Westoby 1996).

However, these models do not tell us how seed mass should vary in relation to plant height, lateral spread or longevity. Geritz has produced a model for perennial species that has predictions similar to the annual models, but in the perennial model the maximum seed mass is set by the yearly resource allocation to reproduction, termed R_i. To predict how maximum seed mass varies with perenniality we need to know how R_i varies with plant longevity. Long-lived plants generally have a higher percentage allocation to structural, non-reproductive structures than annuals; whereas annuals in contrast have higher percentage allocation to reproduction than perennials (Tilman 1988; Wilson & Thompson 1989; Silvertown & Dodd 1996). Hence, if annuals and perennials have the same total mass, annuals will have a larger R_i and hence should produce larger seeds, on average. If, however, perennial plants are larger then this could offset the lower percentage allocation to reproduction with the result that perennials have larger R_is than annuals, which gives the opposite prediction. Therefore, in order to test these ideas we need to know more about R_i and adult longevity.

It has been suggested that plant height might alter the efficiency of seed dispersal, particularly in species with unassisted or wind-dispersed seeds, because small seeds travel further than large ones for a given height of release (Rabinowitz & Rapp 1981; Thompson & Rabinowitz 1989). Hence, short plants might be constrained to have small seeds, whereas tall plants can potentially have large seeds. A corollary of this is that in species dispersed by animals there should be no relationship between plant height and seed mass. The difficulty with these hypotheses is that they are framed in terms of dispersal efficiency and it may not be straightforward to link this with fitness.

A final set of hypotheses link seed mass with mechanisms that allow escape from predators or competition (Janzen 1970; Eriksson 1992). Several hypotheses can be developed. For example, in species with seeds unspecialized for spatial dispersal we might expect those with extensive clonal spread to produce small seeds. There are two potential advantages of this: (1) average dispersal distance might be increased; and (2) more small seeds are produced, which increases the absolute number that disperse a given distance. In each case competition between seedlings and clonal ramets will be decreased, which could increase fitness. A corollary of this is that no decrease in seed mass with clonal extent should be observed in species with wind- or animal-dispersed seeds.

6. DATA AND COMPARATIVE METHODS – SEED MASS

The analyses use data from the Sheffield flora (Grime *et al.* 1988; Hodgson *et al.* 1995). Seed masses were taken from Grime *et al.* 1988 and from the ecological flora database (Fitter & Peat 1994); the resulting dataset contained information on seed masses for 382 species. Species were classified into three dispersal strategies (i.e. unspecialized, wind-dispersed and animal-dispersed) using Hodgson *et al.* (1995). Details of the data coding are given in Hodgson *et al.* (1995) and also section 3. The relationships between height, lateral spread, adult longevity and seed mass were explored using independent contrasts, calculated using the CAIC package (see Purvis & Rambaut 1995 for details). The phylogeny used in the calculation of the contrasts was phylogeny B of Chase *et al.* (1993).

7. RESULTS – SEED MASS

Considering the full dataset there were positive, highly significant relationships between seed mass and plant height and also between seed mass and lateral spread. Note however, in the full model only adult lateral spread entered significantly. There was no significant relationship between seed mass and adult longevity (see table 3). Restricting the analysis to species with seeds unspecialized for dispersal we find that adult height, lateral spread and longevity all enter the multiple regression model significantly; having corrected for height and longevity the relationship between seed mass and lateral spread was negative. Within the wind-dispersed species lateral spread does not enter the regression model significantly but both height and longevity show positive significant relationships. In those species that are animal-dispersed lateral spread is significant when considered in isolation, but in the full model no single factor was significant (see table 3). Excluding a single data point resulted in height being significant in the single variable model (see table 3).

An alternative approach to dividing the dataset into three dispersal categories is to include the effects of wind- and animal-dispersal using dummy variables.

Table 3. *Regression models for log seed mass contrasts*

(In the single effect models only a single term was included in each model, in the full model all three terms were included simultaneously. The table entries give the sign of the relationship, significance levels ($ns = p > 0.05$, $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$), and, for the single variable models, the coefficient of determination. The coefficient of determination for the full model and the number of contrasts in each of the analyses are given in the right hand column. All regressions were forced through the origin. In those species with seeds dispersed by animals two sets of figures are given, those in brackets refer to a reduced dataset where a single outlier was excluded. This outlier was a comparison between *Viburmum opulus* and *Sambucus nigra*.)

