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Life histories, reproductive strategies and allocation

A seed is an embryo plant wrapped in a protective covering of maternal tissue (the testa). It is generally provided with a supply of nutrients contained in a separate tissue (the endosperm), though in many cases all the nutrients are absorbed by the seed leaves (the cotyledons) during the course of development. The primary function of the seed is reproduction. This does not necessarily result in an increase in numbers of the species. In a stable population, each adult is eventually replaced by another adult. This is achieved by the production of large numbers of offspring, most of which will die before reaching maturity. A seed therefore has several functions in addition to multiplication. Its small size (at least in comparison with its parent) renders it well suited for dispersal and the colonization of new areas. In addition, many seeds can withstand a much wider range of environmental conditions than the adult plants, especially extremes of drought and temperature. Their ability to undergo a period of arrested development and persist in a state of diapause is important as a means of persistence for many species, but it is especially crucial for annual plants that do not survive as adults during periods of unfavourable conditions such as seasonal cold or drought.

1.1 Sexual vs. asexual reproduction in plants

An important feature of seeds is their genetic variability. This derives from the fact that (except in the case of apomicts, mentioned below) they are the products of sexual reproduction. Each seed is genetically unique because of the shuffling of the parents' genetic material (by crossing over between the chromosomes) during the formation of the gametes, followed by random combination of the male and female gametes at fertilization. The inherited diversity of

Cambridge University Press
0521653681 - The Ecology of Seeds
Michael Fenner and Ken Thompson
Excerpt
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the offspring provides the species with the genetic flexibility that increases the likelihood of at least some individuals surviving the hazards of natural selection (Harper, 1977).

Seed production is not the only form of reproduction in plants. Many species, especially herbaceous perennials, reproduce asexually by means of vegetative organs. A plant may employ one or both of these forms of reproduction. Annuals and most woody plants generally reproduce only by seed. Plants from habitats that are inimical to seedling establishment (such as rivers and arctic-alpine sites) tend to rely largely on vegetative reproduction. Herbaceous perennials often have both seeds and a means of vegetative propagation. Salisbury (1942) calculated that 68% of the most widespread herbaceous perennials in Britain show some means of vegetative reproduction. This may take the form of ramets (branches that become independently rooted plants) in species with spreading clonal growth such as *Glechoma hederacea*. Plantlets may be produced on distinct stolons (*Ranunculus repens*, *Potentilla reptans*) or may arise from perennating organs such as rhizomes, corms and bulbs, as in *Iris*, *Crocus* and *Lilium*, respectively. In the case of many water plants (such as *Elodea canadensis*), propagation may occur simply by the rooting of detached fragments. Vegetative reproduction may be virtually indistinguishable from growth, as in the case of the formation of rooted tillers in many grass species. The majority of plants with clonal growth also produce seeds, sometimes showing a trade-off in allocation between the two modes of reproduction (Ronsheim & Bever, 2000).

The strategy of producing both vegetative offspring and seeds may maximize fitness by combining the advantages of both forms of reproduction. Asexually reproducing animals such as water fleas and aphids usually have a sexual phase in their life cycle, often after a number of asexual generations. Green & Noakes (1995) provide a model demonstrating that even a small component of sexual reproduction can be highly advantageous in an otherwise clonal life cycle. Plants can often switch between the two modes of reproduction in a phenotypic response to changing conditions, especially to increased density (Abrahamson, 1975; Douglas, 1981). Many species that form large clones have mechanisms for avoiding inbreeding. Nettles (*Urtica dioica*), dog's mercury (*Mercurialis perennis*), creeping thistle (*Cirsium arvense*) and butterbur (*Petasites hybridus*) all have clones that are either male or female (that is, the species are dioecious). This separation of the sexes ensures that only outbreeding between different clones is possible.

Vegetative reproduction facilitates local domination of a site by rapid lateral expansion. Many clonal species form extensive monospecific stands that are able to outcompete other species. Compared with reproduction by seed, the production of vegetative offspring is less costly in terms of energy for the parent plant, largely because the ramets contribute to their own production (Jurik, 1985; Muir, 1995). Another advantage is the relatively high survivorship of ramets in comparison with seedlings. In a study on the demography of the creeping buttercup (*Ranunculus repens*), Sarukhán & Harper (1973) recorded that a clonal offspring had a life expectancy of 1.2–2.1 years as against 0.2–0.6 years for a seedling. A ramet also achieves a greater size in a shorter time than a seedling. However, the close proximity of the offspring to the parent may result in an adverse degree of local crowding (Nishitani *et al.*, 1999).

