Chapter 5 Granivory

Philip E. Hulme and Craig W. Benkman

5.1 Herbivores as predators, seeds as prey

Granivory describes the interaction between plants and the animals (termed granivores or seed-predators) that feed mainly or exclusively on seeds. Seeds are the products of the fertilized ovules of flowering plants and consist of an embryo and food-storage organs surrounded by a protective seed coat (testa). Many animal species feed on seeds (Table 5.1) and they display a wide range of feeding habits: earthworms swallow whole seeds that are subsequently digested by gut enzymes; lygaeid bugs suck out the contents of seeds; certain lepidopteran and coleopteran larvae burrow through and feed within seeds; many birds grind up entire seeds in muscular gizzards; rodents gnaw seeds with their incisors, while ungulates crush seeds in their molar mills. A distinction is often made between pre-dispersal seed-predators that feed on seeds on the parent plant before they are dispersed (e.g. parrots, monkeys, weevils), and post-dispersal seed-predators that scavenge for seeds after they have been dispersed (e.g. pheasants, pigs, earthworms). However, many granivores act as both pre- and post-dispersal predators. Comparison of several studies that have simultaneously quantified pre- and post-dispersal seed predation (Table 5.1) reveals that: (a) a greater diversity of taxa (particularly invertebrates) feed on seeds pre- rather than post-dispersal; (b) while certain plants suffer proportionally more pre- than post-dispersal seed predation the latter is, on average, significantly more severe (47.3% vs. 61.2%); and (c) the intensities of pre- and post-dispersal seed predation are directly correlated. The lack of independence between the intensity of pre- and post-dispersal seed predation might be expected if the granivore assemblage feeding both pre- and post-dispersal were the same. This is generally not the case (Table 5.1), which suggests that there may be certain seed or crop attributes that similarly influence predation by both pre- and post-dispersal granivores. For example, seeds that are poorly defended (either chemically or physically) may be particularly susceptible to the impacts of both pre- and post-dispersal granivores. Alternatively, large seed crops may satiate both pre- and post-dispersal granivores. The limited data available highlight the need for further studies comparing the relative impact of pre- and post-dispersal granivores.

Numerous field studies have identified granivores as having a considerable impact on seed populations (see Crawley 1992; Hulme 1998a for reviews). High rates of predation, often greater than 50%, are typical of many plant species in a number of different ecosystems (Table 5.1). Granivory is thought to play a pivotal role in the regeneration (Sarukhan 1986; Louda et al. 1990; Hulme 1994a, 1996a; Castro et al. 1999), colonization ability (Schupp et al. 1989; Myster & Pickett 1993; Picó & Retana 2000) and spatial distribution (Kollmann 1995; Hulme 1997; Forget et al. 1999) of plants. In addition, granivores have been suggested as agents of natural selection that influence seed traits (Hulme 1998b; Benkman 1999) as well as seed production strategies both within (Ruhren & Dudash 1996) and between seasons (Silvertown 1980; Jensen 1982; Curran & Leighton 2000). They may also shape the characteristics of seed dispersal syndromes involving wind (Casper 1988), ants (Ruhren & Dudash 1996), birds (Traveset 1994; Hulme 1997) and mammals (Traveset 1990; Benkman 1995).

A variety of attributes distinguish granivory from other forms of herbivory (see Chapters 3 and 4) and shape the interaction between plants and granivores:

Not all plants produce seeds. Many plant taxa produce spores rather than seeds (e.g. algae, bryophytes, lycopods, ferns). Sporivory (spore-feeding by animals) is less well documented than granivory but the available evidence suggests that it occurs infrequently. For example, of over

Table 5.1 The percentage of seed predation found in selected field studies which have separately quantified pre- and post-dispersal seed removal.

		Pre-dispersal losses		Post-dispersal losses		
Species	Ecosystem	%	Agent	%	Agent	Author
Cirsium canescens	Temperate grassland	51.8	Tephritid flies	0–99.5	Rodents	Louda et al. (1990)
Cirsium vulgare	Temperate grassland	3–17	Moth larvae	21–66	Rodent	Klinkhammer et al. (1988)
Quercus robur	Deciduous forest	25–80	Knopper galls/weevils	100	Rodents	Crawley & Long (1995)
Fagus crenata	Deciduous forest	36.9	Insects	12.3	Vertebrates	Homma et al. (1999)
Fagus sylvatica	Deciduous forest	3–17	Moth larvae	5–12	Mammals	Nilsson & Wastljung (1987)
Fraxinus excelsior	Deciduous forest	15–75	Moth larvae	25–75	Rodents	Gardner (1977)
Pinus sylvestris	Coniferous forest	80	Crossbills	67–96	Rodents	Castro et al. (1999)
Pistacia terebinthus	Mediterranean shrubland	71.7	Birds/wasps	85	Rodents/ants	Traveset (1994)
Lobularia maritima	Mediterranean shrubland	80–99	*Messor* ants	40–95	*Messor* ants	Picó & Retana (2000)
Leptospermum juniperinum	Sclerophyllous woodland	44	Beetles, wasps, moths	90	Ants	Andersen (1989)
Leptospermum myrsinoides	Heathland	64	Beetles, wasps, moths	90	Ants	Andersen (1989)
Acacia farnesiana	Deciduous tropical forest	0–37.8	Bruchid beetles	35.2–66	Rodents	Traveset (1990; 1991)
Astrocaryum mexicanum	Deciduous tropical forest	50	Squirrels	90	Mice	Sarukhan (1986)
Dryobalanops lanceolata	Malaysian rain forest	32.5	Weevils	9	Vertebrates	Itoh et al. (1995)
Tachigalia versicolor	Panamanian rain forest	20	Bruchids	43	Rodents	Forget et al. (1999)
Cecropia shreberiana	Puerto Rican rain forest	6	Vertebrates, insects	9	Ants	Myster (1997)
Cecropia polyphlebia	Costa Rican rain forest	12	Vertebrates, insects	2	Ants	Myster (1997)

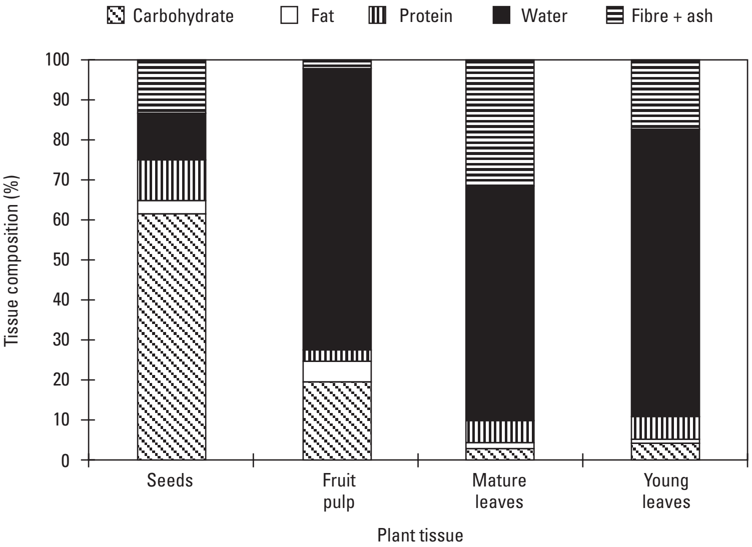


Figure 5.1 Comparison between the average composition of seeds and other plant parts. Seeds provide a concentrated nutrient source that is particularly rich in carbohydrates. (Data from Jordano 1992.)

400 species of arthropod herbivores that feed on ferns, fewer than 10 are sporivores (Balick et al. 1978). Thus, in contrast to other forms of herbivory, granivory is particular to seed plants (e.g. trees, shrubs, herbaceous plants and grasses) that nonetheless comprise the dominant elements of present-day terrestrial vegetation.

Seeds are rich in energy and nutrients. A major biological advantage of seeds over spores is that they provision the developing embryo with nutriment. The food-storage organs may be found within the embryo (e.g. cotyledons) or, in many plant species, elsewhere within the seed (e.g. endosperm). Compared to other plant tissues seeds are nutrient-rich, partly because they contain relatively little water, thus nutrients are concentrated in seed tissues (Fig. 5.1). However, even on a dry-weight basis, seeds generally have a higher energy content than roots, stems or leaves. Not surprisingly, seeds are highly sought after and this may explain why granivory is more widespread than sporivory.

Seeds vary considerably in size and shape. Plant species differ in the extent to which they provision the embryo with resources; this is reflected in the enormous range of seed sizes found in nature. The range encompasses the tiny seeds of orchids (e.g. *Goodyera repens*), weighing approximately 0.001 mg, to the seeds of the double coconut (*Loidocea maldivica*) that often weigh over 20 kg. Even within a single plant community, the sizes of seeds of different plant species may vary across several orders of magnitude, even within a single life-form. For example, in oak–birch woodlands of north-west Europe, tree-seed size varies from 0.2 mg for the seeds of silver birch (*Betula pubescens*) to 6.44 g for the acorns of pedunculate oak (*Quercus robur*). Seeds represent a particularly diverse resource base for potential granivores.

