
Chapter 10

The seedling as part of a plant's life history strategy

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10.1 Introduction

In this chapter, we will describe the intricate links between seedling ecology and life history traits such as seed mass, time to maturity, adult size, and reproductive life span. We will pay particular attention to seed mass, as this is the trait most closely linked to seedling ecology. Seed mass affects the initial size of the seedlings, the amount of reserves seedlings have for establishment, the sites to which seeds are dispersed, and the time seeds spend in the soil before germinating.

Much of our understanding of seed and seedling ecology has been based on the idea that plants face a trade-off between producing a few large seeds, each with high rates of survival as seedlings, versus producing many small seeds, each with lower rates of survival as seedlings. We, therefore, begin by reviewing the evidence for this trade-off. Our review shows that a full understanding of seed and seedling ecology requires consideration of life history variables such as plant height, reproductive life span, and the length of the juvenile period. Then we present a new framework for understanding seed and seedling traits as part of an overall life history strategy. Next we outline relationships between seed and seedling traits and other aspects of plant ecological strategy, such as seed dispersal syndrome, the capability to form soil seed banks, tissue density, and adult plant traits. These data complement previous results, and tend to support the idea that seed and seedling traits can be usefully understood as part of a larger spectrum of life history traits ranging from small, short-lived plants with small seeds, fast growth, low tissue density, and low rates of seedling survival to large, long-lived plants with large seeds, slower growth, denser tissues, and higher rates of survival.

Our focus in this chapter is mostly on between-species variation in seed and seedling strategies. This is because the vast majority of the variation in these traits lies at the between-species level. Across all of the species on earth, seed mass ranges over 11.5 orders of magnitude

(Moles *et al.*, 2005b), while within-species variation in seed mass is typically in the range of two- to fourfold (Leishman *et al.*, 2000). However, variation in seed and seedling traits at the within-species level can have important ecological consequences (Pizo *et al.*, 2006). Thus, we explore variation in seed and seedling traits at the within-species level. We conclude with a discussion of the implications of these data for our understanding of plant regeneration; outlining some areas that we think are ripe for future development. We think that placing seedling ecology in a broader life history context will lead us to new ways of understanding the ecology of plant regeneration.

Some definitions

Many of the terms used in this chapter can be applied to subtly different units/stages. We, therefore, devote this section to clarifying what we mean by seed mass, seedling, juvenile period, and reproductive life span.

By *seed mass*, we mean the dry mass of the unit comprising the seed coat, embryo, and endosperm. In some situations, such as relationships between seed mass and seedling morphology or survival rate, it would be best to know the seed reserve mass (just the embryo and endosperm). In other situations, such as dispersal and seed production, it would be best to know the mass of the whole seed, or even the whole fruit. Fortunately, the various measures of seed mass are tightly correlated. Relationships among seed reserve mass, seed coat mass, and the mass of external protective and/or dispersal structures are approximately isometric across species (Moles *et al.*, 2003; Martínez *et al.*, 2007).

We use the term *seedling* to refer to plants that have germinated but which are still likely to be at least partially dependent on maternal resources. However, there are practical problems in determining whether a young plant is still a true seedling (Fenner & Kitajima, 2000). We, therefore, use the term *juvenile* wherever there is doubt. This term refers to plants at all stages between germination and the time of first reproduction (encompassing seedlings and saplings). Thus, the *juvenile period* is the time between germination and first reproduction. Finally, the *reproductive life span* of a plant is the mean or maximum time between the onset of reproduction and plant death.

10.2 The tradeoff between offspring production and seedling survival

A model for the optimal balance between the size and number of offspring (Fig. 10.1) has been formulated by Smith and Fretwell (1974). This model begins from two observations. First, an organism with a finite amount of energy available for reproduction can either produce a few large offspring or a large number of small offspring. Second, the more energy the organism allocates to each individual offspring, the

greater their expected fitness becomes. Thus, organisms face a fundamental trade-off between using their available energy to produce a few well-provisioned offspring, each with high expected fitness, versus producing more poorly provisioned offspring, each with lower expected fitness.

Much of our research and theory on seedling ecology and plant reproductive strategies has been based on the idea that plants face a tradeoff between producing either a large number of small seeds, each with low rates of survival as seedlings, or a few large seeds, each with a high chance of survival through seedlinghood. This seed number/seedling survival trade-off idea is clearly derived from the Smith-Fretwell theory. However, the Smith-Fretwell theory and the seed number/seedling survival trade-off idea do differ in an important way: the seed number/seedling survival trade-off idea focuses on survival through seedlinghood, while the Smith-Fretwell theory considers the offspring's lifetime fitness.

The focus on the seedling stage in the plant literature is a reflection of the perceived importance of early mortality in shaping plant population and community ecology (Kitajima & Fenner, 2000). A huge proportion of seedlings die within the first few weeks after germination (De Steven, 1991; Alvarez-Buylla & Martinez-Ramos, 1992; Vander Wall, 1994; Horvitz & Schemske, 1995; Bowers & Pierson, 2001) and thus this life history stage is under strong selection pressure. Further, the advantages of large-seededness seem to be short-lived (Leishman *et al.*, 2000). If individuals of large- and small-seeded species are equally likely to survive from the end of the seedling stage to adulthood, then the Smith-Fretwell theory and the seed number/seedling survival idea will be functionally equivalent.

The seed mass/number trade-off

Several field studies have confirmed that there are strong negative relationships between seed mass and the number of seeds a plant produces per year, and between seed mass and the number of seeds produced per unit canopy per year (ShIPLEY & DION, 1992; GREENE & JOHNSON, 1994; JAKOBSSON & ERIKSSON, 2000; AARSSON & JORDAN, 2001; HENERY & WESTOBY, 2001). The trade-off between the size and number of offspring produced for a given amount of energy gives small-seeded species an initial advantage over large-seeded species. However on average, all adult plants must produce exactly one surviving offspring during their lifetime if the population is to remain stable (neither increasing nor decreasing). Thus, the numerical advantage that small-seeded species gain during seed production must be counterbalanced somewhere else in the life cycle. One of the main advantages of producing large seeds is that they produce larger seedlings with higher rates of survival.

The relationship between seed mass and seedling survival

Seed mass affects seedling survival in many ways. First, seedlings from large seeds tend to be taller and/or heavier than seedlings from

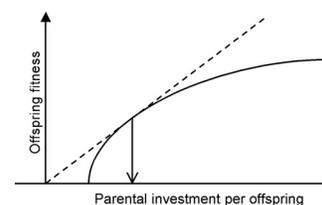


Fig. 10.1 The Smith & Fretwell (1974) model for the optimal size of offspring. This model formalized the idea of a trade-off between producing a few, well provisioned offspring, versus producing many poorly provisioned offspring.