A key feature of vegetative reproduction is that the offspring are all genetically identical to the parent and to each other. All members of a clone, however independent and numerous, can all be considered to be part of the same plant. The offspring of a single individual can cover large areas. In *Phragmites australis*, *Spartina anglica*, *Lemna minor* and *Eichhornia crassipes*, clones may extend to hectares and even square kilometres. The genetic uniformity in these populations is thought to be disadvantageous in the long term because it may render the plant unable to adapt to any change in selective pressures. Clones are also prone to the accumulation of deleterious mutations and viral infections over time. But, in spite of these supposed shortcomings, many clones have been remarkably persistent. Some are thought to be several thousands of years old (Richards, 1986).

Even some seed production is essentially clonal. A number of plants have evolved a means of producing seeds without meiosis or fertilization. This process is called *agamospermy* ('seeds without marriage') and is one form of asexual reproduction or *apomixis*. (The latter term strictly includes vegetative reproduction.) Agamospermy has been recorded in 34 families but is especially frequent in species belonging to certain genera such as *Taraxacum*, *Hieracium* and *Crepis* in the Asteraceae and *Alchemilla*, *Sorbus* and *Rubus* in the Rosaceae. In these species, the seeds from an individual plant are all genetically identical with the parent and with each other. The advantages of agamospermy are not well established. It may be useful in certain circumstances to have the benefits of seeds (multiplication, dispersal, dormancy) without the costs of sexual reproduction. If the plant is well adapted to its niche, then all the offspring will be as fit as the mother plant. Agamospermy does not seem to be an adaptation to an absence of pollinators as many of these species require pollination to induce seed development, even though the male gametes are not used (Richards, 1986).

1.2 Life histories and survival schedules

Natural selection imposes a reproductive strategy on each species. This is a group of life-history traits that enable the plant to survive and transmit its genes to the next generation. It consists of finding the best overall solution to a series of problems faced by the plant, such as the size at which reproduction should start, the subsequent frequency and regularity of reproduction, the amount of resources to allocate on each occasion, and the size and number of the seeds produced. Several of these aspects of reproduction are mutually antagonistic (e.g. allocation level vs. frequency, seed size vs. number), so that the outcome is likely to be the result of a series of simultaneous compromises. See also Box 1.1.

Box 1.1 Trade-offs

Much of ecology is the result of trade-offs (Crawley, 1997). No plant or animal can be good at everything and, in the simplest case, trade-offs reflect the plain fact that resources allocated to one function cannot be allocated to another. One example, sometimes considered so obvious that it hardly needs proving, is the trade-off between seed size and number. In fact, this trade-off is not quite so obvious – a plant could produce both more seeds *and* larger seeds by allocating more resources to reproduction. In reality, allocation of resources to reproduction does not vary greatly between species, and seed number does trade off against seed size (Shipley & Dion, 1992; Turnbull *et al.*, 1999; Jakobsson & Eriksson, 2000). For example, Shipley and Dion (1992) showed that plant weight (a rough measure of resources available for reproduction) and seed weight together accounted for 82% of the variation in annual seed production of 57 herbaceous species. Habitat accounted for 5% of the missing variation, with plants of disturbed habitats (mostly annuals) producing more seeds than equivalent-sized plants from less-disturbed habitats such as old fields and woodlands.

It has been suggested that, to some extent, plants can escape the seed size–number trade-off by modifying the chemical composition of their seeds (Lokesha *et al.*, 1992). There is some evidence that light wind-dispersed seeds are better dispersed than heavier seeds of similar morphology (e.g. Meyer & Carlson, 2001), although this may not apply to all dispersal modes (Hughes *et al.*, 1994a). Since fats yield about twice the energy of carbohydrates per unit mass, a plant could make seeds half as heavy by replacing stored carbohydrate with fats. In fact, the majority of plant species mostly store fats in their seeds, although there are costs: lipid synthesis is more energetically demanding than either protein or carbohydrate production. If lighter seeds are dispersed more effectively by wind, then we might expect fat storage to be more prevalent in wind-dispersed seeds than in those dispersed by other means. An analysis of a large dataset by Lokesha *et al*. (1992) supported this prediction: wind-dispersed seeds averaged about 25% fat, while seeds with no obvious means of dispersal contained about 10% fat. This analysis, however, failed to take account of phylogeny. Very many of the wind-dispersed species were in the Asteraceae, a family in which fat-rich seeds are very common, irrespective of dispersal mode. For example, seeds of Asteraceae tribes in which wind dispersal is absent (e.g. Anthemidae) have the same fat content as tribes in which it is universal (e.g. Lactuceae). A new analysis, using PICs, did not find any relationship between seed fat content and dispersal mode (Thompson *et al*., 2002). The reasons for the absence of any relationship are not entirely clear; it may be that the weight savings associated with fat storage are simply not large enough or that the chemical composition of seeds may be responding to other selective forces.