	single variable model			full model			
	adult height	lateral spread	adult longevity	adult height	lateral spread	adult longevity	r^2 and n for full model
full dataset	+** $r^2 = 0.07$	+*** $r^2 = 0.10$	n.s. $r^2 = 0.02$	n.s.	+*	n.s.	$r^2 = 0.12$ $n = 110$
unspecialized	+* $r^2 = 0.15$	n.s. $r^2 = 0.02$	n.s. $r^2 = 0.05$	+***	−**	+***	$r^2 = 0.45$ $n = 42$
wind-dispersed	+*** $r^2 = 0.45$	n.s. $r^2 = 0.01$	+*** $r^2 = 0.48$	+**	n.s.	+***	$r^2 = 0.65$ $n = 33$
animal-dispersed	n.s. $r^2 = 0.06$ (+** $r^2 = 0.18$)	+* $r^2 = 0.10$ (+** $r^2 = 0.14$)	n.s. $r^2 = 0.03$ (n.s. $r^2 = 0.04$)	n.s. (n.s.)	n.s. (n.s.)	n.s. (n.s.)	$r^2 = 0.11$ $n = 48$ ($r = 0.21$ $n = 47$)

To do this one needs to code two variables, one for wind dispersal that contains a 1 if the species has wind-dispersed seeds and a 0 otherwise: in a similar fashion a variable was coded for animal dispersal. In effect this allows different intercepts to be fitted in the regression models. The full model contained six explanatory variables, adult longevity, height, lateral spread, wind dispersal, animal dispersal, and seed bank scores. The resulting regression model had the following form,

$$\text{seed weight contrast} = 0.36^{***}\ \text{height} - 0.48^{**}\ \text{lateral spread} + 0.32^{*}\ \text{longevity} - 0.56^{***}\ \text{seed bank} - 0.07\ \text{wind} + 0.20^{*}\ \text{animal},$$

where the superscripts indicate the significance levels (see legend to table 3 for details), overall $r^2 = 0.44$, $n = 93$. In this multiple regression model only the effect of wind dispersal was not significant. Seed mass was positively related to plant height, longevity, and animal dispersal, and negatively related to lateral spread and seed bank score. Hence, tall plants, long-lived plants and those that are dispersed by animals tend to have heavy seeds, whereas species with extensive lateral spread or that have long-lived seed banks have lighter ones.

8. DISCUSSION

The results of the comparative analysis of p1 and seed bank scores strongly support the predictions of simple bet-hedging theories (Venable & Brown 1988; Rees 1993, 1994). Evidence for spatial and temporal risk-spreading strategies being negatively correlated with dormancy is found for both adult longevity and lateral spread. The relationships between p1, seed bank scores and seed mass are more difficult to interpret because increased seed mass is linked with both increased establishment success, which reduces expected dormancy levels (Venable & Brown 1987), and also increased levels of predation (Thompson 1987). Increased predation levels make the cost of forming a seed bank greater, which selects for less seed dormancy. In this respect it is perhaps significant that the clearest relationship between dormancy and seed mass occurs in animal dispersed species.

The impact of spatial seed dispersal was difficult to assess in the current datasets because dispersal traits are relatively deeply rooted in the phylogenetic tree resulting in few contrasts (for Roberts's data 171 species yielded only eight contrasts, seven of which were positive suggesting that species with efficient seed spatial dispersal mechanisms have less dormancy, $p = 0.075$). Analysis of the Sheffield dataset was equally uninformative as this problem is compounded with the three-point seed bank score, which results in many uninformative, zero contrasts.

The analyses of seed mass are particularly interesting, suggesting an interplay between dispersal limitation, escaping competition with clonal ramets and differences in establishment success linked with plant height and longevity. As predicted by the escape hypotheses the only negative relationship between seed mass and lateral spread was found in those species with seeds unspecialized for dispersal (Eriksson 1992). In the full model (see table 3) plant height was most strongly related to seed mass in those species with seeds unspecialized for spatial dispersal or wind dispersed, in agreement with Thompson and Rabinowitz's ideas on dispersal limitation (Thompson & Rabinowitz 1989).