The curved line represents the relationship between the amount of energy invested in each offspring and the lifetime fitness of that offspring. This line will be curved if there is a diminishing return on parental investment, e.g. if a given increase in allocation increases the fitness of small offspring more than it increases the fitness of large offspring.

The optimum allocation strategy for the parent occurs at the point where the steepest possible straight line from the origin just touches the fitness curve (represented by the arrow). Increasing the amount of energy allocated to each offspring from this point would increase each offspring's fitness, but this increase would not be sufficient to balance the reduction in the number of offspring that could be made for a given amount of energy. Decreasing the amount of energy allocated to each offspring from this point would result in decreases in offspring fitness and this decrease in fitness would outweigh the increase in the number of offspring that can be made for a given amount of energy. Reproduced with permission from the University of Chicago Press.

small seeds, both within and across species (Jurado & Westoby, 1992; Cornelissen, 1999; Jakobsson & Eriksson, 2000; Vaughton & Ramsey, 2001; Baraloto *et al.*, 2005a; Zanne *et al.*, 2005). This larger initial size might give seedlings from large seeds better access to water and light, as well as a competitive advantage (Leishman *et al.*, 2000). Second, seedlings from larger seeds tend to have a greater proportion of their reserves uncommitted, and thus available to support the seedling in times of carbon stress (Kitajima, 1996a; Green & Juniper, 2004b; Zanne *et al.*, 2005). Third, the negative relationship between seed mass and the relative growth rate of seedlings (Maranon & Grubb, 1993; Kitajima, 1994; Grubb *et al.*, 1996; Wright & Westoby, 1999; Fenner & Thompson, 2005; Paz *et al.*, 2005; Poorter & Rose, 2005) might reflect a slower metabolic rate in large-seeded species (Green & Juniper, 2004b). This slower metabolic rate would allow seedlings to persist for longer on a given amount of reserves in times of carbon stress. As is often the case, it is likely that all of these mechanisms contribute to the greater survival rates associated with large-seededness.

Numerous studies have demonstrated that seedlings from large seeds are better able to withstand many of the different stresses that seedlings face in natural environments, including competition from established vegetation, competition with other seedlings, prolonged periods in deep shade, defoliation, nutrient shortage, and burial under soil or litter (Westoby *et al.*, 2002). The survival advantage of seedlings from large-seeded species is also seen under natural conditions (Moles & Westoby, 2004a; Baraloto *et al.*, 2005a), where seedlings are exposed to the full suite of natural hazards, and often face multiple hazards simultaneously.

The survival advantage for seedlings from large-seeded species, plus the evidence for a seed mass/number trade-off seem to support the seed number/seedling survival trade-off theory. However, for this theory to work, the survival advantage of large-seeded species would have to counterbalance exactly the seed production advantage of the small-seeded species. For example, if species A produces seeds 10 times as big as species B, then species A will only make $1/10^{\text{th}}$ as many seeds for a given amount of energy. To recoup this disadvantage, species A's seedlings would have to be ten times more likely to survive than the seedlings of species B. Is this the case?

Moles and Westoby (2004a) analyzed the slope of the relationship between seed mass and seedling survival to determine whether the advantage that large-seeded species accrue during seedling establishment is sufficient to counterbalance the negative relationship between seed mass and the number of seeds produced per unit of energy. First, they looked at the slope of the relationship between seed mass and seedling survival through the first week after emergence. The slope of this relationship was nowhere near steep enough to counterbalance the seed production advantage of small-seeded species (Fig. 10.2). However, seedlings typically take much more than a week to establish. If the survival advantage of large-seeded species

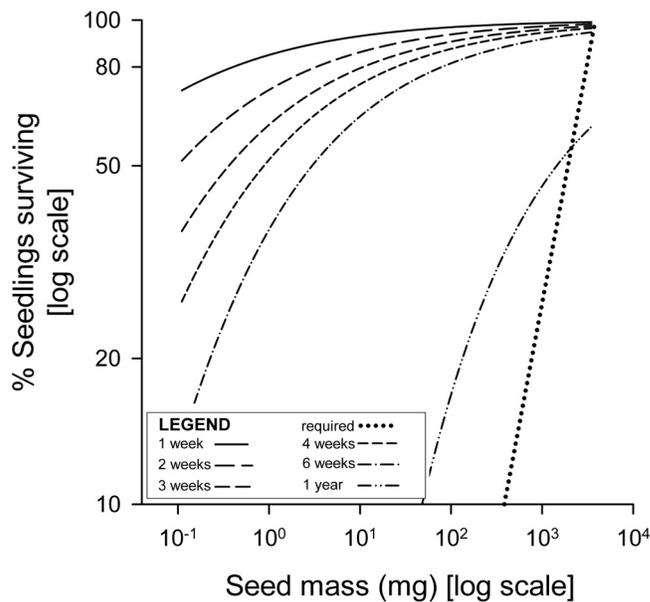


Fig. 10.2 The relationship between seed mass and seedling survival. The solid line represents the relationship between seed mass and seedling survival through one week (data shown in Fig. 10.4a). The other lines show the predicted relationship between seed mass and seedling survival through various amounts of time, assuming that mortality proceeds at the same rate as in the first week (see Moles & Westoby, 2004a). The dotted line represents the slope of the relationship required for the survival advantage of large-seeded species to counterbalance the greater seed production (per unit energy invested) of small-seeded species. When the survival lines reach the same slope as the required line, the small-seeded species and the large-seeded species produce an equal number of surviving offspring. Modified from Moles & Westoby (2004a), published with permission from Blackwell Publishing, Ltd.

accrued for long enough, they would reach the point where they have as many surviving seedlings remaining as do the small-seeded species.

Moles and Westoby (2004a) also calculated how long the survival advantage of seedlings from large-seeded species would have to persist for them to reach the point where they have as many surviving offspring remaining as do small-seeded species (Fig. 10.2). A curve in the relationship between seed mass and seedling survival means that the answer to this question depends on the species' seed mass. At the small-seeded end of the seed mass spectrum, a large-seeded species would break even with a species with 10-fold smaller seeds after 8.8 weeks. This seems quite plausible. Many species take several weeks to establish, and the survival advantage of large-seeded species could easily persist for this long. However, at the larger-seeded end of the seed mass spectrum, the survival advantage of the large-seeded species would have to continue at the same rate as in the first week after emergence for 4.2 years before the large-seeded species had as many surviving offspring as a species with 10-fold smaller

seeds. This is not so plausible because most of the available data show no relationship between seed mass and survival rates of later-stage seedlings or saplings (Saverimuttu & Westoby, 1996a; George & Bazzaz, 1999; Walters & Reich, 2000; Dalling & Hubbell, 2002; Baraloto *et al.*, 2005a); but see Moles & Westoby, 2004a). That is, the advantage of large-seededness is generally temporary, probably expiring when the seed reserves have all been deployed. The time taken for this to happen does vary among species, and there may be correlations between seed mass and aspects of the growth strategy of juvenile and adult plants (Poorter, 2007). However, it seems unlikely that any large-seeded species retains a survival advantage for as long as 4 years. Thus, the available evidence strongly suggests that the survival advantage of large-seeded species is not sufficient to counter the seed production advantage of small-seeded species.