Seeds are frequently well defended physically and/or chemically. Due to their high nutritional value, seeds often require a greater investment in anti-herbivore defence than vegetative tissue (Janzen 1971). Seeds of many plant species are contained in dry fruit that dehisce and liberate seeds when ripe (e.g. capsules, cones, follicles, legumes) or are indehiscent (e.g. nuts). These structures often form the first line of defence against granivores, and the fruit wall may be thick and woody and/or covered in spines, bristles or irritant hairs (Fig. 5.2). To crush hickory nuts (*Carya ovata*) requires a force of over 75 kg, which takes over 30 hours of processing in the gizzards of turkeys (Stiles 1989). In contrast, fleshy fruit often rely on a fibrous seed-coat to physically protect seeds (Fig. 5.3). However, plant species differ in their allocation to physical defences, which may account for as little as 5% of seed mass in spindle (*Euonymus europaeus*) to almost 90% in hawthorn (*Crataegus monogyna*). Finally, the endosperm of some seeds may be so hard that only the most deter-

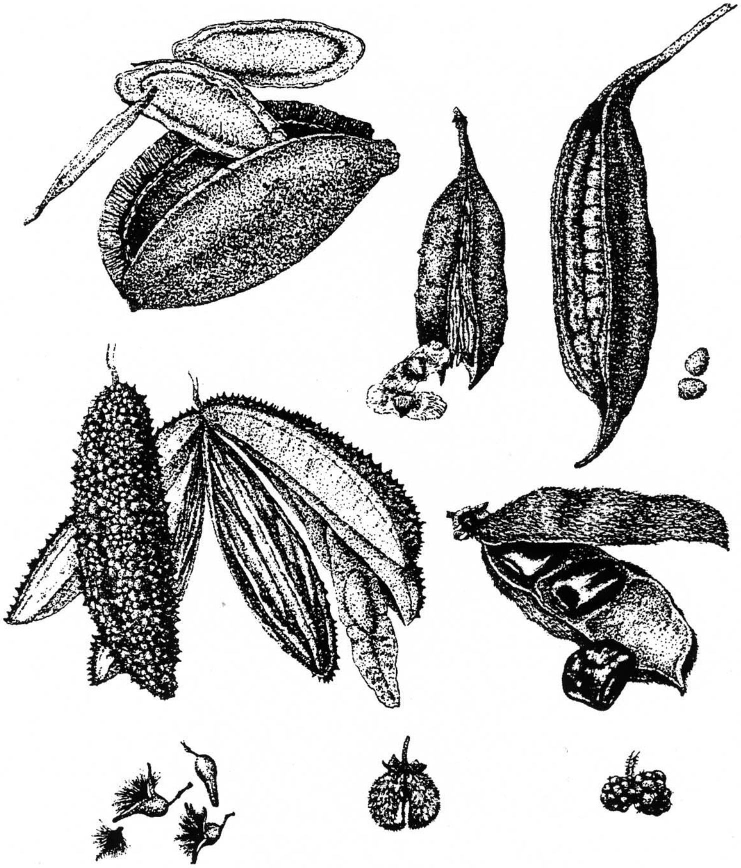


Figure 5.2 Examples of protective fruit structures from lowland tropical rainforest in Australia (redrawn from Grubb et al. 1998): top row (left to right) *Cardwellia sublimis* (Proteaceae) woody follicle, *Neosepicaea jucunda* (Bignoniaceae) woody capsule, *Brachychiton acerifolius* (Sterculiaceae) woody follicle with irritant hairs on seeds; second row *Flindersia bourjotiana* (Rutaceae) spiny woody capsule, *Mucuna gigantea* (Fabaceae) woody legume covered by irritant hairs; third row *Doryphora aromatica* (Monimiaceae) woody receptacular tissue, *Lethedon setosa* (Thymelaeaceae) woody capsule covered by irritant hairs, *Dendrocnide moroides* (Urticaceae) berries with stinging hairs.

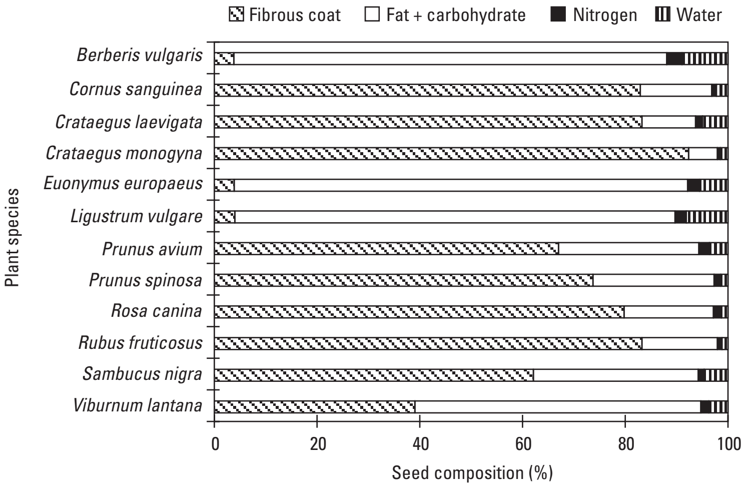


Figure 5.3 Differences in the composition of the seeds of twelve fleshy-fruited shrub species. The seeds differ considerably in their allocation to physical structures such as fibrous seed coats. (Data from Kollmann et al. 1998.)

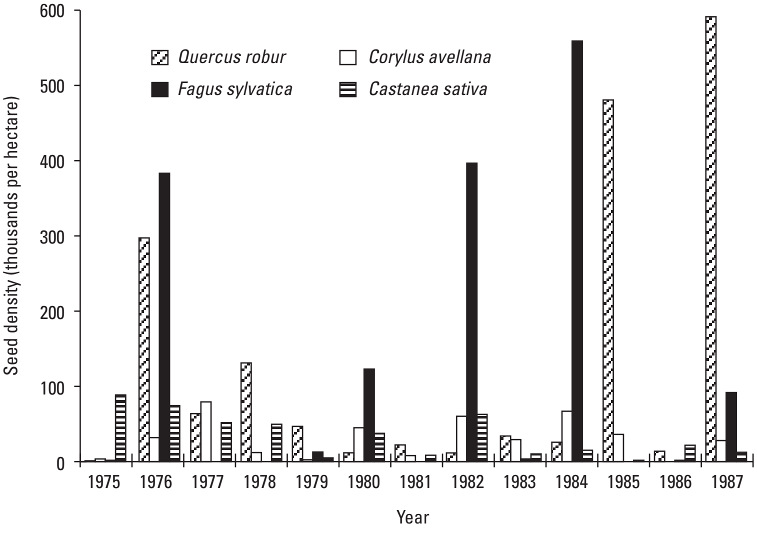


Figure 5.4 Variation over 13 years in the sizes of seed crops of four tree species within a single deciduous woodland. (Data from Gurnell 1993.)

mined granivore attempts to feed on them; such is the case of the Tagua palm nut (*Phytelephas macrocarpa*), the endosperm of which is tough enough to be used commercially as an ivory substitute. The absence of marked physical defence mechanisms in the seeds of some plant species may reflect their reliance on chemical defence. Likewise, seeds that invest in physical defence may often have low levels of toxins. Seeds are sources of some of the most toxic natural products known to humans and the secondary chemicals in seeds present formidable challenges to granivores (Bell 1978; Harborne 1993). A broad spectrum of toxins and anti-feedants occur in seeds, including non-protein amino acids (which disrupt protein synthesis), cyanogenic glycosides (which release cyanide following damage), protease and amylase inhibitors (which impede enzyme function) and phytohaemaglutinins (which reduce nutrient absorption). However, seed chemical defences can only be assessed with reference to specific target organisms since a secondary chemical may not be equally toxic to all granivores. For example, the seeds of the jojoba shrub (*Simmondsia chinensis*) contain a cyanogenic glycoside, simmondsin, that is detoxified by one species of pocket mouse (*Perognathus baileyi*) but not by a congeneric species (*P. penicillatus*) that shares the same desert habitat (Sherbrooke 1976).

Seed abundance is variable in space and time. While many seeds possess physical and chemical defences, plants may also manipulate the quantity of seeds in response to granivory. Records of the seed crops of four temperate tree species over 13 years reveal marked asynchronous variation in seed production (Fig. 5.4). In certain years (1981, 1986), few seeds were produced by any trees, whereas on five occasions (1976, 1982, 1984, 1985, 1987) one or more species produced particularly large seed crops. For the two most variable species, pedunculate oak (*Quercus robur*) and beech (*Fagus sylvatica*), seed density varied by over three orders of magnitude between successive years. Furthermore, in addition to marked differences in absolute seed densities among years, the relative abundance of the four species differed in each of the 13 years. Thus a common plant species may, at times, be rare to a granivore.

Seeds directly influence plant populations in several ways. These include: (i) the colonization of new areas at a distance from the parent population; (ii) the local increase in populations; (iii) the replacement of individuals that die in a population; and (iv) survival during unfavourable periods for plant growth. Since granivory often leads to the eradication of individuals in a plant population, whereas most forms of herbivory often result in only the partial removal of tissue from individual plants, we expect granivores to play an especially important role in plant demography and impose strong selection pressures on plants.