The relationship between adult longevity and seed mass in species with seeds unspecialized for spatial dispersal, and those dispersed by wind is consistent with Salisbury's prediction that seed mass should increase in closed habitats (Salisbury 1942, 1974). Differences between open and closed habitats are often confounded with changes in plant longevity and height. For example Salisbury (1942, 1974) showed, by comparing congeneric species, that species from open (early successional) habitats typically had lighter seeds

Table 4. *Regression analyses of independent contrasts for seed mass and height, structured by habitat*

(Each species was classified using its commonest terminal habitat into one of the seven primary habitats, see Hodgson *et al.* 1995 for a detailed description of the habitat classifications.)

habitat	r^2	n	p
skeletal	0.64	26	< 0.0001
grasslands	0.01	29	n.s.
spoil	0.07	23	n.s.
wastelands	0.17	21	0.06
woods	0.01	36	n.s.
wetlands	0.10	41	0.03
arable	0.46	20	< 0.001

than those from closed (later successional) habitats. However, in Salisbury's study, 63% of the species from open habitats were annuals compared with only 2% from the closed habitats. Clearly adult longevity, height and habitat will often be confounded and this will make interpretation of comparative analyses difficult. Why there is no relationship between adult longevity and seed mass in animal dispersed species is unclear.

The coefficients of determination (r^2) for the multiple regression models of seed mass range from 0.11 to 0.65. Might differences in establishment conditions be the primary source of this unaccounted variation? Recently Leishman *et al.* (1995) have argued that this is *not* the case. Their argument rests on two observations: (1) in five floras the variation in seed mass between species is large relative to variation between floras (Leishman *et al.* 1995), and (2) studies that include habitats (e.g. Mazer 1989) find that habitats account for a relatively small proportion of the variance. However, characterizing the establishment conditions within a flora using a single number is clearly an extremely crude form of analysis. For example, the Sheffield flora used in Leishman *et al.*'s analysis contains habitats ranging from scree slopes to mires and deciduous woodland. Within each of these habitats there will be enormous variation in establishment conditions, for example, woodlands contain shaded areas and gaps, and within each of these there will be places with ground cover, some with deep litter and some with shallow litter. It is therefore not surprising given the enormous variation in establishment conditions within each flora that differences between floras account for a small proportion of the variance in seed mass. In addition to this general argument it should be noted that if the success of a particular seed mass in exploiting any given set of establishment conditions depends on the seed masses of the other species present then the interpretation of comparisons between floras becomes even more problematic. Similar arguments can be put forward for why habitat variables often account for a relatively small proportion of the variance in seed mass (but see Hammond & Brown (1995) where gap environment assessed on a three-point scale accounted for 31% for the variance in seed mass). It also appears from preliminary analysis of the Sheffield flora that the relationship between seed mass and height may require the fitting of interaction terms (i.e. different intercepts *and* slopes within each habitat). For example, in the seven primary habitats (arable, wetland, skeletal, grassland, spoil, wasteland and woodland) of the Sheffield flora the coefficients of determination (r^2) for the relationship between seed mass and height range from < 0.01 to 0.64, strongly suggesting the possibility of an interaction between habitat and height (see table 4). Ignoring interaction terms will reduce the explanatory power of both height and habitat in this case.

A common problem with many studies that compare the use of different variables in predicting say, seed mass, is that the variables are often measured on very different scales. For example, height might be measured on a six-point continuous scale whereas longevity might be assessed as annual or perennial. Obviously perenniality will be a much cruder predictor of seed mass than plant height, and we should not be surprised if longevity accounts for a relatively small proportion of the variance in seed mass, which is generally the case (Leishman & Westoby 1994; Leishman *et al.* 1995). Performing a simulation where the scale of measurement can be changed, clearly illustrates this effect. Assuming we can accurately estimate adult longevity we find, for the simulated data, that the coefficient of determination (r^2) between seed mass and adult longevity is 0.98; however, if longevity is assessed on a two-point scale, annual and perennial, the coefficient of determination drops to 0.38. Interestingly in one of the few studies where plant size has been accurately quantified (Wilson & Thompson 1989) the relationship between log seed weight and total plant biomass for annual grass species has a coefficient of determination of 0.97 ($n = 8$, using species as independent data points). Likewise studies which incorporate habitat variables often do not quantify variation in establishment conditions within habitats (but see Mazer (1989), where a four-point scale was used) and so weak descriptive power should be expected.

More theoretical work is required exploring the evolution of seed traits in realistic models. Current models either ignore space completely or assume large-scale dispersal so that the positions of sites relative to one another can be ignored. Likewise most models assume that all plants are the same size, and so make no predictions about how traits should vary in relation to lateral spread or height. Obviously size-dependent spatial models will be difficult to analyse, but have the great advantage that they make predictions about quantities that are easily measured. Coupling careful comparative analyses with modelling studies offers the possibility of rapidly advancing our understanding of the selective forces shaping plant life histories.

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