The gains in seedling survival associated with large seededness do not seem to be great enough to counter the decreases in seed production. Thus, the seed number/seedling survival trade-off idea must be missing some important elements. In the following sections, we describe a new understanding of how seed mass and seedling strategy are part of a much larger correlated suite of life history characteristics.

Lifetime seed production

Most cross-species investigations of seed production have focused on annual seed production or on the number of seeds that can be made for a given amount of canopy per year. However, the critical measure of evolutionary success is the total number of surviving offspring produced by an individual throughout its lifetime.

The slope of the relationship between seed mass and the number of seeds that a species can produce per unit canopy area per year is -1 (Henery & Westoby, 2001, Fig. 10.3a). That is, a 10-fold increase in seed mass is associated with a 10-fold decrease in the number of seeds made from a given amount of canopy each year. The difference between this relationship and the relationship between seed mass and lifetime seed production will depend on the relationships between seed mass and canopy area, and between seed mass and plant life span.

Several studies have reported positive correlations between plant size and seed size or seed mass (Levin, 1974; Leishman *et al.*, 1995; Aarssen, 2005; Moles *et al.*, 2005c), and between seed mass and canopy area (Fig. 10.3b). The reason for this correlation between adult size and offspring size has been the subject of much recent debate (Moles *et al.*, 2004; Aarssen, 2005; Grubb *et al.*, 2005; Moles *et al.*, 2005c). Regardless of the mechanism underlying the observed relationship, we would expect that the larger canopies of large-seeded species would mean that they have more photosynthate to allocate to reproduction. Because of this, we would expect the slope of the relationship between seed mass and the number of seeds produced per individual plant per year to be less steep than the 1 slope of the relationship

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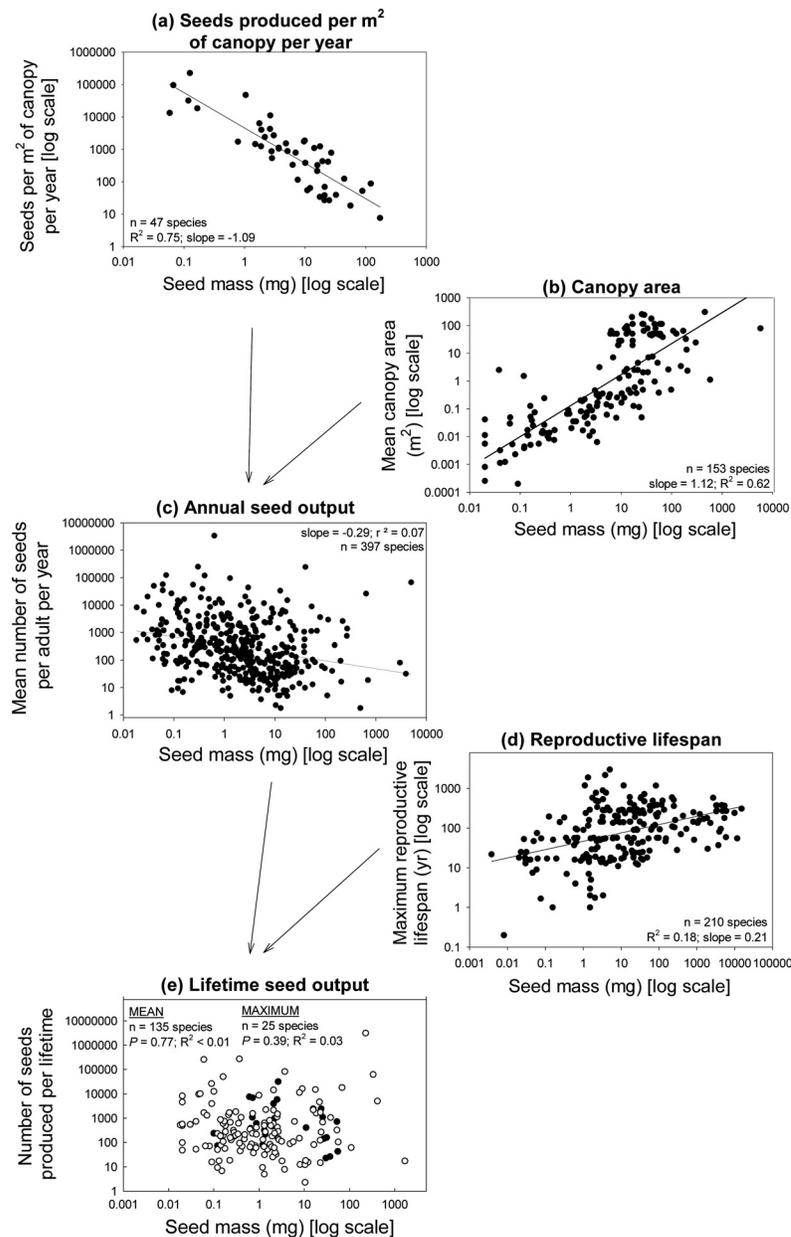


Fig. 10.3 Correlations between seed mass and (a) the number of seeds produced per square meter of canopy per year, (b) canopy area, (c) annual seed production per adult plant, (d) reproductive lifespan, and (e) the total number of seeds produced over a lifetime. Each dot represents the geometric mean value for one species, except in plot e, where open circles represent geometric means and filled circles represent maxima. Lines show the results of model I regressions. Data are from (a) Henny & Westoby (2001), (b–d) from Moles & Westoby (2006), and (e) from Moles *et al.* (2004); published with permission from Blackwell Publishing, Ltd.

