Chapter 2

The Evolutionary Ecology of Seed Size

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Introduction

Seed mass is a trait that occupies a pivotal position in the ecology of a species. It links the ecology of reproduction and seedling establishment with the ecology of vegetative growth, strategy sectors that are otherwise largely disconnected (Grime *et al.*, 1988; Shipley *et al.*, 1989; Leishman and Westoby, 1992).

There is a startling diversity of shapes and sizes of seeds among the plant species of the world. Seeds range from the dust seeds of the *Orchidaceae* and some saprophytic and parasitic species (around 10^{-6} g), across ten orders of magnitude to the double coconut *Lodoicea seychellarum* (10^4 g) (Harper *et al.*, 1970). Within species, seed size typically spans less than half an order of magnitude (about fourfold: Michaels *et al.*, 1988). Most within-species variation occurs within plant rather than among plants or populations (Michaels *et al.*, 1988; Obeso, 1993; Vaughton and Ramsey, 1998), indicating environmental effects during development rather than genetic differences between mothers. This chapter is concerned with the differences in seed size among species, and the consequences for vegetation dynamics and community composition.

During the last 10–15 years, there has been considerable progress in the ecology of seed mass. Unlike many other areas of comparative plant ecology, we have substantial published information from several different scales and research styles. As well as field experiments and demographic studies with a few species at a time, we have simple experiments with larger numbers of species (ten to 50), quantification of seed mass and its correlates in whole-vegetation types (hundreds of species) and tests of consistency across different continents. The wide-scale quantification began as early as Salisbury (1942) and Baker (1972), but has been much added to and consolidated over the past 10 years (e.g. Mazer, 1989, 1990; Leishman and Westoby, 1994a; Leishman *et al.*, 1995; Eriksson and Jakobsson, 1998). The work spanning large numbers of species is complementary to detailed experiments involving only a few species, giving a stronger sense of how widely the results from particular experiments can be generalized.

Much of the literature examines how natural selection on seed size might be influenced by various environmental factors. In this context, it is at first glance surprising that seed size varies within communities across a remarkable five to six orders of magnitude (Leishman *et al.*, 1995; Fig. 2.1). Further, there is strong overlap of seed-size distributions between quite different habitats. Within the temperate zone,
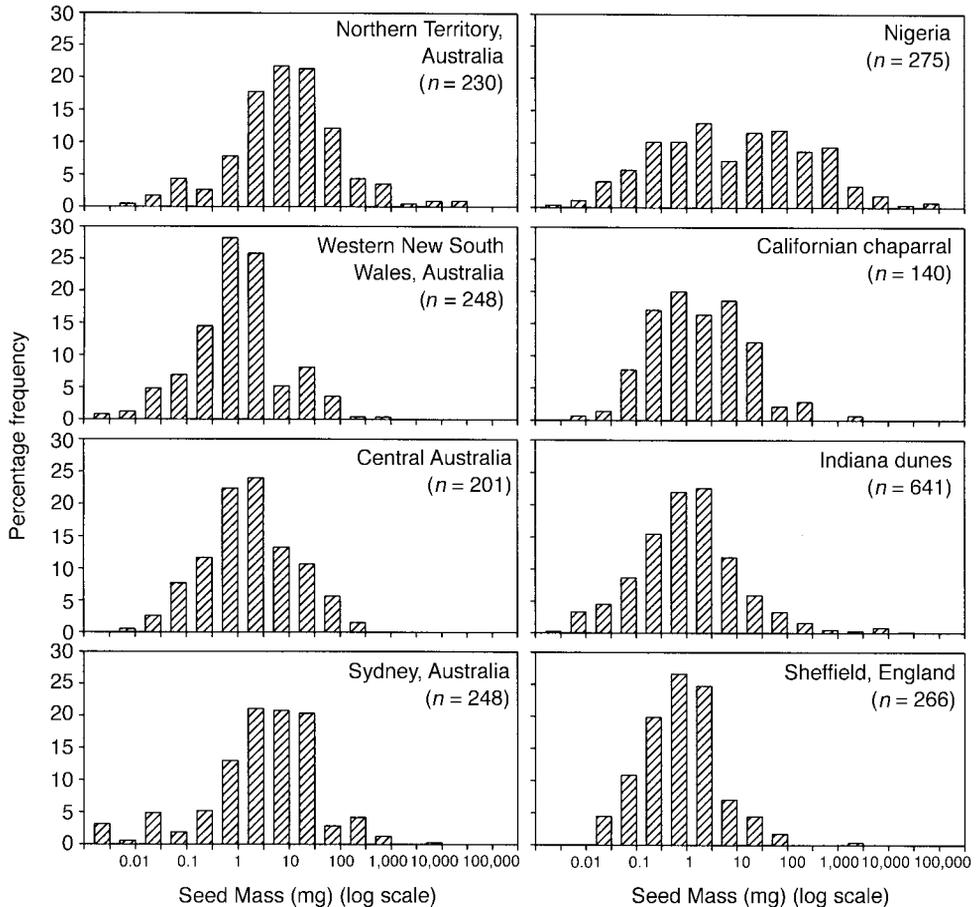
Fig. 2.1. Frequency histograms of seed dry mass from eight floras. The floras originate from four continents and include representatives from tropical and temperate biomes and a diversity of environmental conditions, vegetation types and phylogenetic histories. Data from western New South Wales, central Australia, Sydney (Leishman *et al.*, 1995); Northern Territory, Nigeria (Lord *et al.*, 1997); Californian chaparral (Keeley, 1991); Indiana dunes (Mazer, 1989); and Sheffield (Grime *et al.*, 1988). Seed masses are grouped into half-log classes.

differences between communities account for only about 4% of the variation in seed size between species (Leishman *et al.*, 1995). Differences between the tropics and the temperate zone are somewhat larger (Lord *et al.*, 1995), but variation within a habitat remains a very large component of overall between-species variation. Alternative mechanisms that might shape this wide within-habitat variation have not yet been fully formulated theoretically, much less exposed to strong experimental hypothesis tests.

Components and measurement of seed size

Seeds consist of an embryo plus endosperm (sometimes termed the seed reserve), plus a protective seed-coat or testa. Many seeds have distinctive dispersal appendages attached to the seed, such as plumes and hairs for wind dispersal, hooks and barbs for adhesion dispersal, elaiosomes for ant dispersal and arils or flesh for vertebrate dispersal. These dispersal appendages plus the seed are termed

the diaspore. The mass of dispersal structure and the proportion of seed mass that is seed-coat can vary considerably between species.

There is no single measure of seed size that is ideal for all purposes. For discussing seedling establishment, seed reserve mass best reflects the resources available to the seedling. For discussing the size of the object that has to be moved by a given dispersal mechanism, seed mass including the seed-coat is most relevant. For discussing costs to the mother per seed produced, mass of the whole diaspore is better than seed mass, though still not a complete measure of all costs of reproduction. Westoby (1998) recommended dry seed mass, including seed-coat but excluding dispersal structures, as an ecological strategy axis, partly as a compromise among alternative measures, partly because it is easiest to measure and partly to maintain comparability with the majority of existing data. At the same time, increasing numbers of studies go to the trouble to dissect diaspores into components where it seems relevant (e.g. Westoby *et al.*, 1990; Jurado and Westoby, 1992; Leishman and Westoby, 1994b, c). Fortunately, in data sets spanning a wide range of seed mass, the alternative measures will be strongly correlated. Suppose, for example, that two species have dispersal structure mass 0 and 300% of seed mass: this can only reverse diaspore-mass ranking, relative to seed-mass ranking, for species whose seeds differ in mass by less than a factor of three. Thus, in data sets spanning orders of magnitude of seed mass, there is a strong positive relationship between log dry diaspore mass and log dry seed mass: e.g. in western New South Wales, $n = 243$, $r^2 = 0.71$; central Australia, $n = 199$, $r^2 = 0.83$; Sydney, $n = 286$, $r^2 = 0.97$. On the other hand, among sets of species spanning only (say) three- to fourfold in seed mass, diaspore-mass ranking could be substantially different from seed-mass ranking. Similarly, log seed mass and log seed reserve mass tend to be closely correlated, even though substantial variation exists in the proportion of mass due to the seed-

coat. For example, for the Sydney data set (Westoby *et al.*, 1990) $r^2 = 0.92$, $P < 0.0005$, while the percentage of dry seed mass due to the seed-coat varied between 1.2 and 96%, with a mean value of 43%. In a smaller data set of woody perennials from a range of habitats in New South Wales (Wright and Westoby, 1999), seed mass and reserve mass were again tightly correlated ($r^2 = 0.99$, $P < 0.0005$), while % coat varied from 7 to 57%, with a mean of 30%. In neither data set was there a relationship between % coat and seed mass.