The trade-offs considered above are either inevitable (the same resources cannot be allocated to two competing functions) or have some clear biophysical basis (lighter seeds may be dispersed better). However, trade-offs may derive not from any mechanistic connection between two traits but from shared evolutionary functions. For example, if seed dispersal and seed persistence in the soil both reduce the perception of environmental variability, then the existence of one trait may reduce the adaptive value of the other (Venable & Brown, 1988). Some proposed trade-offs may combine both mechanistic and adaptive origins; if competitive ability depends on substantial allocation to vegetative structures, then good competitors may have fewer resources to allocate to flowers and seeds; poor competitors may then be compelled to escape the competitive dominants by evolving better dispersal ability, thus further reducing the resources available for growth, and so on. Investigating both these trade-offs is hampered by the lack of comparable data for reasonable numbers of species on the traits involved, and by a lack of consensus on exactly how ‘competitive ability’ and ‘dispersal ability’ should be defined and measured. An analysis that divided species into ‘effectively dispersed’ and ‘not effectively dispersed’, using seed morphological criteria, supported the existence of a trade-off between seed dispersal and persistence in the soil in the British flora (Rees, 1993). A more recent analysis, which attempted to quantify effectiveness of dispersal more precisely, but was confined to wind dispersal only, found no evidence for this trade-off (Thompson *et al*., 2002). There may be a number of reasons for these contradictory results, but two are worth mentioning. First, there is a positive, mechanistic relationship between seed persistence and wind dispersal. Both persistence in soil, at least in cool temperate floras (see Chapter 4), and wind dispersal (see Chapter 3) are linked strongly to small seed size. Thus, all things being equal, small seeds may increase the capacity for both wind dispersal and persistence in soil. Second, trade-offs require that traits have both benefits and costs; yet if seeds enter the soil seed bank only if the likely consequence of immediate germination is death, then the cost of persistence may be low. This may often be true, since seeds are remarkably good at assessing whether conditions are suitable for germination and establishment (see Chapter 6). Nor is it clear whether there are significant costs associated with the *capacity* to persist in the soil (Thompson *et al.*, 2002).

For at least 50 years, theoreticians have been attracted by the possibilities that arise from a trade-off between competitive ability and colonising ability (Skellam, 1951). Models that incorporate such a trade-off provide a satisfying explanation for the coexistence of two or more species in a patchy environment. Good competitors (but poor dispersers) always prevail in patches that they occupy, while poorer competitors (but better dispersers) always reach some patches that better competitors fail to reach. Many species can coexist via this mechanism, as long as all show the required competition–colonization trade-off (Tilman, 1994).

Recent studies, however, have questioned both the evidence for the existence of the trade-off and also whether such a trade-off is necessary for species coexistence. A key prediction is that species abundances should often be limited by dispersal and this limitation should be greater for better competitors. That is, good competitors should show the largest increases in abundance when saturating densities of propagules are added experimentally. Several studies have sown enough species to test this idea (Eriksson & Ehrlén, 1992; Thompson & Baster, 1992; Tilman, 1997; Ehrlén & Eriksson, 2000; Jakobsson & Eriksson, 2000), and all have found at least some evidence of seed limitation. In a recent review of the available data, Turnbull *et al.* (2000) concluded that seed limitation is more frequent in early successional habitats and species, i.e. the opposite of the pattern predicted by the competition–colonization hypothesis. A more recent analysis of Turnbull's data confirms that although large-seeded species appear to be more seed-limited in the very short term, there is ultimately no relationship between seed size and the probability of increased recruitment (Moles & Westoby, 2002). More generally, although adult and regenerative traits are clearly not independent (Salisbury, 1942; Rees, 1993; Leishman *et al.*, 1995), there is no compelling evidence that regenerative traits in general are constrained *tightly* by vegetative traits. Thus, plants that combine good competitive ability and effective dispersal certainly exist, e.g. *Typha* spp., *Chamerion angustifolium* and *Phragmites australis*. Several authors have successfully classified local floras into 'strategies' or 'functional types' on the basis of plant traits (Grime *et al.*, 1987; Shipley *et al.*, 1989; Leishman & Westoby, 1992; Díaz & Cabido, 1997), but classes based on vegetative traits are largely independent of those based on seed traits. If this were not generally the case, then the 'regeneration niche' of Grubb (1977) would merely reflect the niche of the mature plant, and there is abundant evidence that it does not. Gross and Werner (1982), Peart (1984) and Thompson *et al.* (1996) all provide good examples of coexisting species that have rather similar ecologies in the mature phase but differ profoundly in one or more of seed size, persistence in soil, dispersal mode and germination phenology. Sometimes, such interspecific differences may appear to represent a competition–colonization trade-off, but closer inspection reveals a more complicated picture. In rainforest in Panama, Dalling & Hubbell (2002) showed that seeds of pioneer tree species varied in size over four orders of magnitude. This variation appears to be maintained by a trade-off between selection for dispersal (favoured by small seed size) and selection for establishment success (favoured by larger seeds). However, seedling densities are too low for competition between them to be important, at least until the seedlings are no longer dependent on seed resources. In fact, small-seeded species have a lower establishment probability for a variety of reasons, including inhibition of germination by litter and mortality from drought during brief dry spells. Although small-seeded species can colonize sites never occupied by larger-seeded species, they simply have a lower probability of survival everywhere, irrespective of competition from larger-seeded competitors.