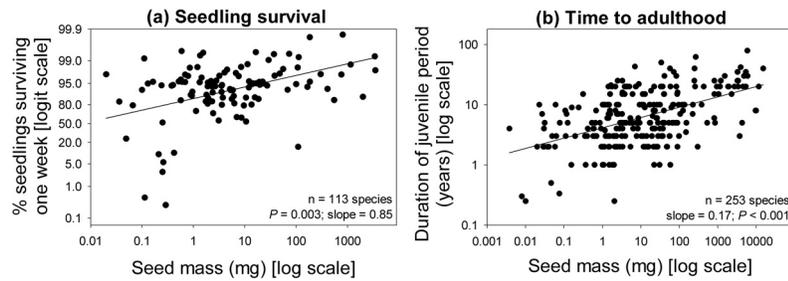


Fig. 10.4 Correlations between seed mass and (a) the percentage of seedlings surviving through their first week after emergence and (b) the time taken for each species to reach reproductive maturity. Each dot represents the geometric mean value for one species. The line in (a) was fit using random effects logistic regression; the line in (b) was fit using model I regression. Data for (a) are from Moles & Westoby (2004a), and (b) from Moles & Westoby (2006); published with permission from Blackwell Publishing, Ltd.

between seed mass and the number of seeds produced per square meter of canopy per year. As predicted, a compilation of data from the literature showed a slope of -0.3 (Fig. 10.3c) (Moles *et al.*, 2004).

Not only do small-seeded species tend to have smaller canopies than do large-seeded species, they also tend to have shorter reproductive life spans (Fig. 10.3e) (Moles *et al.*, 2004; also see Baker, 1972; Silvertown, 1981; Leishman *et al.*, 1995, but note exceptions in Thompson, 1984; Jurado *et al.*, 1991). This further erodes the apparent advantage that small-seeded species have during seed production. In fact, there is no relationship between seed mass and lifetime seed production (Fig. 10.3e) (Moles *et al.*, 2004). Although small-seeded species do make more seeds for a given amount of energy, their smaller canopies and shorter reproductive life spans mean that they do not produce more seeds than large-seeded species over a lifetime.

Seed mass and survival to adulthood

Large-seeded species have a survival advantage over small-seeded species during early establishment (Fig. 10.4a) (Moles & Westoby, 2004a). However, it is not survival through the first week, the first season, or the first year after germination (the time frames most commonly used in studies of juvenile survival in plants) that determines a plant's evolutionary success. Rather, it is the number of offspring that survive to reproductive maturity. Two main factors affect the proportion of a plant's offspring that survive to reproductive maturity, namely the probability of survival through a given amount of time and the amount of time elapsed between emergence and maturity.

A compilation of data from the literature showed that small-seeded species tend to reach reproductive maturity much earlier than do larger-seeded species (Fig. 10.4b) (Moles *et al.*, 2004). This finding is consistent with the relationship between seed mass and plant size (Fig. 10.3b) (Moles *et al.*, 2005c), and the positive relationship between plant height and time to reproductive maturity (Moles *et al.*, 2004).

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That is, small-seeded species tend to have small adult stature and it does not take as long to grow into a small herb as it takes to grow into a large tree.

The longer juvenile period of large-seeded species exposes them to a longer period of juvenile mortality and thus a higher risk of dying before they reach adulthood. This disadvantage counters the higher survival per unit time of seedlings from large-seeded species (full explanation in Box 10.1). Evidence from transition matrix models also supports the idea that later stages of regeneration can be extremely important determinants of population dynamics, especially in long-lived species (Chapter 11). There are not enough data to be certain about the shape of the relationship between seed mass and survival to adulthood. However, the available evidence suggests that there is either no relationship or perhaps a weak negative relationship between seed mass and survival from seedling emergence through to reproductive maturity (Moles & Westoby, 2006a).

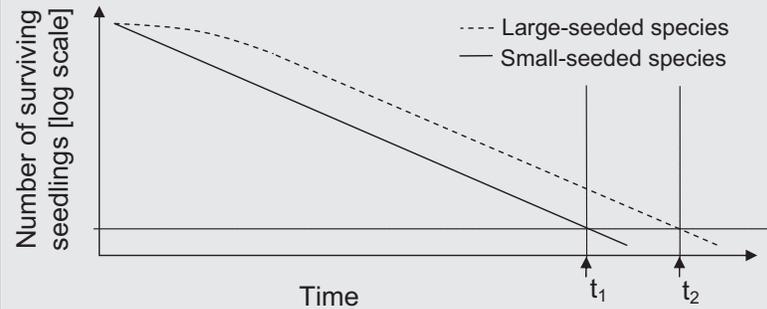
In summary, although small-seeded species produce more seeds per square meter of canopy per year, large-seeded species have larger canopies and longer reproductive life spans. Overall, there is no relationship between seed mass and the total number of offspring produced over a lifetime. Large-seeded species do have higher rates of survival per unit time (at least during the early stages of establishment), but the longer juvenile period of large-seeded species increases the duration of exposure to juvenile mortality. Data are too scarce to make a firm conclusion, however, it is clear that there is not a positive relationship between seed mass and survival from seedling emergence to maturity (the available evidence show that there is no relationship, or perhaps a weak negative relationship between seed mass and survival from seedling emergence to maturity, Moles & Westoby, 2006a).

Our old interpretation of the trade-off between producing a few large seeds, each with high rates of survival as seedlings, versus producing many small seeds, each with low chances of surviving the juvenile period is confounded (at least at the cross-species level) by relationships with other plant life history traits. To understand seed and seedling ecology, we need to consider correlations among seedling survival, seed mass, adult size, time to maturity, and reproductive life span.

10.3 Understanding seed and seedling ecology as parts of a plant's life history strategy

The network of correlations among life history traits can be understood as factors that contribute to one essential variable, the average number of surviving offspring produced during a lifetime. If the population is stable (neither going extinct nor rapidly increasing), then every adult individual will leave, on average, one offspring that survives to reproductive maturity. The number of offspring

Box 10.1 The effects of seed mass, early rates of mortality and time to maturity on seedling survival to adulthood (figure modified from Moles & Westoby, 2006a)



Consider a large-seeded species (dashed line), and a small-seeded species (solid line). The small-seeded species is shown here with exponential rate of mortality, the most common pattern found in empirical studies of seedling mortality (Moles & Westoby, 2004a). Field data suggest that the large-seeded species will have a lower initial rate of mortality than the smaller-seeded species (Moles & Westoby, 2004a). Thus, the number of surviving offspring does not drop as rapidly for the large-seeded species as for the small-seeded species. However, most of the available data suggest that after the seedling from the large-seeded species has deployed all the maternal resources, it will cease to have a survival advantage over the small-seeded species (Westoby *et al.*, 2002). At this point, seedlings from large- and small-seeded species die at approximately the same rate, and the lines on the figure become parallel.

If the large-seeded species and the small-seeded species reached maturity at the same time (say, time t_1) then the lower early mortality of the large-seeded species would translate to a higher number of individuals surviving to adulthood. However, large-seeded species tend to take longer to reach adulthood than do small-seeded species (Moles *et al.*, 2004). Thus, they are exposed to juvenile mortality for longer than are the small-seeded species (say, to t_2). This longer period of mortality decreases the total number of individuals surviving to adulthood. It is possible that this additional time to maturity could completely negate the initial survival advantage of the large-seeded species.