To the extent that mineral nutrients as well as energy are decisive during seedling establishment, the mineral nutrient content of the seed would be just as informative as seed mass. The nutrient content is the product of the nutrient concentration and seed mass, but, since there is much greater cross-species variation in seed mass than in nutrient concentration (e.g. 6.7 versus 1.7 orders of magnitude in the *c.* 1500 species of Barclay and Earle, 1974), in large data sets seed mass and nutrient content tend to be correlated (even if mass and concentration themselves are not). Some authors have reported a negative association between seed mass and nutrient concentration (e.g. Fenner (1983) for 24 species of *Asteraceae*; Grubb and Burslem (1998) within species for the majority of 12 South-East Asian trees; Grubb *et al.* (1998) for 194 species from lowland tropical rainforest) while others have found no correlation (e.g. Kitajima (1996a) for 12 tropical woody species of *Bignoniaceae*, *Bombacaceae*, *Leguminosae*; Grubb and Burslem (1998) across the 12 South-East Asian tree species; Milberg *et al.* (1998) for 21 *Eucalyptus*, *Banksia* and *Hakea* species). Thus, no consistent relationship has emerged between seed mass and nutrient concentration, although evidence is beginning to emerge that variation in these attributes should be considered simultaneously with measures of allocation to seed defence structures, such as seed-coats (Grubb *et al.*, 1998).

The seed size of a species represents the amount of maternal investment in an individual offspring, or how much 'packed

lunch' an embryo is provided with to start its journey in life. Seed size represents a fundamental trade-off, within the strategy of a species, between producing more small seeds versus fewer larger seeds from a given quantity of resource allocated to reproduction. The trade-off and its consequences were formalized in the model by Smith and Fretwell (1974). There is always selection pressure to produce more seeds, since more seeds represent more offspring (although there may be a lower limit to the seed size that permits a functional seedling to be produced (Raven, 1999)). On the other hand, larger, better-provisioned offspring have a greater chance of successful establishment, described by the Smith–Fretwell function in Fig. 2.2. The best outcome from the mother's point of view is to maximize the ratio of seedling establishment chance to provisions invested in each seed, and this occurs where the steepest possible line from the origin just touches the Smith–Fretwell function (Fig. 2.2). Thus a key prediction of

the model is that, if a mother plant is in a position to allocate more resources to seed output, it should produce more seeds of the same size. The physiological machinery of seed provisioning should have been selected to approximate this outcome, rather than increasing the size of a fixed number of seeds. In order to generate this prediction, the exact shape of the Smith–Fretwell function is not important. All that is required is for there to be some minimum size for a seed to have any chance of establishing and for there to be diminishing returns at some stage as seed mass increases further. The curvature of the Smith–Fretwell function ensures that, if resources are reallocated such that one seed has higher seed mass than the optimum while another has less, the gain in fitness in the augmented seed is smaller than the loss in fitness in the diminished seed. The moderate observed variation in seed mass within a species can be attributed either to the machinery of seed provisioning having limited capacity to deliver a
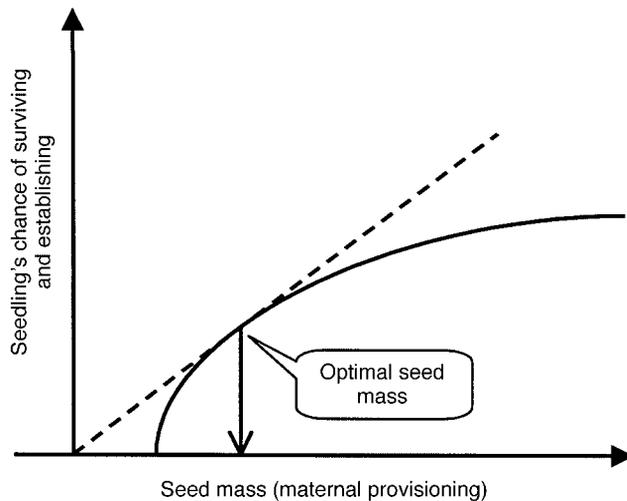
Fig. 2.2. Optimal allocation across seeds of a limited total maternal expenditure on seed provisioning, after Smith and Fretwell (1974). The curved Smith–Fretwell function describes how a seedling's prospects respond to maternal provisioning, the curvature reflecting diminishing returns beyond some point. The best allocation to each seed, from the point of view of genes in the mother, is where the steepest possible straight line from the origin just touches the Smith–Fretwell function. The mother should aim to produce as many seeds as possible of this size. At this point on the curve, if some resource were to be transferred from one seed to another, the fitness gain in the enhanced seed would be smaller than the fitness loss in the diminished seed; hence, maternal fitness would decrease.

completely standardized seed mass or to variability in the Smith–Fretwell function that seedlings are exposed to.

In the Smith–Fretwell treatment, all factors affecting a seedling's chance of establishing and growing to adulthood are amalgamated into the Smith–Fretwell function, including the effects of competition from established vegetation or from other seedlings. Subsequent game-theoretical models (Geritz, 1995; Rees and Westoby, 1997) address frequency-dependent effects among species directly. The question whether these models might be capable of accounting for the wide spread of seed mass observed between species within a habitat is taken up later.

Much of the variation in seed size among species is associated with taxonomy, such as family membership (Hodgson and Mackey, 1986; Mazer, 1989, 1990; Peat and Fitter, 1994; Lord *et al.*, 1995). Some authors believe variation correlated with phylogeny should not be regarded as interpretable in relation to ecology. They regard phylogenetic or correlated-divergence methods of data analysis as compulsory, superseding cross-species correlations rather than complementing them (Kelly and Purvis, 1993; Rees, 1993, 1996; Harvey *et al.*, 1995a, b; Kelly, 1995, 1997). In our view (Leishman *et al.*, 1995; Lord *et al.*, 1995; Westoby *et al.*, 1995a, b, c), phylogenetic and ecological accounts of seed size variation should not be considered mutually exclusive. An important mode of evolution is phylogenetic niche conservatism: a process whereby, because ancestors have a particular constellation of traits, their descendants tend to be most successful using similar ecological opportunities, and so natural selection tends to maintain the same traits among most, if not all, descendant lineages. Niche conservatism: is at least as likely a cause of similarity among related species as constraint – more likely for quantitative traits. It is a process that is phylogenetic and also invokes ecological functionality continuing into the present day. Thus it is simplistic to treat phylogenetic patterns of seed mass as somehow alternatives to ecological patterns.

Dormancy, seed banks and seed mass

In herbaceous vegetation of north-western Europe, persistence in the soil is associated with small and rounded seeds (Thompson, 1987; Thompson *et al.*, 1993; Eriksson, 1995; Bakker *et al.*, 1996; Bekker *et al.*, 1998). Evolutionary divergences in seed size are also correlated with evolutionary divergences in dormancy (Rees, 1993, 1996; Hodkinson *et al.*, 1998) and small seeds dominate the seed bank (Eriksson and Eriksson, 1997). However, it is clear that this pattern is not universal in all floras and vegetation types. Although a few studies in different floras have found similar patterns (e.g. Dalling *et al.* (1997) for species of tropical forest in Panama; Leck (1989) for wetland seed banks; Price and Joyner (1997) for seed banks of the Mojave desert flora of California), other authors have not found this pattern elsewhere. Leishman and Westoby (1994a, 1998) found that small seeds were not more likely to be dormant among species of western New South Wales or among a wide range of Australian species. Lunt (1995) found no relationship between seed size and longevity for six species of Australian grassland. Garner and Witkowski (1997) showed that seeds of three South African woody savannah species were both large and persistent in the soil. Finally, Moles *et al.* (2000) found that dormant species did not consistently have smaller seeds in a data set of 47 native New Zealand species. The relationship between seed size, shape and dormancy for three different floras is shown in Fig. 2.3.