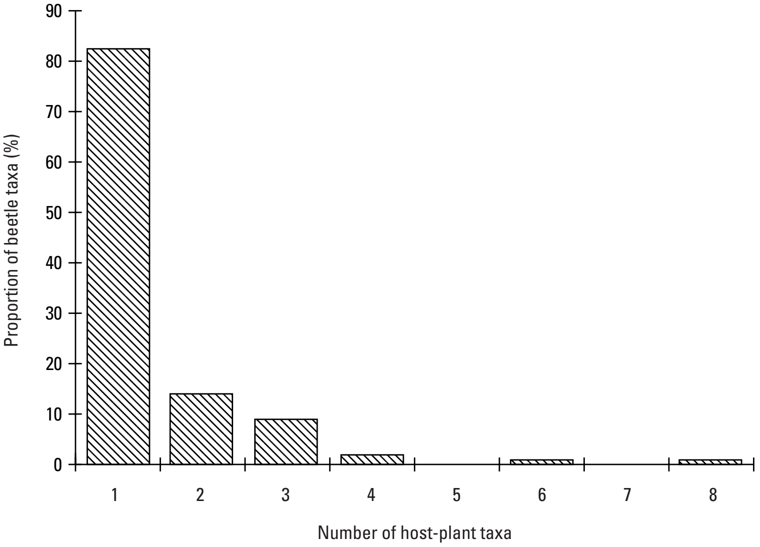


Figure 5.5 The distribution of taxa of beetle seed-predators (families Bruchidae, Curculionidae and Cerambycidae) among 975 species of dicotyledonous plants in a Costa Rican tropical deciduous forest. (From Janzen 1980b.)

5.2 The characteristics of granivory

5.2.1 The different guilds of granivores: their dependence on seeds and their impact

Most pre-dispersal seed-predators are specialists (Janzen 1971; Crawley 1992; Fig. 5.5). Seed-predators can specialize because seeds are clumped and conspicuous prior to dispersal. For the same reason selection for increased seed defences is especially strong, which leads to enhanced defences that exclude less specialized seed-predators. Plants may even respond directly to pre-dispersal seed predation by compensating for seed loss, modifying phenology to avoid predators, or by the induction of secondary chemicals to inhibit further damage (Harborne 1993). The result is the exclusion of generalists, which further favours specialists.

Pre-dispersal seed-predators not only require countermeasures to seed defences, they must also time their life cycle to the often ephemeral availability of seeds on one or a few species of plants. As a consequence, most pre-dispersal seed-predators are insects, especially in the orders Hemiptera, Lepidoptera, Coleoptera and Hymenoptera, that have life cycles synchronized with the availability of seeds from just one or a few closely related species of plants (e.g. Huignard et al. 1990). Birds and mammals lack such flexibility, so they usually consume seeds from a variety of plants and rely on seeds for only a fraction of their annual cycle (e.g. Hulme 1993). The most specialized birds (e.g. nutcrackers and crossbills) and mammals (e.g. tree squirrels and heteromyid rodents) either move between areas or store seeds in caches to ensure a more continuous supply. Such behavioural opportunism, however, may have little effect on the extent to which a granivore is morphologically specialized. For example, crossbills regularly forage on seeds of several species of conifers during a year. Yet each of at least five different 'species' of red crossbills (*Loxia curvirostra* complex; i.e. Plate 5.1, facing p. 84) in North America has a bill morphology that approximates the optimum for foraging on the conifer species each crossbill relies upon in late winter (Benkman 1993; Benkman et al. 2001).

A great variety of animals are post-dispersal seed-predators (Crawley 1992; Hulme 1998a): these include insects (especially ants and beetles), molluscs, crabs, fish, birds and mammals (especially rodents). In contrast to pre-dispersal seed-predators, post-dispersal seed-predators feed on a diverse and spatially heterogeneous resource that requires generalist feeding habits. Not only is the assemblage of post-dispersal seed-predators diverse, but its composition varies considerably among different ecosystems. In temperate woodlands, the majority of post-dispersal seed removal is attributable to one or two species of small mammals, whereas in the humid tropics,

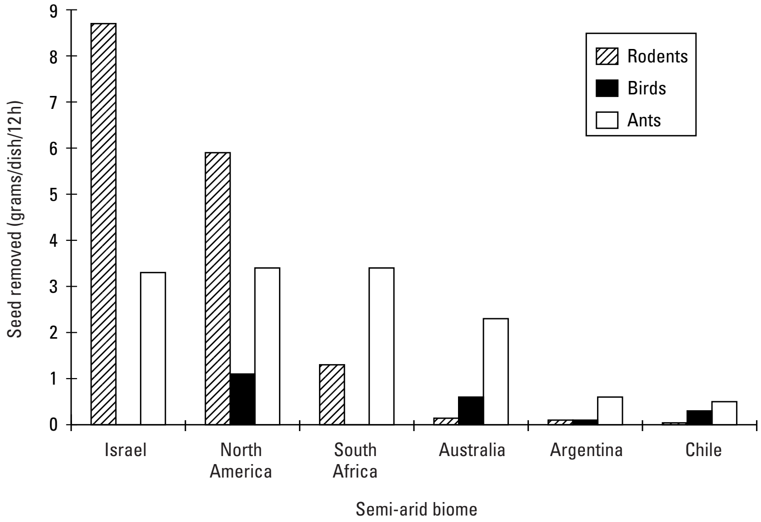


Figure 5.6 Intercontinental comparisons of post-dispersal seed removal by three guilds of post-dispersal seed-predators in semi-arid ecosystems. Data are plotted in order of overall intensity of seed removal and are adapted from sources cited by Hulme (1998b).

important seed-predators include numerous invertebrate taxa (e.g. bruchid beetles, moths and ants) as well a several species of small and large mammals (e.g. in the neotropics: agoutis, pacas, peccaries and tapirs). In arid and semi-arid ecosystems ants are significant post-dispersal seed-predators, whereas in temperate ecosystems they act mainly as seed-dispersers (see Chapter 8). However, these generalizations regarding ecosystem trends should be interpreted with caution. Experimental studies in semi-arid ecosystems reveal marked intercontinental differences in both the overall magnitude of post-dispersal seed predation and the relative importance of different guilds of seed-predator (Fig. 5.6). Rodents play a major role in Northern Hemisphere deserts whereas ants appear more important in the Southern Hemisphere, where overall rates of post-dispersal seed predation are considerably lower. Continental variation in both pre- and post-dispersal predation of *Rhizophora* propagules also reflects differences in the composition of the granivore assemblage in mangrove forests (Farnsworth & Ellison 1997). Further studies are required to assess how granivory varies across a particular plant species' geographical range.

5.2.2 The determinants of seed predation

Pre-dispersal seed-predators are initially attracted to more general features that can be easily detected by vision or olfaction. From a distance plant size and silhouette are probably important, and when closer, fruit size, structure (Mattson 1986; Brody & Waser 1995) and chemistry (e.g. Huignard et al. 1990) and abiotic factors play a role. Pre-dispersal seed-predators are also influenced by the size and maturity of the seed crop (Christensen et al. 1991). The importance of individual seed and fruit characteristics relative to other plant traits in seed and fruit choice is likely to vary depending on when choices are made. At one extreme, individual seed and fruit characteristics might have no direct impact on seed or fruit choice. This is likely when invertebrates oviposit on branches, foliage or buds before the fruits begin to develop (e.g. Brody & Waser 1995); although fruit and seed characteristics could indirectly affect oviposition if successive generations of insects remain near the host plant. In this situation, granivores discriminate between plant species but might not discriminate between individual fruits or even between plants within a species (e.g. Mattson 1986). The impact of a seed-predator is therefore influenced by how well it can deal with the plant's defences (e.g. Zangerl & Berenbaum 1997). At the other extreme, repeated use of mature seeds by many birds and mammals is based on seed characteristics and the ease with which seeds can be harvested and consumed relative to seeds on other plants (e.g. Smith 1970; Benkman 1987).

Animals are expected to forage in a manner that maximizes fitness. Consistent with this, at least some insects choose oviposition sites so as to maximize the growth and survival of their offspring (e.g. Brody & Waser 1995; Moegenburg 1996). For granivores foraging on multiple seeds, the benefits of feeding should be maximized per unit time spent foraging, while minimizing the costs. The benefits relate primarily to the nutritional quality of the seed, which is often equated with seed-energy content. Costs may be related to seed characteristics, such as the energy expended when handling seeds (e.g. penetrating a tough seed coat) and transporting seeds to nests for later consumption (e.g. heavier seeds require more energy to transport them). When energy content and handling time have been measured, at least some ants, birds and mammals have been found to harvest multiple seeds or fruits in a manner consistent with maximizing net energy gain (e.g. Benkman 1987). Moreover, energy intake rates are correlated with measures of fitness in one species of granivore (Lemon 1991).

Seed choice, however, is at times undoubtedly influenced by a variety of other factors. The value of certain seeds may also correspond to concentrations of particular minerals and/or amino acids if these are deficient in the granivore's diet, or concentrations of soluble carbohydrates if water is scarce (Hulme 1993). Costs may be related to digesting or detoxifying seed contents, which will vary among granivores. The constraint of toxins can in theory be incorporated into diet models, but these models have not been tested for granivores, although it is very clear that toxins affect their diets (e.g. Huignard et al. 1990; Hulme 1993). For example, ground-foraging finches worldwide feed mostly on grass seeds (Poaceae), which lack alkaloids, but avoid similar-sized seeds from other plant families (Leguminosae, Malvaceae, Convolvulaceae) commonly having alkaloids in their seeds (Schluter & Repasky 1991). Likewise, birds avoid grass seeds infested with fungal endophytes that produce alkaloids (Madej & Clay 1991). Other variables that will affect seed choice include the distribution (e.g. aggregated or dispersed) and detectability of seeds (e.g. Hulme 1998b), the risk of predation and the abundance of competitors (Mitchell 1977; De Steven 1981). Thus we should expect the interaction between seed predators and seeds to be shaped not only by seed traits (mass, shape, energy content, toxicity) and the characteristics of granivores (body size, susceptibility to toxins, olfactory acuity, hunger), but also by seed distribution, soil texture and habitat characteristics (Myster & Pickett 1993; Hulme 1993, 1994a). Such variation presumably helps to account for the wide differences among plant species in rates of seed predation, even within the same habitat (Table 5.1).