Implications for the relationship between seed mass and plant size

If species with large canopies and long reproductive lifetimes produced very small seeds, they would be able to produce a stupendous number of offspring throughout their lives. However, collation of data for 2589 species from all around the world revealed a positive relationship between seed mass and plant height, and an absence of species with very large adult size that produce very small seeds, despite the inclusion of data for several *Ficus* and *Eucalyptus* species (Moles *et al.*, 2005c). The figure above suggests an explanation for the absence of this *large adult, small seeds*

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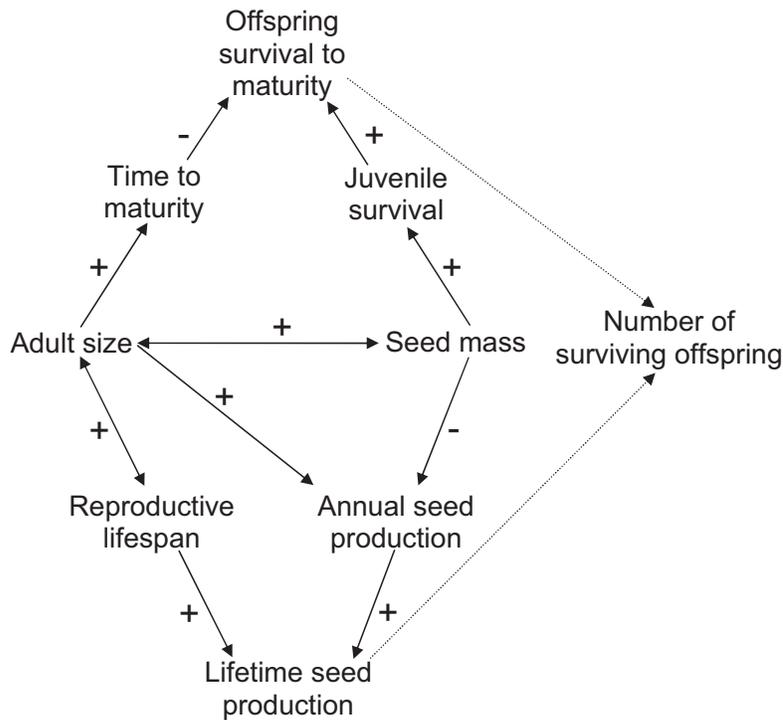


Fig. 10.5 Correlations among the major plant life history traits. Single-headed arrows represent causal relationships, double-headed arrows represent correlations. Plus/minus signs show the direction of correlation.

strategy: A species with large adults will necessarily have a lengthy juvenile period. To have sufficient offspring survive to adulthood, the juveniles of large adults will need to have a relatively low weekly rate of juvenile mortality. This can be achieved by producing large, well-provisioned offspring. A species with large adults and very small seeds would not have enough offspring survive to maturity to replace itself and the strategy would become extinct.

that survive to maturity is a product of lifetime seed production and the proportion of offspring that survive to adulthood (Fig. 10.5). Seed mass, seedling survival, adult plant size, time to maturity, and length of the reproductive period together determine the level of lifetime seed production and offspring survival to maturity. These variables can be usefully organized into two paths, one stemming from correlations with seed mass and the other from correlations with plant size (Fig. 10.5).

The path through seed mass is the original seed number/seedling survival trade-off. Increases in seed mass decrease the number of seeds that a plant can produce in a year, while simultaneously increasing the rate of seedling survival. This increase in juvenile survivorship (per unit time) increases the probability of a given seed surviving to

adulthood. Thus, decreases in annual seed production are balanced by increases in the proportion of seeds surviving to adulthood.

The path through plant height contains variables not usually considered in studies of seedling ecology. However, this path is just as important to the overall life history outcome as the seed mass path. Increasing adult size increases the number of seeds an adult plant can produce because larger plants have larger canopies and, therefore, higher annual photosynthetic incomes, giving the plant more energy to allocate to seed production. However, increases in adult size are associated with increases in time to adulthood and longer juvenile periods carry an increased risk of juvenile mortality. Thus, increases in plant size simultaneously increase seed production and decrease offspring survival to maturity, exactly the opposite effects to increases in seed mass.

10.2 Correlations between seed and seedling strategy and other aspects of plant ecology

In this section, we briefly outline correlations between seed and seedling strategy and other aspects of the species' ecology. The various correlations are presented in the order in which they are encountered during a typical life cycle, beginning with seed dispersal and continuing through seed survival in the soil, germination and seedling emergence, seedling morphology, seedling growth, and ending with the traits of mature plants.

Seed dispersal

As one might expect, there are strong correlations between seed mass and dispersal syndromes (Leishman *et al.*, 1995; Moles *et al.*, 2005a). Species with unassisted dispersal, species that disperse by adhesion to the outside of animals, and species with wind-dispersal tend to have very small seeds, while species that are dispersed by water or via ingestion by animals can be quite large (Moles *et al.*, 2005a). There appears to be a relationship between seed mass and the size of the animals responsible for ingesting/carrying the seeds. Seeds dispersed by mammals tend to be larger than seeds dispersed by birds, which are larger than seeds dispersed by invertebrates.

Differences in dispersal syndrome are likely to affect the shape of the dispersal kernel and the types of environment to which seeds are dispersed (Garcia-Castaño *et al.*, 2006; Russo *et al.*, 2006). These differences in dispersal can affect (1) the relative importance of sibling-sibling competition, intraspecific competition, and interspecific competition among seedlings (Jordano & Godoy, 2002), (2) susceptibility to pathogen attack (Augspurger & Kelly, 1984), and (3) the probability of surviving seed predation (Garcia-Castaño *et al.*, 2006). All of these factors affect a seed's chances of successfully establishing as a seedling. One interesting possibility is that seed and seedling strategies might be affected in the future by selection for dispersal

syndromes that enable plants to migrate rapidly in response to climate change.

Seed survival in the soil

In Europe, there is a tendency for species with small, rounded seeds to have seeds that persist for some years in the soil seed bank (Thompson *et al.*, 1993; Cerabolini *et al.*, 2003). This pattern has also been found in Argentina (Funes *et al.*, 1999), but not in Australia (Leishman & Westoby, 1998), or in the fynbos of South Africa (Holmes & Newton, 2004). In New Zealand (Moles *et al.*, 2000), Iran (Thompson *et al.*, 2001), and central Spain (Peco *et al.*, 2003), there are negative relationships between seed mass and persistence, but no relationships between seed shape and persistence in the soil.