There are two classes of prospective explanations as to why dormancy may be associated with small seed size. First, theory about bet-hedging against zero survivorship predicts that the higher the level of bet-hedging via one mechanism (for example, better dispersal to other sites), the weaker the selection for other mechanisms (for example, bet-hedging seed dormancy) (Venable and Brown, 1988; Philippi and Seger, 1989). Venable and Brown (1988) and Rees (1996) regarded large-seededness
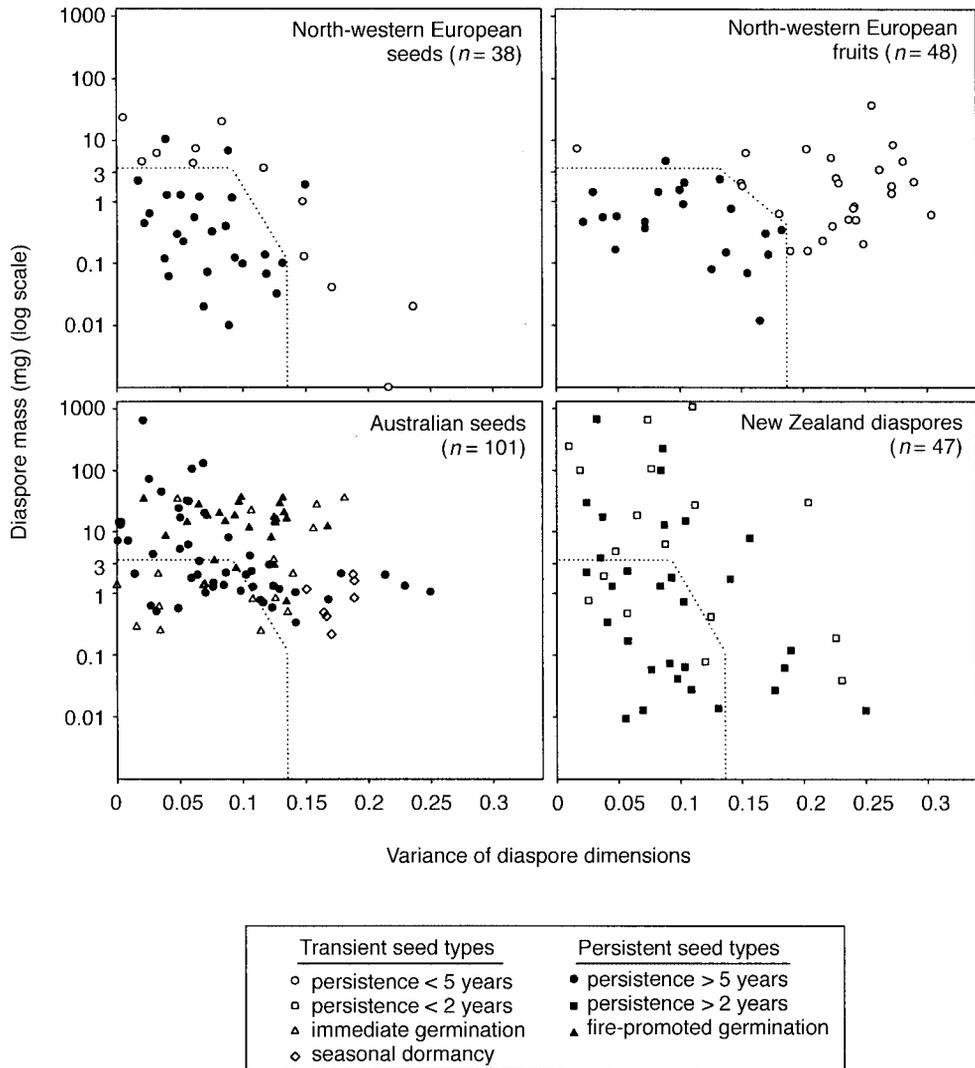
Fig. 2.3. Relationship between mass and variance of dimensions of seeds, fruits or diaspores from north-western Europe (Thompson *et al.*, 1993), Australia (Leishman and Westoby, 1998) and New Zealand (Moles *et al.*, 2000). Variance was calculated from length, width and breadth measurements (standardized such that length equals 1); hence, a perfect sphere has zero variance and a needle or thin disc has a maximum variance of 0.33. Note that, for the Australian data, 'seed' was defined as the diaspore minus any dispersal structures (and thus includes one-seeded fruits, such as achenes); for the New Zealand data, measurements were taken on the part of the diaspore that was most likely to be incorporated into the soil profile (dispersal structures were included if they were permanently attached); and, in the European data set, most 'fruits' were entire diaspores (exceptions are detailed in Thompson *et al.*, 1993).

as contributing to bet-hedging by permitting establishment under a wider range of seedling establishment conditions. Consequently, they predicted that smaller-seeded species would be more strongly

selected for bet-hedging dormancy, as is actually observed in England.

Secondly, although seeds of all sizes are subject to predation from a variety of predators while on the soil surface (Abbott

and Van Heurck, 1985; Meiners and Stiles, 1997; Reader, 1997), only small seeds (which are consumed by invertebrates) can escape predation by quickly becoming incorporated into the soil. In contrast, large seeds are not protected from predation by burial, as vertebrates can find buried seeds (Thompson, 1987). Work by van Tooren (1988) and Chambers *et al.* (1991) has shown that small seeds are both buried more easily and incorporated more quickly into the soil than large seeds. Thompson *et al.* (1994) suggested that small seeds are also more likely to be taken down through the soil profile by earthworms. Thus the proposed mechanism for the association between small seed size and persistence is that only small seeds are able to persist as they are immune from predation once they are beneath the soil surface. Clearly it would be an advantage for persistent seeds to enter the seed bank quickly and thus small seeds may be rounded to facilitate burial. If this is the correct explanation for persistent seeds tending to be small and rounded in European herbaceous vegetation, presumably mechanisms of burial and disturbance are different in Australia (Leishman and Westoby, 1998) and New Zealand (Moles *et al.*, 2000).

Community patterns of seed size variation

Much of the literature on seed size variation considers seed size differences among species in terms of different environmental conditions that seedlings face during establishment. Large seeds are generally considered to be adaptive under harsh establishment conditions (Willson, 1983; Westoby *et al.*, 1992, 1996), and there is considerable evidence for this (discussed later).

The strongest pattern of seed-mass variation in relation to environmental factors is the relationship between large seeds and shaded habitats. This pattern was recognized long ago by Salisbury (1942, 1975), who showed that seed size increased with increasing shadiness of the habitat for British species. The same pattern has been reported for studies on other British species (Hodgson and Mackey, 1986; Hodkinson *et al.*, 1998), other European communities (Luftensteiner, 1979), tropical woody species in Malaysia (Ng, 1978), Peru (Foster and Janson, 1985; Hammond and Brown, 1995), Guyana and Panama (Hammond and Brown, 1995), tropical species in Singapore (Metcalfe and Grubb, 1995) and Australia (between-genera comparisons only: Grubb and Metcalfe, 1996), the Indiana dunes flora of the USA (Mazer, 1989, 1990), annual communities of California (Marañón and Bartolome, 1989) and angiosperm tree species of temperate North America (but not gymnosperms: Hewitt, 1998). The pattern is strongly associated with phylogeny, with particular genera, families or orders tending to contribute more species in shaded than in unshaded situations (Mazer, 1990; Grubb and Metcalfe, 1996; Hodkinson *et al.*, 1998). The pattern is not absolute; for example, some of the smallest-seeded species (< 1 mg) in rainforest sites are very shade-tolerant and are successful in establishing on steep litter-free slopes (Metcalfe and Grubb, 1995, 1997; Grubb and Metcalfe, 1996).

Evidence for an association between large seeds and dry habitats is quite limited. Several within-species studies have reported a tendency for larger seeds in drier habitats (Schimpf, 1977; Sorenson and Miles, 1978; Stromberg and Patten, 1990). In phylogenetically independent contrasts comparing related high- and low-rainfall species, Wright and Westoby (1999) found larger seed mass in three of the five high-rainfall species. The most widely cited study is that of Baker (1972), who compared seed weights of over 2500 Californian taxa with moisture availability of the habitat. He found a positive correlation between moisture stress and seed size among herbaceous species, but not among trees or shrubs. Westoby *et al.* (1992) have argued that Baker's data should be viewed cautiously, as the relationship between seed size and dryness of the habitat is due to very small seeds in flood-prone sites

rather than large seeds in dry sites. Mazer (1989) found no evidence for a relationship between seed size and moisture for 648 species of the Indiana dunes. Similarly, Telenius and Torstensson (1991) found no seed size–moisture relationship among 48 species of the genus *Spergularia*, and Long and Jones (1996) found no relationship in 14 oak species. However, it is not clear that measurements of annual rainfall are a good indicator of moisture stress during establishment for seedlings. Many seedlings only germinate in particular seasons or after suitable rains, and thus establishment conditions for the few weeks after germination may be equivalent in areas of different annual rainfall.

Evidence for larger seeds in low-nutrient soils is also very limited. Patterns of large seed size associated with lower-fertility soils have been found among 12 species of *Chionochloa* in New Zealand (Lee and Fenner, 1989) and for two species pairs in the *Proteaceae* (Mustart and Cowling, 1992) (although, for these habitats, soil moisture and fertility effects could not be separated). In contrast, Grubb and Coomes (1997) found smaller mean seed size among 27 Amazonian forest species on poorer compared with richer soils, while Westoby *et al.* (1990), Hammond and Brown (1995) and Wright and Westoby (1999) found no relationship between seed size and soil types of varying fertilities. Thus the evidence for a relationship between seed size and soil nutrient availability remains equivocal.