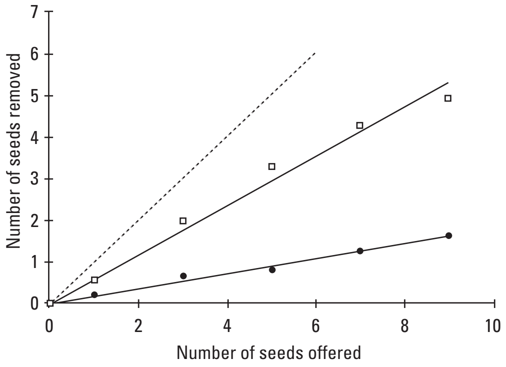
Given the numerous variables influencing seed predation, we might not expect to find that large seeds, for example, are preyed on more frequently than small seeds. However, the premise that granivores prefer large rather than small seeds is widespread in the ecological literature (Crawley 1992; Hulme 1996b). While there is some support for a positive relationship between seed size and predation rate for rodents (e.g. Reader 1993) and perhaps bruchid beetles (Szentesi & Jermy 1995), many studies have found no such relationship (Janzen 1969; Myster & Pickett 1993; Hulme 1994a; Kollmann et al. 1998). Therefore while large seeds may be nutrient-rich they may also possess proportionally greater investment in physical and/or chemical defence (Grubb et al. 1998) or be too heavy for small granivores such as harvester ants to manipulate (Brown & Heske 1990).

5.2.3 Density and dependence on frequency

Granivores may respond positively, negatively or not at all to changes in seed density (Box 5.1). Many pre-dispersal seed-predators have limited abilities to increase seed predation when seed crops increase between years. Consequently, the percentage of the seed crop eaten either varies little with seed-crop size (density-independence; e.g. De Steven 1981), or more often decreases with increases in seed-crop size (inverse density-dependence; e.g. Turgeon et al. 1994). For specialist insect seed-predators especially, the percentage of predation often depends on the relative size differences between successive seed crops (e.g. De Steven 1983). For example, a greater percentage of a conifer seed crop is destroyed if the previous year's seed crop is large, so that insect populations can increase, than when the previous seed crop is small (Turgeon et al. 1994). One result is that the percentage of the seed crop damaged in one year is often positively correlated with the size of the seed crop in the preceding year. Indeed, when annual seed production is more consistent, a higher proportion of the seed crop is eaten (Mattson 1986). Inverse density-dependence can also arise because of social interactions between granivores (Pulliam & Dunning 1987). At low seed abundance sparrows consume most of the seeds and are limited by seed densities, but during years when seed densities are high only a small fraction of the seeds is consumed. Social interactions apparently limit the density of sparrows settling on their wintering grounds.

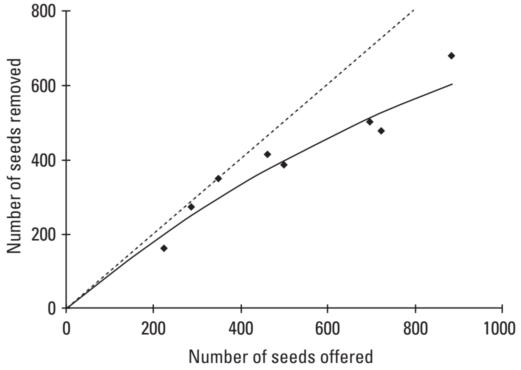
Box 5.1 Forms of response to seed density in granivory

(1) Density-independent seed predation



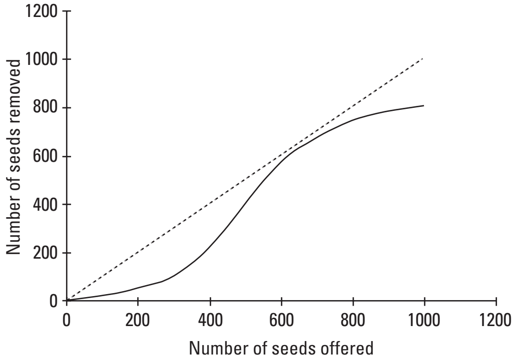
If granivores remove a constant proportion of seeds irrespective of seed density then a linear relationship between seed density and the number of seeds eaten per granivore per unit time is expected. Woodland rodents feeding on low densities of *Fraxinus excelsior* (•) and *Ulmus glabra* (□) seeds removed almost all seeds that they encountered but they encountered seeds only in a proportion of all available microhabitats. (Adapted from Hulme & Hunt 1999.)

(2) Inverse density-dependent seed predation



A declining proportion of available seeds are consumed as seed density increases, which produces an asymptotic curve, with a limit to the number of seeds eaten per granivore perhaps set by gut capacity, tolerance of seed toxins, handling time or intraspecific interference. Over an entire dry season, harvester ants (*Meranoplus* spp.) removed proportionally fewer *Sorghum intrans* seeds in sites where seed densities were high. (Adapted from Watkinson et al. 1989.)

(3) Direct density-dependent seed predation



At low seed densities the proportion of seed consumed increases with increasing seed density until limits similar to those described in (2) occur, resulting in inverse density-dependence which leads to a sigmoid relationship. Most studies that have explicitly examined the effect of seed density on rates of seed removal have examined only two different seed densities and thus no published examples of sigmoid relationships are known.

The level of seed predation by generalist seed-predators or specialist seed-predators that are highly mobile or can complete several generations while feeding on a single crop is less dependent on previous seed crops. As a consequence, the percentage of the seed crop they consume often increases with increasing seed-crop sizes (direct density-dependence; Box 5.1, Fig. 3). Larger seed crops provide greater rewards and are thus more likely to attract seed predators. For example, large conifer cone crops have more seeds per cone, which results in higher feeding rates for crossbills for a greater part of the year (Benkman 1987). Because crossbills do not stay and breed when feeding rates are low, disproportionately more crossbills are attracted to and breed longer when cone crops are large than when they are small (Benkman 1987) and as a result harvest seeds from a greater percentage of the cones.

Generalist post-dispersal seed-predators may also respond to changes in seed density (Hulme 1993; Kunin 1994). For rodents, density-dependence is most commonly found for small seeds (e.g. Casper 1988; Hulme 1994a) whereas removal of relatively large seeds is often density-independent (e.g. Hulme 1996a, 1997). However, the influence of seed density on seed removal is not only a function of seed characteristics, but is also mediated by habitat characteristics, possibly related to local food abundance (Hulme 1993, 1994a).

The availability of alternative food sources may increase seed predation by sustaining granivore populations during periods of food shortage. For example, Douglas fir (*Pseudotsuga menziesii*) suffers greater seed predation by pine squirrels (*Tamiasciurus*) when they can rely on lodgepole pine (*Pinus contorta*) seeds during years that Douglas fir produces few seeds (Smith 1970). Likewise, insect seed-predators that rely on other plant parts during seed failures (e.g. conifer seed-predators that feed or develop on foliage when conifer seeds are unavailable) are less affected by fluctuations in seed crops (Turgeon et al. 1994). As for many specialist insect seed-predators, the percentage of the seed crop eaten by highly mobile specialists is probably dependent on the size differences between successive seed crops but on a larger geographical scale.

On the other hand, alternative food sources may reduce seed predation if these foods are highly preferred or simply more common. Polyphagous granivores may respond not only to the absolute abundance of seeds of a particular plant species but also to its relative abundance in relation to co-occurring seeds of other plant species (Greenwood 1985). Even if the density of seeds of a particular plant species is constant within a habitat, granivores may view the seeds as being either common or rare, depending on the relative abundance of seeds of other plant species. Frequency-dependent foraging may lead to a greater proportion of seeds being taken when the species is common and a smaller proportion when rare (pro-apostatic selection) or alternatively seeds may be preyed upon proportionally more when rare than when common (anti-apostatic selection). Although granivore foraging might be expected to be frequency-dependent (Greenwood 1985) the limited data available suggest that neither ants (Kunin 1994) nor rodents (Hulme & Hunt 1999) respond to changes in the frequency of different seeds. Evidence of frequency-dependent seed predation is limited to selection at the fruit level. Rodents, for example, are more likely to miss seeds in multi-seeded *Scheelea* palm nuts when multi-seeded nuts are rare than when they are common (Bradford & Smith 1977). Seed predation by rodents, therefore, favours a low frequency of multi-seeded nuts, even when predation by bruchids, which usually attack just one seed per nut, is high. Similarly, Mitchell (1977) suggests that frequency-dependent selection by mammals on *Cercidium* pods is responsible for the low frequency of multi-seeded pods.