There has been some confusion in the literature regarding seed persistence in the soil and seed dormancy. Some authors use the terms almost as though they are synonyms. However, there is no strong relationship between dormancy and persistence (Thompson *et al.*, 2003). So, is the tendency for smaller-seeded species to have more persistent seed banks matched by a tendency for smaller-seeded species to have some form of dormancy? It seems so: a study of 1795 species showed that species with some form of dormancy have smaller seeds than do species without dormancy (Jurado & Flores, 2005). However, the magnitude of the difference in seed mass was so small that its ecological significance is doubtful.

The idea that small-seeded species are generally more likely to have persistent seed banks is consistent with the finding that short-lived species, which tend to have smaller seeds, are more likely to have persistent seed banks than are long-lived species (Thompson *et al.*, 1998). There is also some evidence that species with high levels of seedling survival tend to have low levels of seed dormancy (Kiviniemi, 2001). Both of these are examples of situations where seed traits can be understood as simple components of the broader life-history strategy of each species. This is consistent with the work of Venable and Brown (1988), who considered the interaction of dispersal, dormancy, and seed size in reducing the impact of environmental variation. They recognized that associations between seed size and other plant attributes are an important component of a species' life history and that there may be trade-offs between these attributes.

Germination and seedling emergence

The tendency for small-seeded species to have persistent seed banks suggests that these species are well-placed to have their seedlings rapidly emerge and take advantage of favorable establishment conditions. This idea is consistent with the results of a study of seedling establishment after fire in Australia (Moles & Westoby, 2004b). This study showed a positive relationship between seed mass and the amount of time elapsed between the time at which conditions first became favorable for germination and the first emergence of seedlings. There is also a strong correlation between the size of seeds and the depth of burial from which seedlings can emerge (Maun &

Lapierre, 1986; Gulmon, 1992; Jurado & Westoby, 1992; Jurik *et al.*, 1994; Bond *et al.*, 1999). One hypothesis is that this relationship is a simple consequence of the redistribution of mass from the seed to the hypocotyl (Bond *et al.*, 1999).

Seedling morphology

There are strong negative relationships between seed mass and the photosynthetic capacity of a species' cotyledons (Ibarra-Manriquez *et al.*, 2001; Zanne *et al.*, 2005), and between cotyledon thickness and photosynthetic rate (Kitajima, 1992b). Seedlings from large-seeded species also tend to have hypogeal cotyledons that remain below the soil surface or cryptocotylar germination (the cotyledons remain within the fruit wall or seed coat) (Ng, 1978; Garwood, 1996; Wright *et al.*, 2000; Ibarra-Manriquez *et al.*, 2001; Zanne *et al.*, 2005). The correlations between seedling morphology and seed mass may be related to the seedling's ability to resprout after sustaining damage from herbivores. Small-seeded species generally deploy all of their reserves during germination. However, larger-seeded species, with greater reserves, are able to hold some resources in reserve. Seedlings with epigeal cotyledons are usually unable to resprout if their cotyledons and apical bud are removed (Moles & Westoby, 2004b). This is no disadvantage for small-seeded species, which are unlikely to have enough reserves available to resprout, regardless of the availability of buds. However, it would be advantageous for large-seeded species to have their reserves and some meristematic tissue safely stored below-ground, so that they can resprout after sustaining herbivore damage (Harms & Dalling, 1997).

Seedling growth strategies

Many studies have shown negative relationships between seed mass or initial seedling mass and the relative growth rate of young seedlings (Maranon & Grubb, 1993; Kitajima, 1994; Grubb *et al.*, 1996; Wright & Westoby, 1999; Fenner & Thompson, 2005; Paz *et al.*, 2005; Poorter & Rose, 2005). The higher relative growth rate of small-seeded species seems to be associated with low density tissues and a strategy of maximizing surface area. For instance, a study of 33 Australian species showed a positive correlation between relative growth rate and specific root length, and a negative correlation between relative growth rate and leaf mass per area (Wright & Westoby, 1999). In addition, a study of 52 woody species from Europe showed that species whose seedlings had high leaf mass per area had denser, but not thicker leaves (Castro-Diez *et al.*, 2000). These dense-leaved seedlings tended to have more sclerified tissue in the leaf lamina, smaller cells, and lower water and nitrogen concentrations than did species with low leaf mass per area (Castro-Diez *et al.*, 2000). Consistent with this, Cornelissen *et al.* (1997) found a positive correlation between seedling relative growth rate and foliar nitrogen concentrations. Finally, a study of 80 species from Europe showed that seedlings with high relative growth rates tend to have low stem tissue density and wide xylem vessels (Castro-Diez *et al.*, 1998).

The correlations between seed mass, seedling morphology, and seedling growth strategy undoubtedly contribute to the low survival rates of seedlings from small-seeded species (Fig. 10.4a). One might also expect fast-growing, low tissue density seedlings to have low levels of chemical defense. However, experimental data for 19 species of Asteraceae do not appear to support this prediction (Almeida-Cortez & Shipley, 2002).

Traits of mature plants

Seed and seedling traits are often correlated with the traits of adult plants. We have already described correlations among seed size, seedling size, maximum plant height, time to maturity, and longevity. As one might expect, there are also correlations between a species' morphology as a seedling and as an adult. For example, seedling leaf size is correlated with adult leaf size (Cornelissen, 1999).

As the seedling stage makes up a very small fraction of the life span of a plant, one might think that plant traits would be largely determined by the environment in which the adult plants occur. However, seedlinghood is a time of high mortality, and thus exerts a disproportionately strong selective effect on plant traits. Evidence for the importance of the regeneration phase was recently found in a study of 58 plant species from a rain forest in Bolivia (Poorter, 2007). Poorter showed that several ecologically important leaf traits of adult plants, including leaf mass per area, maximum photosynthetic assimilation rate, and leaf nitrogen content, were more closely related to the light conditions the species experienced during its regeneration phase than to the light conditions experienced by the adult plants on which the traits were measured.

Section summary

There is a spectrum of variation of seed and seedling strategies from species with large seeds and slow-growing seedlings with dense tissues and slow tissue turnover to species with small seeds and fast-growing seedlings with lower-density tissues, fast tissue turnover. The fast-growing, small-seeded species also tend to have the ability to persist for long periods in the soil and then rapidly emerge and grow when conditions become favorable. These data fit well with the idea that plant life histories can be seen as a spectrum from tall, long-lived plant species with large seeds and high rates of seedling survival to small, short-lived species with small seeds and low rates of seedling survival (Fig. 10.5). In the future, it would be good to formally incorporate variables such as tissue density and relative growth rate into the scheme depicted in Fig. 10.5.

10.3 | Seed and seedling strategies within species

The focus of this chapter so far has been on interspecific variation in seed and seedling traits. This is largely because the variation

in strategies is so much greater between than within species. However, selection acts within species, so understanding trait variation within species contributes to understanding of the evolution of life history strategies. In this section, we will summarize the state of the literature on seed mass variation, seed production, and seedling survival at the within-species level, and compare this literature to the literature on cross-species relationships.