In summary, there is a clear and consistent pattern of larger seeds being associated with shaded habitats. However, any association between large seeds and dry or low-nutrient soils appears much more marginal.

Experimental evidence for the role of large seed size during seedling establishment

Seedlings face a variety of hazards during establishment. Mortality rates are often very high (Harper, 1977); consequently, natural selection may operate strongly during this early stage of a plant's life cycle. Many studies have shown that initial seedling size is positively related to seed size, both within species (Dolan, 1984; Wulff, 1986; Zhang and Maun, 1991; Moegenburg, 1996) and among species (Stebbins (1976) for 15 Mediterranean annuals; Jurado and Westoby (1992) for 32 central Australian species; Seiwa and Kikuzawa (1991, 1996) for Japanese tree species; Cornelissen (1999) for 58 semi-woody British species). Within particular establishment sites, larger seeds have better seedling survival, again both within species (Stanton, 1984; Morse and Schmitt, 1985; Winn, 1988; Tripathi and Khan, 1990; Wood and Morris, 1990) and among species (Marshall, 1986; Chambers, 1995; Greene and Johnson, 1998).

For natural selection to favour larger seeds under particular hazards, it is not sufficient that larger-seeded species have better seedling survival. The relative advantage of larger-seeded species has to be greater under the hazard than in its absence. In this section, we review evidence from manipulative experiments that the advantage of larger-seeded over smaller-seeded species is indeed greater in the presence than in the absence of particular hazards.

Competition

In most manipulative experiments on the role of seed size in competitive environments, adult plant cover is removed to reduce competition. These experiments have shown that small-seeded species are less successful below closed canopies than large-seeded species (Gross and Werner, 1982; Gross, 1984; McConnaughay and Bazzaz, 1987; Reader, 1993; Ryser, 1993) in a variety of (mostly herbaceous) environments. Similarly, Burke and Grime (1996) and Eriksson and Eriksson (1997) have shown that small-seeded species are more dependent on disturbance (and hence reduced competition) than large-seeded species. There are some exceptions: both

Fenner (1978) and Reader (1991) have reported no correlation between seed size and competitive ability among a range of species.

Only two experiments have been reported where seedlings from different seed sizes competed soon after germination and survivorship was traced. Black (1958) grew seedlings of *Trifolium subterraneum* with different initial seed sizes in swards and showed that large seeds were more successful. Leishman (2001) grew multi-species mixtures of three seed size classes and showed that there is a competitive hierarchy among seedlings based on seed size, such that large seeds consistently win over smaller seeds.

Shade

Early work by Grime and Jeffrey (1965) and Hutchinson (1967) showed that small-seeded species suffer higher seedling mortality in shaded conditions. Grime and Jeffrey (1965) grew seedlings in vertical tubes with varying light gradients and found that, among nine tree species, longevity in deep shade was greatest for large-seeded species. Hutchinson (1967) grew seedlings in the dark and also found a correlation between seed size and longevity. More recent experiments that have examined mortality of seedlings during early life and in dense shade have also found that seed size is positively related to longevity (e.g. Leishman and Westoby (1994b) for 23 Australian species grown in the glasshouse for 6 weeks under 1% photosynthetically active radiation (PAR); Saverimuttu and Westoby (1996) for 11 pairs of Australian species grown in the glasshouse under < 1% PAR; Walters and Reich (2000) for ten North American species grown in the glasshouse under 2% PAR). Seiwa and Kikuzawa (1996) grew seedlings in large gaps, in small gaps and in the forest understorey and found higher mortality of small-seeded species in the forest understorey after canopy closure. Many other experiments have measured growth of seedlings in non-lethal shade

and have shown consistently that growth of smaller-seeded species is relatively more depressed than that of larger-seeded species (e.g. Piper, 1986; Seiwa and Kikuzawa, 1991; Osunkoya *et al.*, 1993, 1994; Leishman and Westoby, 1994b).

Other experiments where longevity in shade has not been correlated with seed mass have extended over longer periods, and have applied shading levels permitting at least some photosynthesis. For example, Augspurger (1984) found for 18 neotropical tree species that survival measured over 1 year was not correlated with seed mass, but rather with seedling characteristics, such as density of wood and leaf tissue. Experiments by Saverimuttu and Westoby (1996) and Walters and Reich (2000) deliberately compared outcomes during the cotyledon stage with outcomes during the later stages of seedling growth, and showed that seed mass was influential during early but not during later stages. This makes sense in terms of mechanism (discussed below), and seems capable of accounting for the discrepancy between the Augspurger study and the others cited.

Low soil moisture

There is limited and equivocal experimental evidence about the advantage of large seeds for establishment under low soil moisture conditions. Within-species studies have shown that larger seeds had better (Wulff, 1986) or worse (Hendrix *et al.*, 1991) survival in drier conditions. Buckley (1982) studied four arid dune-crest species and showed that larger seeds resulted in lower post-emergence mortality in the field. Leishman and Westoby (1994c) found, in a field experiment using 18 species from semi-arid Australia, that seedlings from large seeds had higher percentage emergence and survival than small-seeded species, but there was no evidence of a relatively greater advantage of large seeds in less-watered treatments. However, the climatic conditions were particularly harsh during the field experiment, so that survival was low even in watered

treatments. In a repeat experiment in the glasshouse, using 23 species, larger seeds did confer a relatively greater advantage under increasingly dry soil conditions, and longevity was positively related to seed size.

Nutrient deprivation

Within-species (Krannitz *et al.*, 1991) and between-species studies (Jurado and Westoby, 1992) have shown that seedlings from large seeds survive longer in conditions of nutrient deprivation. Stock *et al.* (1990) found among five *Proteaceae* species that seedling survival in nutrient-deficient soils was not associated with seed size. However, the small range of seed sizes among these five species (10–30 mg) may have made a significant effect less likely.

Burial

Given that large seeds produce large seedlings, it is not surprising that seedlings from large seeds are able to emerge from greater soil depths. This has been shown experimentally in several studies (Maun and Lapierre, 1986; Gulmon, 1992; Jurado and Westoby, 1992; Jurik *et al.*, 1994) for a variety of species and habitats. The relative ability of seedlings to emerge through leaf litter may also be an important determinant of species composition in some habitats (Sydes and Grime, 1981; Bergelson, 1991; Facelli and Pickett, 1991; Facelli and Facelli, 1993; Facelli, 1994). As for depth of burial, large robust seedlings would be expected to emerge more successfully through litter. Experiments by Gulmon (1992), Vazquez-Yanes and Orozco-Segovia (1992) and Seiwa and Kikuzawa (1996) have shown that seedling emergence through litter is also positively associated with seed size. Buckley (1982) argued that for desert sand-dunes, larger seeds permitted germination from deeper in the soil, where moisture conditions are more favourable.

Herbivory

A few experiments have suggested that seedlings from large seeds tolerate defoliation (simulating herbivory) better than small-seeded seedlings. Armstrong and Westoby (1993) showed that capacity to survive removal of 95% of cotyledons was positively associated with seed size within genera and families, but not across all species, for 40 Australian species. Bonfil (1998) removed the entire cotyledons from two species of *Quercus* and found that seed mass was positively correlated with survival and growth for both species. In a slightly different approach, Harms and Dalling (1997) removed the entire shoot at 1 cm above the soil surface, at first-leaf stage, for 13 neotropical woody species. They found that only the largest-seeded species (at least 5 g) were capable of resprouting, while smaller-seeded species, which failed to resprout, died after clipping.

Mechanisms for tolerating establishment hazards

Thus, in experiments, larger-seeded species perform better under a diversity of adverse establishment conditions, including competition, shade, low soil moisture and nutrients, burial and herbivory. Might a common mechanism underlie these results, or are different effects or correlates of large-seededness responsible under different conditions or at different developmental stages? Under shading, at least, the advantage of larger seeds is confined to cotyledon-stage seedlings and does not persist into later seedling life, so any common mechanism would need to account for that. Westoby *et al.* (1996) distinguished three mechanisms by which larger seed mass might translate into greater success in the face of various hazards:

1. Seedling size effect: larger seeds result in larger seedlings, enabling better access to light (through penetration of soil or litter layer or relative to competing vegetation) and/or a reliable water-supply (via a longer radicle).

2. Reserve effect (Westoby et al., 1996), also called cotyledon functional morphology hypothesis (Hladik and Miquel, 1990; Garwood, 1995; Kitajima, 1996a, b) or larger-seed–slower-deployment hypothesis (Kidson and Westoby, 2000): obviously larger-seeded species will have larger total resources in their seeds. But this will not sustain their seedlings longer under a carbon deficit unless more resources remain uncommitted at a given time after germination, not just absolutely, but relative to the functional size of the seedling.