Recent work has also cast doubt on some of the assumptions of the simple competition–colonization model. In its usual form (e.g. Nee & May, 1992; Tilman, 1994), the model assumes both global dispersal and instantaneous competitive displacement. Neither of these assumptions is particularly realistic, and relaxing either allows species to coexist without a competition–colonization trade-off (Higgins & Cain, 2002). In more realistic models, local dispersal creates spatial refuges for poor competitors, while temporal refuges arise from the ability of poor competitors to survive, even if only briefly, before being excluded by superior competitors (Pacala & Rees, 1998).

The idea of trade-offs between vital activities is well exemplified in the 'principle of allocation' formulated by Cody (1966). Every organism has a finite amount of resources available to it during its lifetime. These resources may be in the form of nutrients, energy or time. The organism partitions these resources between its various vital activities: maintenance, growth, defence and reproduction. It follows that resources devoted to any one activity can only be allocated to that function at the expense of the others, and so there is a trade-off between the resources devoted to each activity. The actual balance of resource allocation to each function is thought to be the optimum compromise brought about by natural selection. Although originally formulated in relation to animals, the principle can be readily applied to plants. They too have to allocate resources to growth, competition with neighbours, defence against predators, and reproduction. For example, a plant exposed to a high risk of herbivory will have to devote resources to mechanical or chemical defence at the expense of resources needed for other activities. In a highly competitive environment, a plant's survival may depend on a high level of resource allocation to vegetative expansion rather than to reproduction. Lovett Doust (1989) and Reekie (1999) provide useful reviews of allocation trade-offs in plants.

The evolution of different levels of allocation to reproduction is thought to be driven largely by the level of disturbance in the habitat. In habitats with a high degree of disturbance (e.g. subject to periodic, unpredictable events such as landslides, floods, fire, burrowing by animals and ploughing by humans), the vegetation remains open and seedlings colonize newly exposed soil. Mortality is mainly density-independent and is highest at the adult stage. Under these conditions, selection would favour an early onset of reproduction and a short life cycle culminating in a single reproductive event. Any individuals that do not reproduce quickly may not have any offspring at all, and fitness will probably be related directly to the number of seeds produced. Short life cycles and early maturity are also associated with small adult size (Kozlowski & Wiegert, 1986). In less disturbed habitats, where the vegetation forms a closed, stable community, selection will favour perennial plants of large adult size that devote more resources to competing with their neighbours. In such plants, we would expect allocation to favour vegetative growth and possibly defence against herbivores, reducing allocation to reproduction. Mortality will be largely density-dependent and concentrated in the early stages of establishment. The high juvenile mortality would itself select in favour of long-lived individuals that have repeated opportunities for reproduction during their lifetime. These two contrasting plant types represent two extremes of a continuum, corresponding to Gadgil & Solbrig's (1972) categories of r- and *K*-selected plants, based on the original ideas of MacArthur & Wilson (1967).