Seed mass variation

Seed mass typically varies two- to fourfold within species (Michaels *et al.*, 1988; Jacquemyn *et al.*, 2001), compared to seed mass variation within communities of five to six orders of magnitude (Leishman *et al.*, 2000) and 11.5 orders across all species (Moles *et al.*, 2005b). Numerous studies have shown that seed size is a heritable trait (e.g. Schaal, 1980; Byers *et al.*, 1997; Wheelwright, 2004, but see Silvertown, 1989; Wolfe, 1995).

Seed mass variation within species mostly occurs within plants rather than among plants or populations and is largely related to seed position within pods and fruits (Wolf *et al.*, 1986; Wulff, 1986a; Michaels *et al.*, 1988; Winn, 1991; Obeso, 1993; Mendez, 1997; Vaughton & Ramsey, 1997; Willis & Hulme, 2004; Pizo *et al.*, 2006). This suggests that much of within-species seed mass variation is due to physiological or morphological constraints on optimum resource allocation to seeds. Sakai and Sakai (2005) argue that greater allocation to reproductive output should result in increases in seed number rather than individual seed mass because of greater resource use efficiency (the terminal stream limitation model). Seed mass variation among individual plants has also been shown to increase in response to fungal infection in some species of *Hydrophyllum* (Hydrophyllaceae) (Marr & Marshall, 2006). Variation in seed mass among populations has also been attributed to population size (Kery *et al.*, 2000; Jacquemyn *et al.*, 2001; Hensen & Oberprieler, 2005) and resource availability (Willis & Hulme, 2004). Finally, there is some evidence that seed mass varies according to pollen source. Self-pollination is associated with decreased seed mass in *Swertia perennis* (Gentianaceae) (Lienert & Fischer, 2004), *Asclepias incarnata* (Apocynaceae) (Lipow & Wyatt, 2000), *Chamaecrista fasciculata* (Leguminosae) (Fenster, 1991), and *Banksia spinulosa* (Proteaceae) (Vaughton & Ramsey, 1997). However, a few studies have found no difference in mass of seeds from self- and cross-pollination (Winn, 1991; Ashworth & Galetto, 2001; Leimu, 2004).

The heritability of seed mass and the relatively small variation in seed mass within species suggests that seed size is determined via a process of stabilizing selection. This can operate through selection via trade-offs in seedling survival, dormancy, dispersal, predation, and seed number (Venable & Brown, 1988). For example, in *Quercus ilex* (Fagaceae), selection pressure on fitness components relating to establishment success favors larger seeds while selection pressure relating to predation pressure favors small seeds (Gomez, 2004). Much of the

literature focuses on the central role of the seed number/seedling survival trade-off in determining an optimum seed mass for plant fitness.

The Smith–Fretwell model that formalizes the seed number/seedling survival trade-off produces a curve relating fitness to offspring size that predicts a single optimal seed mass (Fig. 10.1). A key prediction of the Smith–Fretwell model is that if a mother plant can allocate more resources to reproductive output, it should produce more seeds of the same size. The small variation within species in seed mass that is observed is attributed to limitations of a plant's ability to produce completely standardized seed mass or to variability in the shape of the Smith–Fretwell function within species (Leishman *et al.*, 2000). Variations in seed mass among individuals or populations of a species would provide evidence for the role of variability in the seedling environment in producing variation in seed mass. In contrast, variation in seed mass within individuals would provide evidence for the role of the limitation in a plant's capacity to produce completely standardized seeds. Venable (1992) modified the Smith–Fretwell model to account for variation in resource availability and relaxed the assumption of linear fitness returns from offspring number. He showed that within-species trade-offs between seed mass and number may be masked by variation in resource availability and plant size. Further work by Geritz (1995) extended the Smith–Fretwell model into a game-theoretical context. He showed that variation in seedling density favors the evolution of seed mass variation within individuals, based on the idea that seedlings from large seeds win in competition with seedlings from small seeds, but small seeds are able to colonize more sites because of their numerical advantage.

Intraspecific relationships between seed mass and seed production

What evidence is there for intraspecific seed mass/number trade-offs? In studies where plant size is accounted for, the predicted negative relationship between seed mass and number is apparent (e.g. Harper *et al.*, 1970; Ågren, 1989). That is, small-seeded individuals produce more seeds per unit biomass per year. However, when seed mass and number relationships are examined at the whole-plant level, the relationships are either negative (e.g. Aniszewski *et al.*, 2001) or neutral (e.g. Schaal, 1980; Wulff, 1986a; Winn & Werner, 1987). Some authors have argued that these neutral patterns at the whole-plant level can be understood in the context of variation in plant size, where larger plants produce more seeds (Henery & Westoby, 2001). This argument is consistent with Venable's (1992) model. The patterns found in within-species studies are relatively similar to the results of the cross-species studies described in section 9.2. However, no within-species studies have taken the approach of quantifying the slope of the seed mass/number relationship or considered seed mass variation in relation to lifetime seed production.

Intraspecific relationships between seed mass and seedling survival

Many studies have shown that seed mass is positively related to initial seedling size within species (e.g. Dolan, 1984; Wulff, 1986b; Zhang & Maun, 1991; Moegenburg, 1996) and that seedlings from larger seeds can emerge from greater soil depths (Wulff, 1986b). Within particular establishment sites, larger seeds have been shown to have better seedling survival (Stanton, 1984; Morse & Schmitt, 1985; Stanton, 1985; Winn, 1988; Tripathi & Khan, 1990; Wood & Morris, 1990) and greater reproductive output (Stanton, 1985). There is evidence that larger seeds provide an advantage in drier habitats (Schimpf, 1977; Sorenson & Miles, 1978; Wulff, 1986b; Stromberg & Patten, 1990; Parciak, 2002; but see Hendrix, 1991) and that seedlings from large seeds survive longer in conditions of nutrient deprivation (Krannitz *et al.*, 1991) or are more competitive in low fertility conditions (Tungate *et al.*, 2006). Early experiments by Black (1958) showed that large seeds were more successful in seedling–seedling competition. These studies are generally in relation to initial seedling success rather than to success through to reproductive maturity (with the exception of Stanton, 1985).

Cross-species studies show that the greater survival per unit time associated with large-seeded species is countered by the greater time to maturity (section 10.2). We wondered whether this confounding might also occur at the within-species level. We therefore searched BIOSIS (<http://www.biosis.org/>) to find studies that reported seed mass and plant size, seed mass and plant longevity, and seed mass and time to maturity relationships within species, excluding crop cultivars. The relationship between seed mass and maternal plant size is reported as either neutral (Klinkhamer & De Jong, 1987; Hendrix & Sun, 1989; Dudash, 1991; Stocklin & Favre, 1994; Vaughton & Ramsey, 1997) or positive (Hendrix & Sun, 1989; Klinkhamer & De Jong, 1993; Stocklin & Favre, 1994; see Moles *et al.*, 2004, Appendix 4). Some of these apparently neutral relationships might be due to a lack of statistical power. We were not able to find any information about intraspecific relationships between seed mass and time to maturity. However, variation in time to maturity is probably quite small within species, so may not be an important consideration at this scale.