3. Metabolic effect: lower relative growth rate (RGR) and perhaps lower respiration rate in larger-seeded species enables longer survival under adverse conditions.

Seedling size effects

Seedlings need to reach light, whether by penetrating the soil or a litter layer or by overtopping competing vegetation. At shading below the compensation point, any seedling, whether large- or small-seeded, will eventually die. In the field, there may be steep gradients of light and soil water within a few centimetres of the soil surface, and under these circumstances centimetres or even millimetres of extra shoot or root length could be important. Light gradients near the ground would be steepest in closed herbaceous vegetation. Larger seedlings with larger root systems (e.g. Evans and Etherington, 1991; Jurado and Westoby, 1992) may gain access to soil moisture at deeper levels.

Seed mass is the largest influence on a seedling's initial reach above and below the ground, but etiolation should also be considered. The ability to etiolate under low light (by increased extension of the hypocotyl relative to that occurring under high light) is roughly similar in both small- and large-seeded species. However, the apparent cost is greater in smaller-seeded species, as etiolation is achieved via a greater drop in hypocotyl tissue density and a proportionally greater decrease in root mass and length (Ganade and Westoby, 1999). Analogous to the etiolation response

in shoots, several studies have shown that some species have a root elongation response in low soil moisture conditions (Osonubi and Davies, 1981; Molyneux and Davies, 1983; Sydes and Grime, 1984; Evans and Etherington, 1991).

The seedling size effect cannot account for increased seedling survivorship under hazards where there is no gradient of resource (e.g. light or soil moisture) away from the soil surface. Although resource gradients may be common in the field, experiments with nutrient deficiency and defoliation have not provided such gradients, nor have most shading experiments, with the exception of those of Grime and Jeffrey (1965). Consequently, seedling size effects cannot provide a universal mechanism accounting for the better survival of seedlings from larger seeds under hazards.

Larger-seed–slower-deployment effect

A spectrum of cotyledon types exists from thin, leaf-like, high-specific leaf area (SLA), primarily photosynthetic cotyledons to thick, low-SLA, non-photosynthetic storage organs (Hladik and Miquel, 1990; Garwood, 1995; Kitajima, 1996a, b; Wright and Westoby, 1999). Thicker cotyledons are generally found in larger seeds. The extreme case of non-photosynthetic cotyledons is cryptocotylar cotyledons, which remain protected within the testa. A strong association has been found between large seed size and cryptocotyly (Ng, 1978; Wright *et al.*, 2000), although small-seeded cryptocotylar species are also known.

Storage tissue is not always in cotyledons. Sometimes it is in the endosperm, and occasionally in the hypocotyl. There are no publications that compare seedling survivorship under hazards specifically across a broad range of endospermic species. Consequently, the following discussion will be couched in terms of cotyledon reserve storage. It seems reasonable that the same mechanisms would apply to storage in other locations, but there is little evidence to discuss on this issue.

The reserve effect requires not only

that the cotyledons have a storage role but that, across species, storage mass increases at a greater rate than seedling mass. Thus, for large-seeded species, greater proportions of the seed reserve remain uncommitted at any given stage during deployment. Consequently, the resources available to support respiration under carbon deficit would tend to be greater, relative to the autotrophic functioning parts of the seedling, in larger seeds. This would remain true up until the stage when all stored resources had been deployed into the functioning structures of the seedling. Recent quantitative surveys confirm that seedlings from larger-seeded species do indeed tend to have greater reserves relative to functioning parts of the seedling (Ganade and Westoby, 1999; Kidson and Westoby, 2000), in both cross-species and evolutionary divergences (phylogenetic analyses).

If species with large stored seed reserves committed all those resources very quickly into leaves, roots or other fixed structures of the seedling, the resources would no longer be available to support the seedling in adversity. The phrase 'larger-seed–slower-deployment' serves as a reminder that it is not sufficient for large-seeded species to have proportionately greater stored reserves: these reserves must also be held back from commitment to fixed structures over a longer period. In large seeds, the period of reserve transfer may be very considerable (e.g. a full year for *Chlorocardium rodiei* (ter Steege *et al.*, 1994)). Transfer may (Kitajima, 1996b) or may not (ter Steege *et al.*, 1994) be accelerated if the seedling is growing in the light, but in either event the slow deployment of reserves represents an opportunity cost if the seedling is not shaded or subjected to some other hazard. That is, if the reserves had been transferred quickly, the initial leaf area and root length of the seedling would have been greater, and it would have had a continuing growth advantage in the light. The same would, of course, have been true if the resources had been built into potentially autotrophic parts of the embryo within the seed, instead of placed in storage tissues.

In dense shade below the compensation point, slow deployment from reserves confers greater longevity in large-seeded species, but the longevity is not indefinite, so how might this translate into improved fitness? Longer survival would increase the chance of a seedling surviving until the formation of a tree-fall gap. However, not all forests have dynamics driven by tree-fall gaps. Also, Thompson (1987) and Seiwa and Kikuzawa (1996) point out that many deciduous forest seedlings germinate in winter or early spring, when the overstorey is leafless.

Further, in experiments where dense shade is applied, a tenfold increase in seed mass confers a gain in longevity that is considerably less than tenfold (e.g. Saverimuttu and Westoby, 1996). In other words, considering the effects of shading alone, the total seedling-days produced in the understorey per gram of seed decreases with seed mass. This should mean that the average number of seedlings still alive when a gap opens above them, per gram of seed produced, should be lower for larger-seeded species. Most probably, shading experiments in shade houses or growth chambers overestimate the likely longevity of small-seeded species. In the field, seedlings 'waiting' in shaded understorey will also be exposed to herbivores, pathogens and physical damage, and the slowly deployed reserves in large seeds will be beneficial in surviving these hazards, as well as in supporting respiration below the compensation point (Metcalfe and Grubb, 1995, 1997; Grubb and Metcalfe, 1996).

Metabolic effect and correlates of slow metabolism

Across species, a negative correlation has commonly been found between the seed mass and the potential relative growth rate (RGR) of seedlings grown under favourable conditions (e.g. Grime and Hunt, 1975; Shipley and Peters, 1990; Jurado and Westoby, 1992; Marañón and Grubb, 1993; Rincón and Huante, 1993; Osunkoya *et al.*,

1994). However, there is no known mechanism through which larger seed mass might directly cause lower potential RGR. Rather, low potential RGR and large seed mass appear to be part of a trait syndrome also involving sturdy tissue construction (low-SLA and specific root length) (Reich *et al.,* 1998; Wright and Westoby, 1999; Fig. 2.4) and low rates of tissue turnover (Bongers and Popma, 1990; Seiwa and Kikuzawa, 1991). Conversely, smaller-seeded species generally have higher potential RGR under near-optimal conditions, which is due in part to the seedlings being constructed of thinner or lower-density tissue with high turnover rates. Under unfavourable growth conditions (e.g. under low light or nutrients), the realized RGR of large- and small-seeded species may be similar, and (larger-seeded) species with more robust leaf and root tissue may survive longer than smaller-seeded species (e.g. Gross, 1984; Seiwa and Kikuzawa, 1991; Leishman and Westoby, 1994b; Walters and Reich, 2000).

Summary about mechanisms

In experiments that expose seedlings to hazards, a striking feature is the variety of different hazards under which larger seed mass confers improved survival. To the extent that this is underpinned by a common mechanism, this must be the larger-seed–slower-deployment effect. At the same time, effects of initial seedling size are clearly important in certain situations.

It has become clear that there are two sets of mechanisms in the determination of seedling survival under adverse conditions. The two sets operate at different stages. Early after germination, for cotyledon-stage seedlings, survival is influenced mostly by stored reserves and by initial seedling size. The experiments of Grime and Jeffrey (1965), Hutchinson (1967), Leishman and Westoby (1994b) and Saverimuttu and Westoby (1996) for cotyledon-stage seedlings provide good examples of cases in which these mechanisms are likely to be operating under shaded conditions. Later on, growth and survival are largely determined by seedling morphology and physiology (e.g. interactions of light and nutrient availability with leaf-area ratio, net assimilation rate, RGR, etc.), and seed size is no longer directly relevant. The studies by Augspurger (1984), Kitajima (1984) and Saverimuttu and Westoby (1996) for leaf-stage seedlings and by Grubb and Metcalfe (Metcalfe and Grubb, 1995, 1997; Grubb and Metcalfe, 1996) provide good evidence of the operation of this second stage in determining seedling survival. By recognizing the two sets of mechanisms and the two phases of seedling life, some apparent inconsistencies in experimental results are resolved.