5.2.4 Spatial and temporal heterogeneity

Seed predation varies across a hierarchy of spatial scales, including along topographic gradients and across a species' range, between habitats (e.g. woodland vs. grassland), among microhabitats within a single habitat (forest understorey vs. treefall gap) and at an even finer scale within a single microhabitat (Hulme 1994a, 1998a; Hulme & Borelli 1999). As might be expected, spatial variation arises because some habitats, irrespective of seed availability, are more suitable for certain granivores than others or because seed defences might vary spatially (Hulme 1998a). Frequently, fewer seeds are removed from open microhabitats (Myster & Pickett 1993; Hulme 1994a, 1996a, 1997). This appears to occur when rodents are the principal granivores since their abundance tends to be positively associated with vegetative cover which provides them with a screen from avian predators (Hulme 1993). In contrast, harvester ants appear to forage preferentially in open areas and avoid dense vegetation (Hulme 1997). Similarly, variation in granivory among habitats has also been attributed to differences in vegetation cover (Kollmann et al. 1998; Hulme & Borelli 1999). Seed-

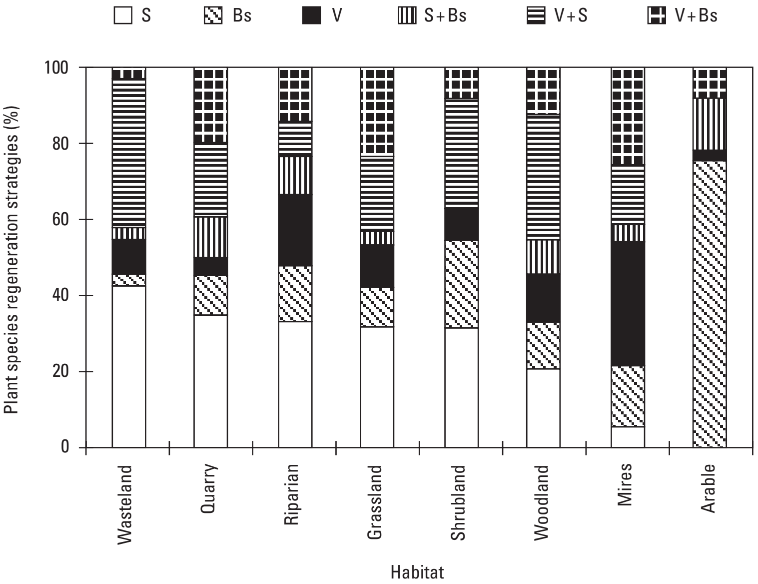


Figure 5.7 Distribution of major regenerative strategies of plant species found in the principal habitats of the Sheffield region (UK). Data and nomenclature are drawn from Hodgson et al. (1994). Key: V, regeneration by vegetative spread; Bs, regeneration via a persistent buried seed bank; S, seasonal regeneration by seed.

predators may therefore significantly modify the seed shadows of plants, both within and between habitats. We suspect that spatial variation in seed predation is widespread, and that the idiosyncrasies of the particular seed-predators and plants will play a prominent role in determining the patterns of variation.

Seed predation may vary both within and between years (Hulme 1994a, 1998a). In a study of predation on seeds of 12 species of fleshy-fruited shrubs, rates of seed removal by rodents were consistent in two different years and showed a similar seasonal trend with removal highest in summer and least in winter and spring (Kollmann et al. 1998). Temporal variation in granivory of a particular plant species may result from changes in the abundance of its seed (e.g. Gardner 1977; Nilsson & Wästljung 1987), as well as changes in other food resources (Hulme 1993) and/or in granivore densities (Hulme 1994a, 1997).

5.3 Demographic implications of seed predation

5.3.1 When is seed predation important in plant population dynamics?

The role of seed-predators in the dynamics of plant populations has received detailed attention (Andersen 1989; Crawley 1992; Hulme 1998a). Seed predation may play only a minor role in the demography of plants if: (1) plants regenerate primarily by vegetative means; (2) seed losses to predators are buffered by the presence of a large persistent seed bank; (3) seed predators are satiated by large seed crops; (4) regeneration is microsite-limited rather than seed-limited and/or (5) granivore densities are limited by factors other than seed density (e.g. predation or parasitism) such that they cannot fully exploit seed resources.

Three major, though not mutually exclusive, regenerative strategies have been identified for flowering plants (Fig. 5.7): vegetative expansion through the formation of persistent rhizomes, stolons or suckers, and regeneration by seeds which either do or don't form a persistent bank of viable but dormant seeds in the soil. In all but two of the dominant habitats of northern England, species that reproduce exclusively by short-lived seeds are better represented than species that rely exclusively on vegetative reproduction or regeneration from a persistent soil seed bank. Even among those plant species that adopt more than one regenerative strategy, species relying to some extent on non-persistent seeds are more common than those that don't. For these species, regeneration by seed is often as or more important than vegetative reproduction or regeneration from a seed bank (Turnbull et al. 2000). It is evident that the importance of granivory will vary among

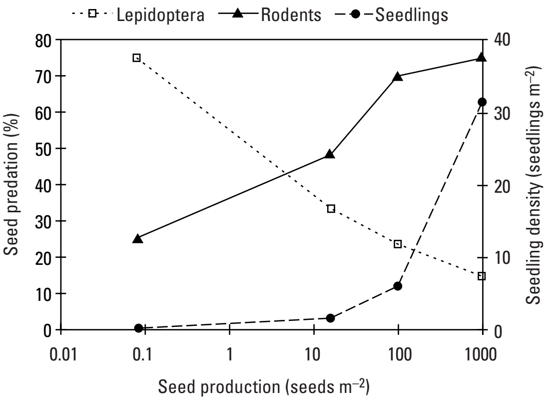


Figure 5.8 The influence of ash (*Fraxinus excelsior*) seed-crop size on seedling densities in relation to the levels of pre-dispersal seed predation by a specialist moth (*Pseudargyrotoza conwagana*) and post-dispersal seed predation by generalist rodents. (Data from Gardner 1977.)

different habitats and among species within a single habitat. Although these trends can only be taken as being representative of the flora of north-west Europe, the data suggest many plant species may potentially be influenced by seed predation.

Through the synchronous production of large seed crops at irregular time intervals (often described as masting; Fig. 5.4) plants are thought to satiate seed-predators and enhance their regenerative capacity (Silvertown 1980). The seed production of most polycarpic woody plants varies annually, with most seed crops either large or small rather than intermediate in size (Herrera et al. 1998). Large, irregular seed crops (masts) are probably more successful at limiting the impacts of specialist pre-dispersal seed-predators than generalist post-dispersal seed predators (Gardner 1977; De Steven 1983; Nilsson & Wästljung 1987; Crawley & Long 1995). Vertebrates, however, are often satiated when there is community-wide synchrony among plant species (Itoh et al. 1995; Curran & Leighton 2000) or when the plant community is dominated by one or a few species (Nilsson & Wästljung 1987; Homma et al. 1999). For example, the irregular seed crops produced by ash (*Fraxinus excelsior*) reduce the proportion of seed destroyed by invertebrates in mast years whereas, in contrast, the proportion consumed by rodents was actually higher in mast years (Fig. 5.8). This reflects the generalist feeding habit of rodents which enables them to persist in non-mast years by feeding on seeds of other species (Fig. 5.4). In years of abundant food their numbers increase (Jensen 1982) and they also have the ability to exploit supra-abundant food supplies through storing food in caches (Vander Wall 1990). Perhaps the high frequency of supra-annual reproductive synchrony in New Zealand is in response to both the presence of specialist insect seed-predators and the absence of generalist seed-predators like rodents (Kelly 1994).

Densities of seedlings are often higher after mast years than non-mast years (Gardner 1977; Crawley & Long 1995; Itoh et al. 1995; Curran & Leighton 2000) since more seeds escape predation in mast years. Although the proportion of seeds destroyed by post-dispersal seed-predators remains little changed, overall more seeds escape predation in mast years. This is not the equivalent of stating that granivores have no effect during mast years, since the number of seedlings recruiting in the absence of predators is not known and could potentially be much greater. These findings for masting trees also suggest that recruitment is seed-limited for these species, since more seed production results in more seedlings (Fig. 5.8).

The extent to which plant populations are either microsite- or seed-limited is unclear because only a few field studies have simultaneously combined seed addition, disturbance and exclosure of seed predators in a factorial design (Reader 1993; Edwards & Crawley 1999). However, the few studies of plant establishment which also considered seed-predators suggest that the failure of many species to establish in dense vegetation may sometimes be due to higher rates of post-dispersal seed predation rather than to increased interference from established vegetation (Reader 1993; Edwards & Crawley 1999). These studies lend support to the view that the importance of seed limitation in communities of perennial plants may currently be underestimated (Turnbull et al. 2000). It can be argued that, to influence plant demography, seed-predators must reduce seed densities below the density of available microsites, thus reducing establishment (Crawley 1992). However, even when microsites are rare, seed predators play a pivotal role in mediating pre-emptive competition for microsites through differential mortality of seeds of various species (Brown & Heske 1990; Edwards & Crawley 1999). In microsites where seed predation is intense (e.g. beneath nurse plants), predators may markedly affect establishment probabilities even when these microsites are limiting (Hulme 1996a).