10.4 Implications of a holistic understanding of plant life history strategies

Merging theory for plants and other taxa

The idea that seed and seedling strategies are just part of a broader life history syndrome is a departure from most recent thinking about seed mass/offspring survival strategies. However, it is not really a very novel idea. In fact, we seem to have returned to the r-K spectrum

of ecological strategies (Pianka, 1970). Species with small-seeds, high rates of juvenile mortality, short life spans, and small adult size are clearly r-selected species, while species with large seeds, low rates of juvenile mortality, long life spans and large adult size are K-selected species. The present theory (Fig. 10.5) also has much in common with Charnov's (1993) theories on life history, originally developed for understanding animal life history strategies.

The parallels between our present understanding of seed and seedling ecology and these older theory lineages have not been fully explored. It seems certain that applying ideas developed in these other areas of biology will lead to some interesting advances in our understanding of plant life history strategies.

Reassessing theory on the coexistence of multiple recruitment strategies

In the past, theories on plant life history strategy have sought to relate suites of attributes to particular habitats. These habitats may be defined in terms of disturbance, competition, adversity, or demographic factors such as growth rates and mortality schedules (Pianka, 1970; Grime, 1979; Begon, 1985; Sibly & Calow, 1985; Tilman, 1988). However, much of this body of theory fails to account for the wide variation in seed and seedling traits found within communities. The fact that differences in seed size are much greater between species within a community than between very different communities (Leishman *et al.*, 2000) suggests that seed size is more strongly related to other plant attributes than to establishment conditions. Consistent with this, a study of 12 987 species showed that evolutionary divergences in seed mass have been much more consistently associated with divergences in plant traits such as seed dispersal syndrome and growth form than with divergences in environmental variables such as latitude, net primary productivity, temperature, precipitation, and leaf area index (Moles *et al.*, 2005a).

A game-theoretical approach has been used to explain the coexistence of different seed size strategies, both within and across species (Geritz, 1995; Rees & Westoby, 1997; Geritz *et al.*, 1999). In these models, the landscape is seen as a grid of spaces available for seedling establishment. If a large seed and a small seed land in the same grid square, then the seedling from the large seed will outcompete the seedling from the small seed because of its greater resources and larger size. However, the large-seeded strategy can never exclude the small-seeded strategy because the small-seeded strategy is able to produce more seeds than the large-seeded strategy and will, therefore, reach some sites that are not reached by the large-seeded strategy.

Competition/colonization models seemed for some time to be the most plausible explanation for the wide differences in seed mass among coexisting species. Experiments showed that seedlings from large seeds usually have a competitive advantage over seedlings from small seeds (Leishman, 2001; Coomes & Grubb, 2003) and

observational studies have supported the idea that small-seeded species produce more seeds per individual per year, and per square meter of canopy per year (Shipley & Dion, 1992; Greene & Johnson, 1994; Jakobsson & Eriksson, 2000; Aarssen & Jordan, 2001; Henery & Westoby, 2001). However, several lines of evidence have recently cast doubt on the relevance of the competition/colonization theory to real-world situations. Leishman (2001) showed that the expected relationship between seed mass and colonization ability was obscured in the field by differences in abundance between species. Further, a compilation of field data showed that (1) competition between seedlings is a relatively minor cause of death compared to drought, herbivory, and pathogen attack and (2) seedlings seldom germinate at high enough densities for interspecific competition to be a major determinant of seedling mortality until after the seedlings have passed the stage at which seed mass might affect the outcome of competition (Moles & Westoby, 2004c). Finally, data from two detailed field studies strongly suggest that the competition/colonization trade-off cannot explain the coexistence of different seed mass strategies. Eriksson (2005) studied plant regeneration in Swedish grassland. He found that recruitment was not related to seed mass, and that larger seeded species did not generally win in competition with small-seeded species. In fact, there was no case in which a larger-seeded species had negative effects on a smaller-seeded species, even though the seeds had been sown at densities at least as great as those found under natural conditions. Thus, Eriksson (2005) soundly rejected the idea that game-theoretical competition/colonization models explained the coexistence of multiple seed-size strategies in this ecosystem. Turnbull *et al.* (2004) studied recruitment in annual plants in limestone grassland in South Wales. Although these authors found some evidence for a competition/colonization trade-off, the trade-off was not strong enough to be the sole explanation for species coexistence (Turnbull *et al.*, 2004). Thus, there is growing consensus that the competition/colonization theory does not provide a general explanation for seed mass variation within communities (Coomes & Grubb, 2003; Eriksson, 2005).

All this leaves us wondering how the vast range of different seed and seedling strategies coexist and how such different strategies were ever selected for in the first place. One possible explanation is that different species utilize different regeneration niches within each environment (Grubb, 1977; Coomes & Grubb, 2003; Turnbull *et al.*, 2004). There is some evidence that different species do perform better under subtly different establishment conditions. However, it is difficult to imagine how subtle differences between microsites within ecosystems could account for the vast differences in coexisting seed and seedling strategies (Eriksson, 2005).

Perhaps understanding seed and seedling strategies as components of a larger life history strategy will help us to resolve this mystery of strategy coexistence. For instance, incorporating information about adult niches along with information about regeneration niches might help us to understand how different plant strategies can coexist. In

any case, this strategy coexistence problem is certainly an interesting direction for future research.

10.5 | Conclusion

Our past focus on the trade-off between producing many small seeds each with low levels of survival as seedlings, versus producing a few large seeds, each with higher levels of survival was missing several important elements. It appears that seed and seedling ecology are better understood as components of a larger life history strategy, at least at the cross-species level. Plant strategies seem to fall largely along a spectrum from small-seeded species with low rates of seedling survival, short life spans, small stature, rapid growth, and the ability to disperse through time and space to take advantage of short-lived recruitment opportunities (r-selected species) through to large-seeded species with high rates of seedling survival, long life spans, large adult size, slower growth, and seedlings that can tolerate a wide range of conditions during establishment (K-selected species). Of course, there are many exceptions to this generalization. Much of the variation can be understood as species responses to particular combinations of biotic and abiotic stress. However, we think that viewing seed and seedling ecology as part of a broader life history strategy will give us new tools that might help to answer some of the outstanding questions regarding the ecology of plant regeneration.