Associations between seed size and other plant attributes

Dispersal mode

It has long been recognized that the dispersal mode employed by seeds is associated with seed size (Harper *et al.*, 1970; Primack, 1987). Early work by Foster and Janson (1985) showed that, among 203 tropical woody plants of Peruvian forest, species with mammal-dispersal syndrome had significantly larger seeds than species with bird-dispersal syndrome. These results have been confirmed in other tropical forest woody species by Hammond and Brown (1995). In arid and semi-arid habitats of Australia, Jurado *et al.* (1991) and Leishman and Westoby (1994a) found that animal-syndrome (including both ant- and vertebrate-syndrome) seeds were, on average, significantly larger than unassisted, wind- or adhesion-syndrome seeds. Leishman *et al.* (1995) found that the relationship between seed mass and dispersal mode was broadly similar in five very different temperate habitats (central Australia, western New South Wales and Sydney in Australia, Indiana dunes in the USA and Sheffield, UK). Dispersal mode was associated with 29% of variation in seed mass between species. While the pattern of association of seed size with
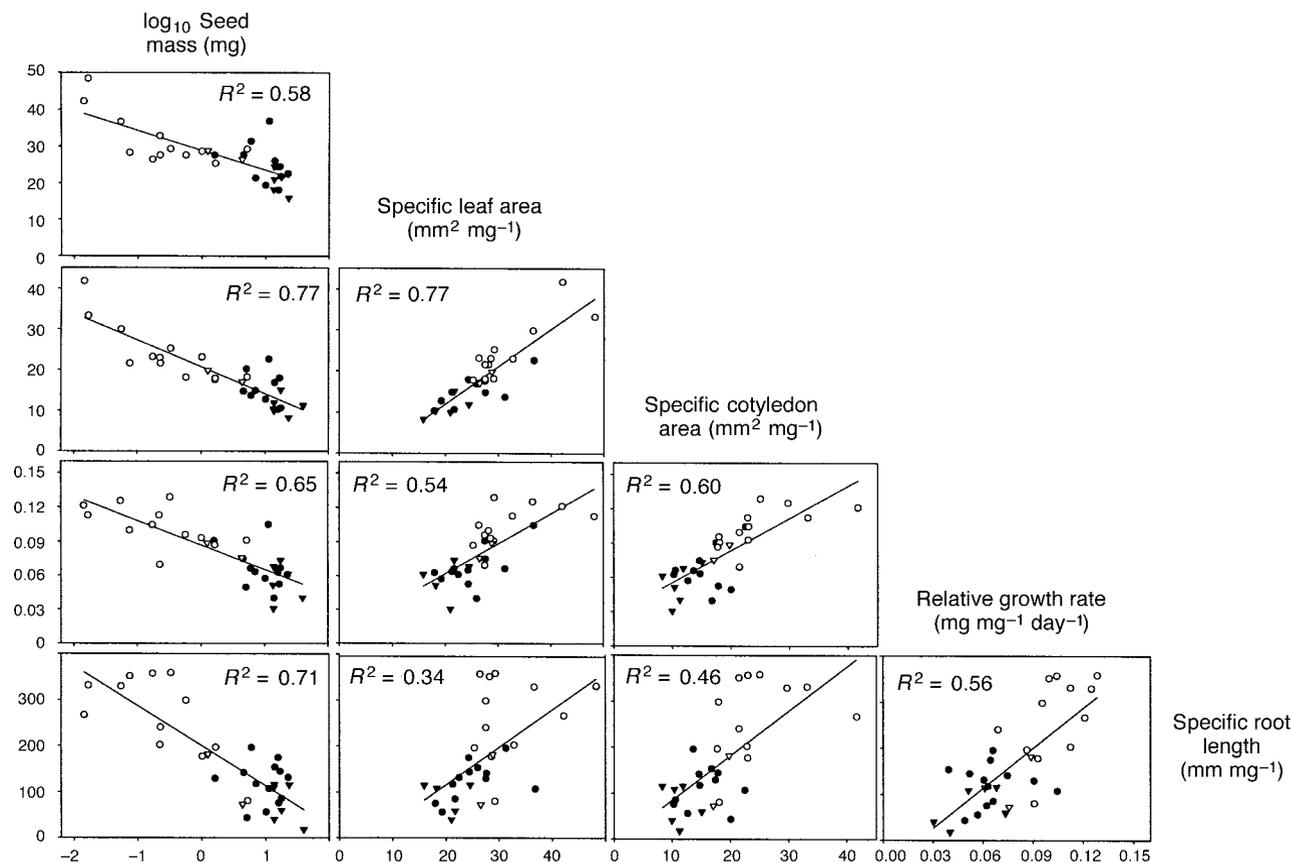
Fig. 2.4. Relationships between five seedling attributes for 33 woody species from New South Wales, Australia (data from Wright and Westoby, 1999). Low relative growth rate and large seed mass appear to be part of a trait syndrome also involving sturdy tissue construction (low area per unit dry mass of cotyledons and seedling leaves, and low root length per unit dry mass), although the advantages of such traits may operate at different stages of a seedling's life (see text). ●, *Fabales*; ○, *Myrtaceae*; ▼, *Proteaceae*; ▽, species from other clades. All relationships are significant at $P < 0.01$.

dispersal mode was different among the five floras (dispersal mode × flora interaction, $r^2 = 0.03$), this effect was about ten times smaller than the overall seed size/dispersal mode relationship ($r^2 = 0.29$). Note that the r^2 of 0.29 means that 71% of all seed-mass variation is within rather than between dispersal modes.

Hughes *et al.* (1994) have shown that the nature of this relationship is that seeds larger than about 100 mg tend to be adapted for dispersal by vertebrates, and seeds smaller than 0.1 mg tend to be unassisted, but between 0.1 and 100 mg many dispersal modes are feasible (Fig. 2.5). The fact that seeds < *c.* 0.1 mg tend to be unassisted presumably comes about both because the effectiveness of unassisted dispersal decreases above this size, and also because the relative cost of attaching an
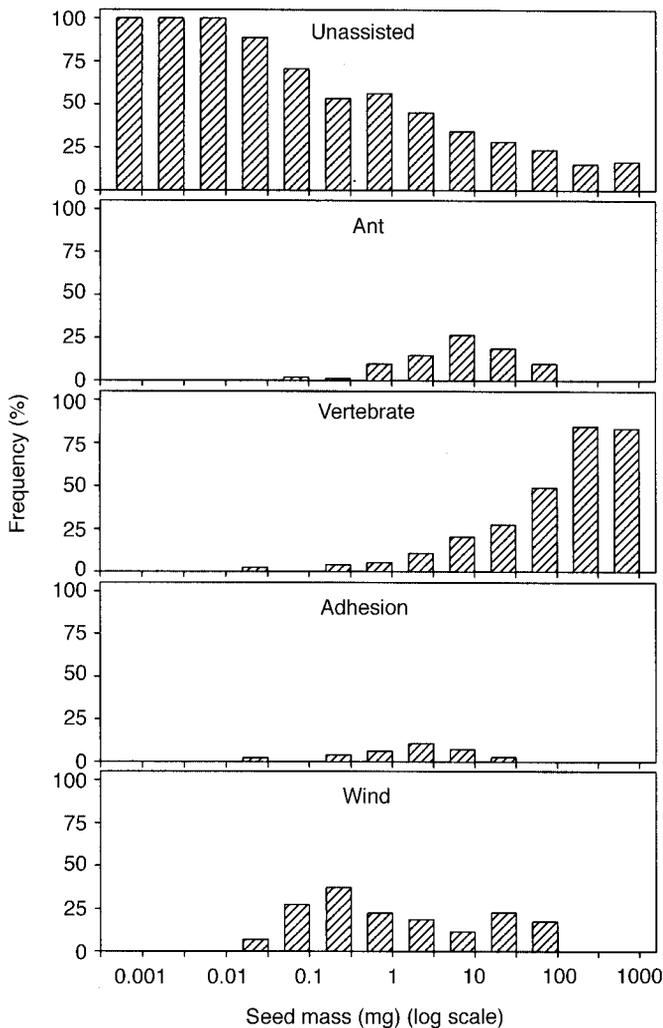
Fig. 2.5. Seed size distributions for unassisted and ant-, vertebrate-, adhesion- and wind-dispersed seeds from five floras: western New South Wales (Australia), central Australia, Sydney (Australia), Indiana dunes (USA) and Sheffield (England). Data compiled by Hughes *et al.* (1994). Note that all dispersal modes occur for seeds between 0.1 and 100 mg, while the smallest seeds tend to be unassisted and the largest seeds unassisted or adapted for dispersal by vertebrates.

effective dispersal structure is high below this size (Leishman and Westoby, 1994a).