If the population size of granivores is limited by seed abundance, then, potentially, granivores may limit seed populations and pose a strong selective force on plants. Alternatively, if predators limit the size of granivore populations to a level sufficient to restrict impacts on seed populations, then seed predation may play a minor role in plant demography. A variety of insect (Janzen 1969; De Steven 1983; Andersen 1989; Turgeon et al. 1994; Gómez & García 1997), mammalian (Gurnell 1993; Hulme 1993) and avian (Grant 1986; Schluter & Repasky 1991) granivores appear to be food- rather than predator-limited. However, in other cases granivores are predator-limited or jointly limited by predators and seeds. For example, Schluter and Repasky (1991) found evidence that ground-feeding finches in Africa and North and South America were limited jointly by predators and seed abundance; however, in the Galápagos, where predators are rare, Darwin's finches are food-limited. Janzen (1975) has argued that parasitoids on bruchids are rare in the tropics because it is difficult for a parasitoid to locate and utilize seed-predators that are so specialized. In temperate regions, however, parasitoids might often limit insect seed predators. For example, at high elevation in the Sierra Nevada (Spain), Gómez and Zamora (1994) found that predation by weevils on the shrubby crucifer *Hormathophylla spinosa* doubles when parasitoids are excluded. Yet, in another study near the same location, parasites had little impact on seed predators (a moth and two species of weevils) of a different shrub species (Gómez & García 1997). It is impossible to generalize from so few studies since it is likely that the relative importance of food and predator limitation will vary in relation to the type of granivore (e.g. pre-dispersal specialist invertebrate vs. post-dispersal generalist vertebrate), if granivores lay their eggs on the surface of the fruit or inside (e.g. Mattson 1986), whether they feed on the ground or in the canopy (e.g. Benkman 1991) and the ecosystem (e.g. tropics vs. temperate). It should nevertheless be borne in mind that whether or not granivore populations are limited by predation, predators can influence the plant–herbivore interaction through mediating where and when granivores forage (Lima & Dill 1990).

5.3.2 How does granivory influence plant demography?

By altering the size and distribution of seed populations, granivores may directly influence plant populations in several ways.

5.3.2.1 The colonization of new areas at a distance from the parent population

When certain granivores (e.g. rodents, birds and ants) encounter a seed, rather than consuming it immediately, they may move it to another location where it may be stored (often buried) for consumption at a later time. The behaviour of storing food for later consumption is termed caching, and if recovery of seed stores (caches) is less than perfect, seeds may survive to germinate. Thus the overall effect on plant populations of certain vertebrate seed-feeders may in fact be positive, resulting in a particular form of seed dispersal (see Chapter 7: Box 7.1). In these instances, seed predation is the cost of reliable seed dispersal (Janzen 1971). Two types of caching behaviour are recognized: larder-hoarding, where seeds are placed in a single large store; and scatter-hoarding, where seeds are placed in several small caches (Vander Wall 1990). Successful seed dispersal is more likely through scatter-hoarding since seeds are buried in many shallow caches, distributed among a variety of microhabitats. The large number of caches often results in less than perfect seed recovery (Vander Wall 1990). In contrast, larder-hoards are often buried more deeply (frequently within animal burrows) and the single location makes recovery of seeds highly probable (Vander Wall 1990). Even where recovery is less than perfect, the depth of burial may prevent successful germination from larder-hoards. Moreover, larder-hoards are often repeatedly used from year to year and the disturbance resulting from burying and recovering seeds often kills seedlings. Marked taxonomic differences occur in the type of caching undertaken. Certain seed-feeding birds, e.g. jays and nutcrackers, generally scatter-hoard, whereas most granivorous mammals larder-hoard, with the important exceptions of tree squirrels (*Sciurus*), chipmunks and caviomorph rodents (Vander Wall 1990).

Detailed studies of cached seeds have shown the survival and germination from naturally scatter-hoarded seeds is low: 0.02% for *Oryzopsis hymenoides* (McAdoo et al. 1983); 0–2% for *Dipteryx panamensis* (Forget 1993); 0–4% for *Fagus sylvatica* (Jensen 1982); 5–8.5% for *Purshia tridentata* (Vander Wall 1994) and 0.75–10% for *Gustavia superba* (Forget 1992). Although survivorship is low, if sufficient numbers of seeds are cached, these low percentages may translate to significant numbers of seedlings. Few studies have monitored the subsequent survival of seedlings, and those that have record high seedling mortality (Forget 1993; Vander Wall 1994) suggesting that cache locations may not necessarily be suitable for establishment. It therefore remains unclear whether regeneration is higher in the presence of scatter-hoarding seed-feeders than in their absence. Nevertheless, caution must be applied when interpreting seed removal by scatter-hoarding vertebrates as seed predation, since although most seeds removed are consumed, a small fraction may be dispersed to suitable microsites (albeit at a remarkably high cost). However, this uncertainty as regards seed fate is greatest for large-seeded species, e.g. trees, for which most evidence of scatter-hoarding exists (Vander Wall 1990).

Granivores may also significantly reduce rates and distances of seed dispersal (Sallabanks & Courtney 1992). Certain vertebrate seed-dispersal agents may preferentially disperse seeds that have not suffered pre-dispersal seed predation by invertebrate granivores. Jays (Hubbard & McPherson 1997) and mice (Crawley 1992) reject weevilled seeds, although squirrels appear not to (Steele et al. 1996). Similarly, frugivores feeding on fleshy fruit may respond to cues such as fruit colour that indicate whether or not pre-dispersal seed predation has occurred (Sallabanks & Courtney 1992). Pre-dispersal seed-predators will often reduce the size of the seed crop available for dispersal. Fewer seeds on the plant means that fewer seeds will reach any particular microsite following dispersal, thus sites a long distance away from the parent plant are less likely to receive seeds. Furthermore, if seed dispersers respond positively to seed-crop size, they may visit significantly less frequently plants that have suffered pre-dispersal seed predation (Sallabanks & Courtney 1992).

Frugivores may disperse seeds to microsites that suffer high post-dispersal seed predation, e.g. beneath shrubs (Kollmann 1995; Hulme 1996a). Often the association between shrubs and regeneration is maintained even in the face of intense seed predation. This suggests that regeneration requirements other than the escape from seed predation probably determine the spatial distribution of regeneration, e.g. requirements for shade (Hulme 1996a, 1997). However, the prevalence of high rates of seed predation in many shrub microhabitats suggests that seed predators may exert a considerable influence on the regeneration of these species (Kollmann 1995).

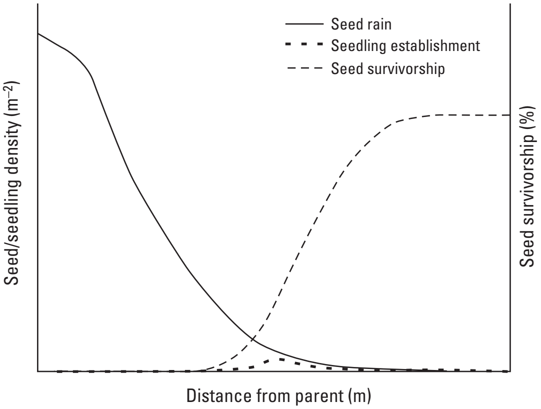


Figure 5.9 A schematic model of how distance- and/or density-responsive granivores might influence seed survival in relation to the distance from the parent plant and the consequences of granivory in terms of the distance at which peak seedling regeneration occurs. Granivores are hypothesized to prevent regeneration close to the parent plant, leading to seedling regeneration occurring farther away from the parent then if granivores were not present. (Adapted from Janzen 1970.)

5.3.2.2 The local increase in populations

Independently of the mode of seed dispersal, for many plant species most seeds fall close to the parent plant (Stiles 1989). If microsites do not vary as a function of distance from the parent plant (e.g. allelopathic and shading effects of the parent plant are negligible), then regeneration is likely to occur close to the parent. Both Janzen (1970) and Connell (1971) suggested that if granivores preferentially feed on seeds beneath the parent plant, either because they respond to the increased seed density (density-responsive granivores) or they are specialist granivores whose foraging is limited to within a certain distance of the parent (distance-responsive granivores), then maximum seedling regeneration occurs some distance from the parent (Fig. 5.9). Evidence for the Janzen–Connell hypothesis is equivocal, but suggests that invertebrate granivores are more likely to feed in a distance- and/or density-responsive manner than vertebrates (Hammond & Brown 1998). However, it is uncertain whether this spatial pattern in granivory is sufficient to limit local colonization since (a) vertebrate granivores may remove a greater proportion of seeds than invertebrates, irrespective of distance (Hulme 1998a); (b) even where a distance effect is found, it may be over such a short scale as to have negligible consequences on the spatial pattern of regeneration (Hubbell 1980); (c) microsites may also vary as a function of distance from the parent plant.

5.3.2.3 Survival during unfavourable periods for plant growth

Plants may survive unfavourable periods for growth as seeds within a soil seed bank. In almost all published studies, seed burial reduces post-dispersal seed predation (Hulme 1993). In addition, burial augments density effects by reducing losses of seeds at low density proportionally more than seeds at higher densities (Hulme 1994a). Comparisons between invertebrates and rodents show that only rodents significantly reduce buried seed populations (Hulme 1994a; Hulme & Borelli 1999). Exclusion of rodents from plant communities can therefore lead to less of a reduction of the seed bank (Kelly & Parker 1990). For buried seed, rodents locate and exploit large seeds more effectively than small seeds. It is perhaps no coincidence that the majority of plants that possess permanent seed banks (seeds remain viable but dormant in soil for >1 year) have small seeds and thus are relatively safe from predation, while most species with transient seed banks (seeds remain viable in soil for <1 year) tend to be relatively large-seeded (Hulme 1998b). Indirect support for this hypothesis is found in the arid zones of Australia where granivory by rodents, and therefore of buried seeds, is negligible (Fig. 5.10) and no relationship exists between seed-bank persistence and seed size (Leishman et al. 1995). Furthermore, and separate from any effect of seed size, rodents tend to remove a smaller proportion of buried seeds with persistent rather than transient seed banks (Fig. 5.10). Thus seeds with persistent seed banks apparently possess features than make them less easy to detect when buried. One such factor might be an impermeable seed coat that seals in any attractive odour a seed might have.