The life history of a plant is thus a consequence of its age-specific risk of mortality. Plants are usefully classified into two categories: monocarpic, in which seeds are produced only once, after which the plant dies; and polycarpic, in which seeds are produced repeatedly for an indefinite period. Monocarpic plants are dependent on the success of reproduction by seed on every occasion that they produce seeds, whereas polycarpic plants can reproduce even after repeated failures. The lifespan of a monocarpic plant may be up to one year (an annual), two years (a biennial) or several years (a perennial monocarp). Annuals often have a life cycle of only a few weeks and, in some cases, can have several generations in a year. Biennials usually spend the first year building up a reserve of resources on which they draw in the second year for reproduction. Long-lived monocarpic plants are rare. They include some species of bamboo (*Bambusa* species) and century plants (*Agave* species). These species often have very high levels of reproductive allocation, having accumulated reserves over a long period. Since they have only one opportunity for reproduction, they would be expected to allocate the maximum possible resources to seeds in a 'big bang' reproductive event (Gadgil & Bossert, 1970; Janzen, 1976). On the same reasoning, perennials would be expected to have a lower annual allocation, thereby avoiding exhaustion that would jeopardize future reproduction. Surveys of allocation in the two groups largely support these expectations. In a comparative study of 40 grass species, Wilson & Thompson (1989) found that most annuals had a reproductive allocation of over 50% and that the corresponding figure for stoloniferous and rhizomatous perennials was much lower (less than 10%). However, Willson (1983) lists many cases where reproductive effort in annuals, biennials and perennials defies expectations, so the differences between the categories in this respect is far from clear-cut. The biomass fraction that a plant devotes to reproduction in a given environment is genetically programmed. This is indicated by the variation in reproductive allocation found in different populations within the same species (Schmid & Weiner, 1993; Lotz, 1990; Reekie, 1998; Sugiyama & Bazzaz, 1998).

The age of first reproduction is an important determinant of an organism's potential population growth rate. A relatively small delay in this has a disproportionate numerical penalty (Lewontin, 1965). For example, a plant that delayed its time to first reproduction by 44% would need to increase its fecundity by a factor of three to compensate in the long term (Willson, 1983). In many plants (as in most animals), there is a threshold size that has to be attained before reproduction is possible. This is exemplified by *Aster lanceolatus*, *Solidago altissima* and *S. canadensis* (Schmid *et al.*, 1995; Schmid & Weiner, 1993). In many plants, the threshold size may be due simply to the structural requirement to form the necessary flower initials. The importance of these developmental constraints is emphasized by Watson (1984). Environmental factors such as nutrient levels and competition may also influence the age at first reproduction (Sugiyama & Bazzaz, 1998), but the number of seeds produced is determined mainly by size rather than age (Schmid & Weiner, 1993). In some cases (such as in *Oenothera erythrosepala*), flowering may be induced by a photoperiodic cue to which the plant is incapable of responding until a critical minimum leaf area (not mass) has been attained (Kachi & Hirose, 1983).

In a natural population, the local growing conditions of every plant will be different, so the individuals will vary in size (due to the availability of, for example, light, water and nutrients, in the immediate vicinity). The fraction of biomass allocated to reproduction can also vary phenotypically, especially with plant size. Hara *et al.* (1988) investigated the relationship between individual biomass and reproductive allocation in 16 annuals, 2 biennials and 14 perennial herbs from wild populations in Japan at both flowering and fruiting stages. They were able to recognize two broad strategies: annuals and biennials showed huge variation in the sizes of flowering individuals but, in spite of this, reproductive allocation was more or less constant within a species. No matter what size the parent plant was, it devoted much the same fraction of its resources to flowering, so the cost of reproduction remained fixed. This is consistent with other studies on annuals (Fenner, 1986b; Kawano & Miyake, 1983). In contrast, the perennials had a smaller variation in individual mass and showed a clear decrease in reproductive allocation with increasing size within a species. Other studies, however, show that this is not a universal distinction between annuals and perennials. There are exceptions on both sides. For the annual *Abutilon theophrasti*, Sugiyama & Bazzaz (1998) found a log-log regression between seed mass and vegetative mass. Conversely, four alpine perennial species of *Ranunculus* were shown to have a constant reproductive allocation, independent of plant size (Pickering, 1994). From a survey of the literature, Samson & Werk (1986) go so far as to say they could find no consistent differences between annuals and perennials in respect of size dependence on reproductive effort.

In studies where the relationships between mass of reproductive structures and mass of whole plants have been recorded in natural populations, there is usually a positive linear relationship between the two (Thompson *et al.*, 1991; Schmid & Weiner, 1993; Pickering, 1994). Aarssen & Taylor (1992) also found mainly straight-line relationships between fecundity (number of seeds per plant) and parent plant biomass in 21 herbaceous species. Fig. 1.1 shows a generalized diagram (based on Klinkhamer *et al.*, 1992) plotting (a) the relationship between reproductive mass and total plant mass and (b) the corresponding proportional reproductive allocation vs. plant mass. This is shown for two plants: one with and one without a threshold requirement for reproduction. The intercept on