Most information about distance travelled by seeds is anecdotal (Hughes *et al.*, 1994); consequently, an r^2 between seed mass and distance travelled cannot be given. It seems to be widely believed that smaller seeds travel further, because seeds falling freely during dispersal have a slower terminal velocity if small and consequently would be expected to travel further in a given wind. However, a number of factors counteract this. Larger-seeded species tend to have wings or hairs that slow the rate of fall if wind-dispersed. Among species with wings or hairs, typically the wing area increases with seed mass. Other larger-seeded species use animals or ballistic mechanisms for dispersal (Fig. 2.5). Even among unassisted species, those with larger seeds tend to be taller. That is, the height from which seeds are released tends to be greater, as does the time to reach the ground and the lateral distance travelled at a given wind speed. Taking these factors together, there is little evidence for any coherent relationship between seed mass and distance travelled across the full range of species and dispersal modes (Hughes *et al.*, 1994).

Growth form and plant height

A relationship between seed size and growth form has been well documented for a variety of floras from a range of habitats. Seed size generally increases from forbs and grasses through shrubs to trees and vines (Salisbury, 1942; Baker, 1972; Foster and Janson, 1985; Mazer, 1989; Jurado *et al.*, 1991; Leishman and Westoby, 1994a; Hammond and Brown, 1995; Leishman *et al.*, 1995; Metcalfe and Grubb, 1995; Fig. 2.6). Leishman *et al.* (1995) showed that this association between growth form and seed size was reasonably consistent across five temperate floras. The average relationship between seed size and growth form accounted for 20% of seed-size variation, while differences between floras (the growth form × flora interaction) accounted for only 2%.

Given that there is a correlation between growth form and plant height, it is not surprising that a positive correlation between seed size and plant height has also been reported consistently for different floras (Foster and Janson, 1985; Thompson and Rabinowitz, 1989; Leishman and Westoby, 1994a; Peat and Fitter, 1994; Leishman *et al.*, 1995; Rees, 1996). Interestingly, work by Leishman *et al.* (1995) on five quite different temperate floras showed that, although there is a large overlap in the amount of seed-size variation accounted for by plant height and growth form, both variables are able to account for a small but significant amount of variation after each other, in each of the floras.

What prospective explanations might there be for a relationship between seed size and growth form or plant height? Thompson and Rabinowitz (1989) invoked allometry, but, in the absence of a plausible mechanism, whether developmental or evolutionary, this merely restates the correlation. One plausible mechanism of natural selection might be that a greater height of release can compensate for a larger seed size in achieving a given dispersal distance. Under this argument, we would expect the plant height–seed size relationship to hold for species dispersed by wind or gravity, but not for animal-dispersed species. In fact, Leishman *et al.* (1995) found that the relationship between seed size and growth form/plant height was just as strong for animal-dispersed species as for wind-assisted and unassisted species. Similar results have also been found by Thompson and Rabinowitz (1989) for herbaceous species of *Asteraceae* and *Fabaceae*. In summary, the present situation is that no plausible mechanism is known that might account for the strong association between seed size and plant height or growth form.

Longevity of parent plant

In some studies, longer-lived plants tend to have larger seeds (Baker, 1972; Silvertown, 1981; Telenius and Torstensson, 1991).
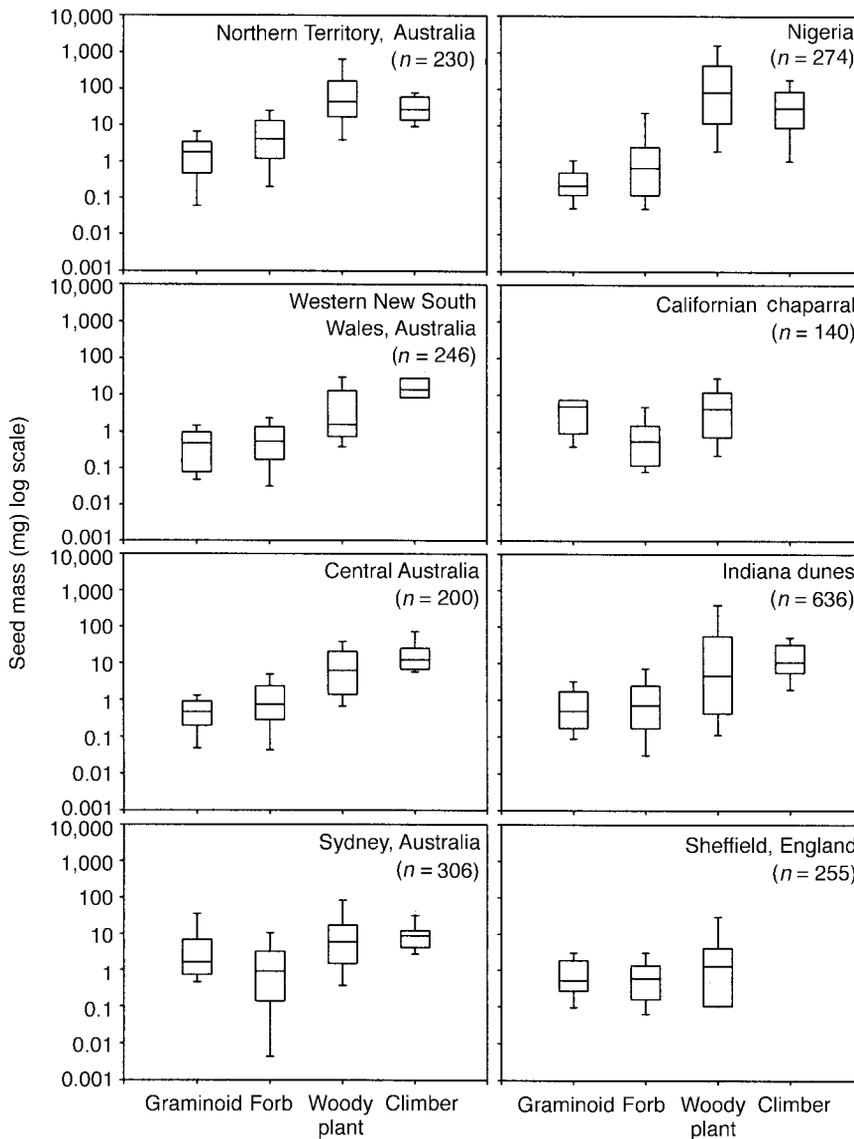
Fig. 2.6. Seed dry masses in four growth forms in eight floras: western New South Wales, central Australia, Sydney (Leishman *et al.*, 1995); Northern Territory, Nigeria (Lord *et al.*, 1997); Californian chaparral (Keeley, 1991); Indiana dunes (Mazer, 1989); and Sheffield (Grime *et al.*, 1988). The boxes span from the 25th percentile to the 75th percentile, with the line inside the box representing the sample median. Whiskers indicate the 10th and 90th percentiles. Outliers have not been shown.

Other studies have found no such relationship (Thompson, 1984; Mazer, 1989; Rydin and Borgegard, 1991). In studies where a number of plant attributes have been considered simultaneously, it has been shown that any relationship between seed size and plant longevity can be explained via secondary correlations of both seed size and plant longevity with plant height/growth form (Jurado *et al.*, 1991; Leishman and Westoby, 1994a; Leishman *et al.*, 1995).

Genome size

Larger-seeded species have been found to have a larger 2C DNA content, among mainly herbaceous and north-temperate species. Thompson (1990) found a positive association between seed size and 2C DNA values for 131 herbaceous species. Within-genus studies have also found consistent positive associations between seed size and 2C DNA content (e.g. Davies (1977) for 12 species of *Vicia*; Bennet (1987) and Peat and Fitter (1994) for a range of genera; Marañón and Grubb (1993) within 12 *Poaceae* but not within seven *Asteraceae*). In contrast, Lawrence (1985) found no such relationship within *Senecio*. Grassland species of the Sheffield flora that have large seeds and large nuclear DNA contents have longer cell cycles and tend to be more frost-resistant than seeds with smaller genomes, as cell division is less constrained by low temperatures (Thompson, 1990; Macgillivray and Grime, 1995).

Other miscellaneous seed-size associations

Several macroscale patterns of seed-size associations are of interest. Lord *et al.* (1997) compared data from five floras (two Australian temperate, one Australian tropical, two tropical from other continents). Seed size of tropical species was consistently larger than that of temperate species, independent of growth form and dispersal-mode differences between the floras. They suggested that the higher temperatures of tropical systems might result in higher metabolic costs of seedling growth and hence select for larger seed size.