5.3.3 Seed-predators and plant species diversity

In addition to its impact on seed survival, dispersal, colonization and seed-bank persistence of seeds of particular plant species, granivory may also influence plant community structure. Granivores may prevent competitive exclusion among plant species within a particular plant community and hence enhance plant species diversity. This may occur through a number of different mechanisms (Hulme 1996b).

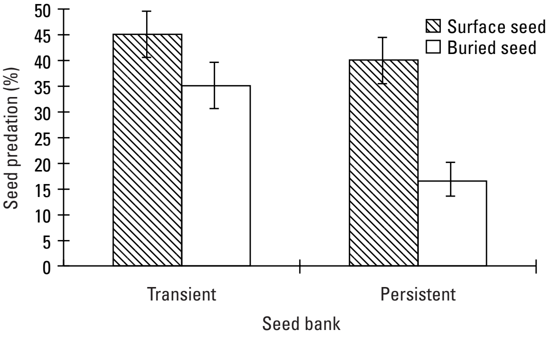


Figure 5.10 The relationship between the persistence of seeds within seed banks and seed predation by rodents on 19 species of grassland seeds either buried or placed on the soil surface. Seeds with persistent seed banks are proportionally less likely to be removed when buried than seeds with transient seed banks. (Data from Hulme 1998b.)

Trade-offs between granivory and plant competitive ability. A large seed facilitates establishment in the face of interference competition from established plants or other seedlings (Leishman et al. 1995). If large seeds are at a greater risk from predation (Section 5.2.2) and seeds compete for microsites, then granivores may permit less competitive species (e.g. those with smaller seeds) to establish. This tradeoff would act to promote species coexistence and may enhance species diversity.

Frequency-dependence. Pro-apostatic frequency-dependent foraging by seed-predators will select against the commonest seeds within a habitat (Section 5.2.3). This may facilitate the establishment of rare species and prevent any one plant species dominating the entire habitat. Frequency-dependence can therefore strongly stabilize the dynamics of granivory and may lead to greater permissible niche overlaps between plant species. But again, there is no evidence of such frequency-dependent foraging by granivores.

Spatially heterogeneous granivory. Different species of granivores exhibit different seed preferences (Section 5.2.2) and may forage in different microhabitats (Section 5.2.4). Spatial heterogeneity in granivory may lead to different plant species regenerating more successfully in some microhabitats than others. If maintained for a relatively long period of time with respect to the lifespan of plants, consistent spatial patterns in the location where plant species regenerate may promote plant species coexistence.

The Janzen-Connell spacing model. According to this model (Fig. 5.9) granivory may lead to greater survival of seeds at a distance from the parent plant if granivores feed in a distance- or density-responsive manner. This feeding behaviour would preferentially select against regeneration of offspring within a particular distance from parent plants and therefore lead to a more uniform distribution of conspecifics. Seeds of heterospecifics could survive within this distance since they would not be fed upon by specialist distance-responsive granivores and would occur at too low a density to elicit a response from density-responsive granivores. This spacing mechanism would act to prevent any one species from dominating the plant community and thus enable more plant species to coexist.

As has been discussed above in Sections 5.2.2 and 5.3.2 of this chapter, consistent experimental evidence for any one of these mechanisms is weak. Nevertheless, granivores do appear to influence the diversity of plant communities, particularly where they preferentially feed on large seeds. This has been demonstrated in the Chihuahuan Desert, where removal of rodent granivores led to an increase in large-seeded perennials and a subsequent reduction in plant species diversity (Brown & Heske 1990). In neotropical forest gaps, high rates of predation on the relatively large seeds of primary tree species facilitate colonization by smaller-seeded pioneer species (Schupp et al. 1989). Similarly, in temperate grasslands, seed-predators may maintain species diversity by limiting tree invasion and the rate of development of woodlands (Myster & Pickett 1993).

5.4 Evolutionary implications of seed predation

5.4.1 Natural selection and seed-predators

Seed-predators potentially affect plant evolution whenever they differentially depress seed production among plants in relation to variation in some heritable plant trait. Seed-predators commonly have this potential. They have an impact on seed production (Table 5.1), and seed predation usually varies in relation to seed and fruit traits (e.g. Smith 1970) that are often heritable (e.g. seed size (Leishman et al. 1995, but see also Silvertown 1989), seed chemistry (Zangerl & Berenbaum 1997; Berenbaum & Zangerl 1998) and fruit structure (Primack 1987)). Likewise, if certain heritable traits of a seed-predator affect its ability to exploit seeds and as a consequence affects its fitness, then seed-predators can be expected to evolve to increase their feeding efficiency. Variation between seed-predators affects both feeding abilities and fitness components (e.g. Grant & Grant 1995; Carroll et al. 1997). Moreover, traits affecting feeding ability are often heritable (e.g. detoxification capability (Berenbaum & Zangerl 1998), insect beak lengths (Carroll et al. 1997), and birds' bill size (Grant & Grant 1995)). Thus, we might expect the evolutionary interactions between seed-predators and plants to be dynamic. Well, the answer is both yes and no. In the rest of this section we would like to focus on the 'no'.

Many seemingly adaptive traits might not be heritable. For example, juniper titmice (*Baeolophus griseus*) feed on juniper (*Juniperus osteosperma*) seeds, but can distinguish empty from full seeds only after removing the surrounding pulp. As expected, titmice avoid trees with relatively high frequencies of empty seeds, which should favour trees that produce proportionately more empty seeds (Fuentes & Schupp 1998). However, the proportion of empty seeds might have very low heritability. Empty seeds are often frequent because fertilization in many gymnosperms and some angiosperms occurs well after pollination and the start of fruit development (Willson 1983). Thus, a high proportion of empty seeds might result from, for example, a high frequency of self-fertilization (e.g. Nilsson & Wästljung 1987). The benefits arising from increased numbers of empty seeds, therefore, are possibly fortuitous consequences of development and not the result of selection by seed predators (Fuentes & Schupp 1998). On the other hand, the continuing investment in the development of empty fruits so that fruits or empty seeds might act as decoys or deterrents (e.g. Fuentes & Schupp 1998) is more likely subject to selection.

Even if traits are heritable, evolutionary change can be limited when, for example, selection on seed-predators oscillates from year to year with changes in the availability of seeds (Grant & Grant 1995) or if tradeoffs exist. Tradeoffs are fundamental to life-history evolution, and tradeoffs between seed predation, dispersal and germination affect the evolution of seed and fruit characteristics (Janzen 1969; Primack 1987). For example, selection by parsnip webworms (*Depressaria pastinacella*) favours increases in two furanocoumarins, bergapten and sphondin, in seeds of wild parsnip (*Pastinaca sativa*). Apparently limiting, however, are the precursor molecules in the common biosynthetic pathways producing these two furanocoumarins. Thus, selection by webworms has led to an evolutionary stalemate because increases in bergapten result in decreases in sphondin and vice versa (Zangerl & Berenbaum 1997; Berenbaum & Zangerl 1998).

Perhaps the most evident tradeoff between seed predation and dispersal occurs for animal-dispersed seeds because protecting seeds from predators is often incompatible with enhancing the accessibility and attractiveness of seeds to dispersers. Thus, for example, fruit pulp might be less well protected because secondary chemicals deter not only seed-predators but also seed-dispersers (Janzen 1978 and Chapter 7 in this volume). This might explain why most seed defences of legumes seem to occur in the seeds rather than the pods even though most seed-predators oviposit on the pods (e.g. Johnson 1990). Likewise, a tradeoff between satiating seed predators and saturating mutualist seed-dispersers presumably causes endozoochorous woody plants to produce less variable seed crops than woody plants that are dispersed by wind or seed-predators (Herrera et al. 1998). If the tradeoffs are strong and seed predation great, selection by seed-predators might even cause plants to rely on dispersal by wind rather than by animals (Benkman 1995).

Because of tradeoffs the equilibrium level of defence depends on the strength of selection exerted by seed-predators. At least two general hypotheses might account for variation in the intensity of selection exerted by seed-predators on seed defences. First, seed-predators prefer larger seeds with higher concentrations of nutrients with a concomitant increase in the intensity of selection for seed defences (Grubb et al. 1998). (Seed preference studies (see Section 5.2.3) usually cannot address this because seed size is confounded with seed defences.) Consequently, plants with larger seeds or with, for example, higher concentrations of nitrogen in their seeds should invest more heavily in seed defences. A comparative study of 194 species of Australian rainforest plants supports this hypothesis (Grubb et al. 1998). Second, when seed crops fluctuate in size from year to year seeds may escape predation because of predator satiation (Section 5.3.1). The more seed crops vary from year to year the greater the proportion of seeds that potentially escape predation. Thus, plants whose seed crops fluctuate (and hold seeds for brief periods of time) tend to invest less in seed defences than plants that produce more consistent seed crops (Janzen 1969, 1971; Smith 1970). In the following sections we discuss various seed defences and counter-defences by seed-predators, and evaluate these hypotheses further.