Two large cross-species studies have found positive correlations between geographical range size and seed number (Peat and Fitter, 1994; Eriksson and Jakobsson, 1998); hence, given the seed size/number trade-off, larger-seeded species have smaller range sizes. However, both Oakwood *et al.* (1993) and Edwards and Westoby (1996) showed that, although larger seed size was associated with smaller range size, this correlation could be understood as arising from secondary correlations via growth form and dispersal mode.

There is conflicting evidence on the association between seed size and mycorrhizal infection. Janos (1980) found that late successional species of tropical forests (which tend to have large seeds) were more likely to have mycorrhizas. Peat and Fitter (1994) found similar results for the British flora analysed at the family level. Westoby *et al.* (1992) found no evidence at species level for a correlation between seed size and mycorrhizal infection among the British grassland species of Grime *et al.* (1988). Allsopp and Stock (1992, 1995) found that, among South African species, mycorrhizal dependency increases with smaller seed size. Thus, the evidence for any association between seed size and tendency to mycorrhizal infection remains equivocal.

Summary about correlations with other plant attributes

Growth form, plant height and dispersal mode are the only attributes known to be correlated with substantial variation in seed size, independently of other attributes. There appears to be a positive correlation between seed size and genome size, but the potential for this to be understood as a secondary correlation via some third attribute has not yet been investigated, and the pattern itself has yet to be generalized across habitats other than cool-temperate grasslands. There is also an intriguing pattern of larger seeds in tropical floras, independent of growth form, height and dispersal mode, but as yet we have no understanding of the selection processes resulting in this pattern.

The broad spread of seed size among coexisting species

A striking and consistent pattern is the broad span of seed sizes within assemblages (typically five to six orders of magni-

tude), together with a strong overlap in seed sizes among assemblages (Fig. 2.1). Among five very different temperate communities from three continents, ranging from arid woodlands through coastal rainforest and sclerophyll woodlands to closed herbaceous communities, Leishman *et al.* (1995) showed that differences between the floras accounted for only 4% of seed-size variation. Much of the research literature on seed size has been directed towards understanding the hazards that seedlings face during establishment. However, the observation that such different habitats have very similar seed-size distributions points to the possibility that the prevalence of different physical conditions for establishment is not the main influence on seed size.

Grime *et al.* (1997) have shown for 43 British species that most of the trait variation for the regenerative stage is accounted for by the trade-off between seed size and number. Coexisting plant species are spread along a spectrum of different solutions, or strategies, along the seed size–number trade-off. The question is, are they spread along this spectrum simply because different solutions are equally competent and there is nothing to prevent them spreading? Or are there frequency-dependent processes that spread coexisting species out along the spectrum, with a high abundance of small-seeded species favouring an increase of larger-seeded species, and vice versa?

Frequency-dependent or game-theoretical models are indeed capable of predicting an evolutionarily stable strategy (ESS) consisting of a broad mix of seed-size strategies (Geritz, 1995; Rees and Westoby, 1997). In this, they contrast with the prediction of a single optimal seed-size strategy, in a given establishment environment, from the Smith–Fretwell model (Smith and Fretwell, 1974). The difference arises because the game-theoretical models express the idea that a seed's chance of producing an adult depends on what other seeds, of what sizes, are present in the competing mixture. Specifically, the models are driven by competition between

seedlings and by a colonization–competition trade-off. The adult that establishes at each patch or living site is assumed to come from the largest seed reaching the patch. Hence, a strategy mixture can be invaded by larger seeds because they will win in competition with small seeds. On the other hand, since smaller seeds are produced in larger numbers, they will reach some patches that are not reached by any larger seeds, and thus can persist in the mixture.

These game-theoretical models predict the broad spread of seed size that is actually observed among coexisting species, but how likely is it that they are a true description of the processes involved? One key mechanism, that large seeds win in competition with small seeds, appears generally true during early seedling competition (reviewed above). There is also consistent evidence that larger-seeded species produce fewer seeds per unit biomass than smaller-seeded species (Shipley and Dion, 1992; Greene and Johnson, 1994; Eriksson and Jakobsson, 1998; Leishman, 2001; M.L. Henery and M. Westoby, unpublished data). How widely might it be true that the species mixture (and hence the seed-size mixture) is decided mainly by competition between seedlings? This seems plausible in assemblages of annuals, in fire-prone and arid assemblages and in vegetation with gap dynamics. In these assemblages, most seedling establishment occurs at a common time (after fire, rain or gap creation), and growth to adulthood is arguably decided by competition among seedlings rather than with adults. But this list does not cover all possible vegetation types.

At ESS in the game-theoretical-strategy-mixture models, more establishment opportunities (vacant patches) must be reached by small-seeded species than by large-seeded species. There is little quantitative evidence available that small seeds dominate the seed rain. Spence (1990) found that small seeds dominated the seed rain of four New Zealand alpine communities, but Leishman (2001) found the opposite for a calcareous grassland community

in the UK. Several studies have shown that small seeds dominate the seed bank (e.g. Leck, 1989; Eriksson and Eriksson, 1997; Price and Joyner 1997), which may also contribute to colonization opportunities. Clearly, this is an area where additional data are needed.

Also at ESS in the game-theoretical-strategy-mixture models, a negative correlation is expected between seed size and species abundance, measured as biomass or cover (M.R. Leishman and B.R. Murray, unpublished data). This is because the smaller-seeded species have to produce enough seeds to disperse successfully not just to patches not reached by one of their larger-seeded competitors, but to patches not reached by any of their larger-seeded competitors. This requires high abundance, as well as large numbers of seed produced from each unit of biomass or cover. The evidence is against this prediction, on the whole. Rabinowitz (1978) and Mitchley and Grubb (1986) found positive correlations between seed size and abundance for limited subsets of species within US tallgrass prairie and UK chalk grassland communities, respectively. However, other studies have found a negative correlation (Rees, 1995) or none (Eriksson and Jakobsson, 1998). M.R. Leishman and B.R. Murray (unpublished data) examined 12 different communities from four geographical regions, including both tropical and temperate, and found no evidence for consistent seed size/abundance patterns. In the four communities where significant seed size/abundance correlations were found, the relationships were positive.

In summary, we do not yet have a satisfactory biological interpretation for the consistently broad spread of seed mass within vegetation types. Existing game-theoretical models are driven by competition among seedlings (which in reality is unlikely to decide the species mixture in all vegetation types) and make some predictions that do not seem to be satisfied with any consistency. The logically possible alternatives are: (i) that, within each assemblage, there is a broad variety of establishment conditions (i.e. a variety of Smith–Fretwell functions), and each seed size does best in its own specific situation; (ii) that, within assemblages, many species occur as sink populations, supported by dispersal from source populations in other habitats; and (iii) that game-theoretical or frequency-dependent processes spread out the ESS mixture of some other species attribute, which in turn is correlated with seed size.

Conclusion

The last 10 years have seen considerable progress in understanding the evolutionary ecology of seed size. Substantial numbers of experiments have accumulated comparing ten to 50 species at a time. Correlative information across hundreds of species on several continents serves to place the experiments in context and to characterize the field distribution of seed mass and its relationships to other traits.

Larger seeds tend to produce seedlings with a greater proportion of their mass as stored reserve relative to autotrophically functioning structure of the seedling. These larger reserves are deployed progressively rather than immediately into structures. The consequence must be that, at any given stage during deployment, seedlings of larger-seeded species tend to have more reserves uncommitted and available to compensate for various hazards. Experiments have compared species across a range of seed sizes, both across species and as phylogenetically independent contrasts, and have applied competing vegetation, dense shade, drought, mineral nutrient deficiency, clipping and burial under litter and soil. Larger-seeded species have been advantaged under all these hazards. The larger initial seedling size is important in some situations, as well as the holding of uncommitted reserves. Later in seedling life, after reserves have been fully deployed into seedling structures, larger seed size no longer confers any direct advantage. Rather, shade tolerance is conferred by slow turnover of well-defended tissues, which may be loosely correlated with larger seed mass.

Seed mass is correlated with height, growth form and dispersal mode. These relationships have similar form in different temperate vegetation types from different continents. Although larger seed mass has been shown experimentally to confer improved tolerance against a wide variety of hazards, the only clear habitat pattern in the field is that species establishing under shade tend to have larger seeds. Seeds tend to be larger in the tropics, independent of growth form and dispersal mode. The reason for this remains unclear.

There is a markedly wide spread of seed mass among species within vegetation types. Recent game-theoretical models predict this, but the limited empirical evidence suggests that some key mechanisms in the models are not realistic in the field. In other words, the models make the right predictions for the wrong reasons. Understanding the broad spread of coexisting seed-mass strategies remains an outstanding challenge.

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