5.4.2 Selection on physiological seed traits and counter-adaptations of animals

Some seeds are so toxic that all seed-predators avoid them, so why aren't more seeds this toxic? One explanation is that plants are confronted with a problem of how to simultaneously maximize protection and stored reserves within a restricted space. Evidence of this tradeoff is the narrow range of concentrations of toxins within a species (Bell 1978). Presumably plants producing lower concentrations of toxins are more susceptible to predation and those producing higher levels produce seedlings that are disadvantaged in competition with seedlings having greater reserves. A potential solution to such a constraint is to have toxins that can also act as storage products, like toxic lipids and non-protein amino acids that can be metabolized and translocated in the seedling (Harborne 1993). The capacity to serve as nourishment to a seedling may favour the use of, for example, less toxic non-protein amino acids over more toxic alkaloids (Bell 1978). Another solution is to have toxins that are effective at low dosages. Most toxins are usually in small concentrations (<5%) in the seed and some alkaloids, for example, can be lethal at concentrations as low as 0.1% (Harborne 1993). An alternative explanation limiting chemical defences is autotoxicity. Chemical defences that might be autotoxic (e.g. tannins, saponins), however, are usually compartmentalized in specialized cavities, often in the seed coat or fruit (Janzen 1978). Finally, defensive chemicals can be costly to the plant. Producing more toxic chemicals deters seed-predators but at the expense of producing fewer seeds (Zangerl & Berenbaum 1997).

Like many herbivores (see Chapters 3 and 4), numerous insect seed-predators have biochemical adaptations to deal with secondary compounds, including various detoxification and sequestration mechanisms. Many bruchids, for example, have the ability to avoid incorporating toxins during biosynthesis, and at least a few species can even detoxify and degrade the toxins and then use the by-products in their metabolism (Johnson 1990). However, the difficulties of dealing with more than a few different kinds of defensive compounds has favoured the evolution of specialization in seed-predators (Johnson 1990) and helps explain why a large fraction of seed-predators are specialists (Fig. 5.5; Janzen 1980b). In contrast to insects, few if any species of bird or mammal are highly specialized on one or a few highly toxic seeds. Although some rodents can tolerate relatively toxic seeds (Sherbrooke 1976), most birds and mammals avoid toxic seeds (e.g. those with alkaloids) or use them sparingly (Harborne 1993; Hulme 1993). Many birds and mammals eat tannin-rich acorns, and several species at least can subsist on a diet consisting exclusively of acorns (Gurnell 1993). Parrots are possibly able to deal with plant toxins better than any other group of vertebrate granivores. Parrots often feed on unripe and often toxic seeds (and fruits), and can tolerate high levels of alkaloids and phenols, in part because parrots selectively feed on soil (geophagy) containing minerals with high capacities to bind plant toxins (Gilardi et al. 1999).

Two processes have potentially played a role in generating the diversity of specialist seed-predators and the diversity of chemically defended seeds. The first process is escape-and-radiate coevolution developed for herbivores and plants (see Chapters 2 and 3), which can be summarized as follows. By mutation and recombination new chemical defences arise that allow plants to escape seed-predators. These plants then radiate. Eventually seed-predators evolve counter-measures then radiate on the plants. This is roughly the scenario envisioned for bruchids and legumes by Janzen (1969). As an example, the evolution of endopeptidase inhibitors in legumes may have freed them of many seed-predators and perhaps enabled further radiation. The subsequent loss of inhibitable endopeptidases in bruchids may have enabled them to then radiate onto legumes (Janzen 1969). Given the increasing number of studies showing that seed-predators have strong impacts on plant populations, and the increasing evidence for escape-and-radiate coevolution in herbivores and plants (e.g. Chapter 3), we believe studies testing this hypothesis for seed-predators and their victims would be well worthwhile.

The second process is the result of apparent competition (*sensu* Holt 1984). This would favour divergence in chemical defences and could even provide a mechanism for escape-and-radiate coevolution. As Janzen noted, 'any pair of species with the same defence would jointly present a larger and more reliable food source to the seed predator, thereby creating strong selection favoring any mutant that caused them to diverge in secondary seed chemistry' (Janzen 1978). Such a process could contribute to the tremendous diversity of chemical defences in seeds and in turn the diversity of seed specialists. However, comparative and experimental studies designed to elucidate the importance of this mechanism for seed diversity, as has been done for other forms of competition, are lacking.

5.4.3 Selection on physical seed traits and counter-adaptations of animals

It is not surprising that granivores lack a consistent preference for larger seeds, given the tremendous variation in other seed traits between plant species (see Section 5.2.2). Such variation also appears to explain the absence of seed-size preferences by granivores within a plant species (Smith 1970). Nonetheless, several studies have found that granivores preferentially feed or oviposit on larger seeds within a plant species (Moegenburg 1996) indicating that some granivores exert selection on seed size. Seed-size selection appears most likely when seeds are outside the fruit (i.e. dispersed) and the seed-predator is specialized on one or a few species of seed. However, seed size might still not evolve much in response to seed predation for at least four reasons. First, seed-size differences between plants can often be largely the result of environmental variation rather than heritable variation (Silvertown 1989). Second, most of the variance in seed size is accounted for by variation within crops (e.g. at a level within individuals) rather than among individuals. Consequently, differential predation by seed size might not cause differential reproductive success (i.e. selection) between individual plants. Third, selection on seed size by seed-predators could be countered by selection from a variety of sources (Primack 1987). For example, the advantage of larger seed size soon after germination (Westoby et al. 1996) may counter and perhaps overwhelm selection by seed-predators. Furthermore, both studies mentioned above, showing seed-predators preferentially preying on larger seeds, also found that larger seeds had germination advantages. Moreover, in one of these studies (Moegenburg 1996) environmental variation appeared to have a large impact on seed size. Finally, a change in seed size might reduce predation by one seed-predator but increase predation from another (Willson 1983).

In contrast to the few data indicating that seed-predators influence seed-size evolution, there is considerable evidence that seed-predators have favoured the maintenance and elaboration of many structural features of the seeds and fruit. These features include background matching of dispersed seeds (Nystrand & Granström 1997), the texture, thickness and hardness of seed coats or fruits (Smith 1970; Johnson 1990; Grubb et al. 1998), pubescence or irritant hairs or spines (Grubb et al. 1998; Coffey et al. 1999) and the number of seeds per fruit (Smith 1970, but see also Casper 1988). This evidence is especially compelling for spines on pine cones, where foraging experiments and explicit phylogenetic models were combined to show that increases in spine length are related to deterring seed-predators foraging for seeds in open cones (Coffey et al. 1999). In sum, these studies support Smith's (1970) hypothesis that selection pressures from the physical environment mostly affect seed size, whereas selection pressures from seed-predators mostly affect the type and amount of tissue that protect seeds. As Smith (1970) noted, this is an oversimplification. Nevertheless, this hypothesis has been useful in guiding research.

Many studies show that variation in the physical characteristics of seeds and fruits have influenced the evolution of seed-predators. Two examples should suffice. The beak in different soapberry bug (*Jadera haematoloma*) populations has evolved to different lengths to reach the seeds of the various species of plants the bug has colonized in the past century (Carroll et al. 1997). The extensive studies by Peter and Rosemary Grant, Dolph Schluter and others (e.g. Grant 1986) show that the size and hardness of seeds available during the dry season have influenced the evolution of bill structure in Darwin's finches (*Geospiza* spp.). Moreover, bill size is highly heritable and has evolved rapidly in response to changes in seed availability (Grant & Grant 1995).

5.4.4 Selection on seed dispersal behaviour and counter-adaptations of animals

Annual variation in seed-crop size is thought to be adaptive because of the economies of scale (Norton and Kelly 1988; Kelly 1994). That is, the cost per seed and seedling declines with increasing flower or seed-crop size. The result is that for a given average amount of investment the reward from alternately producing large and small seed crops is greater than the reward of a consistent intermediate-sized seed crop (Fig. 5.11). Variable seed crops should be favoured as long as the number of seeds or seedlings surviving increases in an accelerating manner with increases in seed production (i.e. the second derivative is positive). Such an increase could result from predator satiation or, especially if unpollinated flowers are costly, improved pollination success (Lalonde & Roitberg 1992).

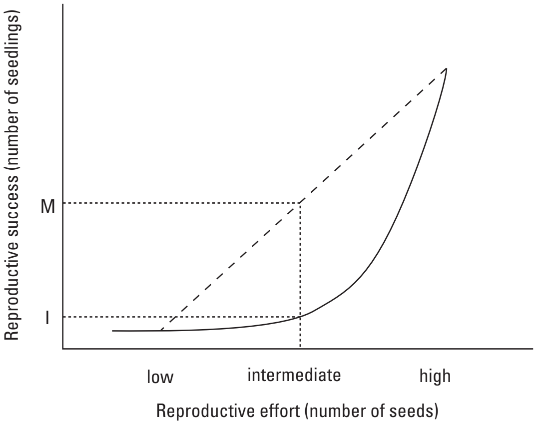


Figure 5.11 The solid curve represents a hypothetical relationship (but see Fig. 5.8) between the reproductive success of a plant and its reproductive effort. When the curve is concave-up (as shown, and as expected with the economies of scale), alternating reproductive effort between low and high seed years yields a greater average reproductive success (M) than when an intermediate (same mean) effort is made every year (I).

Selection by seed-predators has undoubtedly favored supra-annual reproductive synchrony (Kelly 1994). Evidence for selection by seed-predators is the reduction in annual variation in the absence of seed predators (Kelly 1994), a greater range of variation in seed production by plants dispersed by wind than by animals (Herrera et al. 1998), and experimental evidence that asynchronous individuals suffer higher predation rates (Crawley & Long 1995). The examples of supra-annual community-wide synchrony, including temperate conifers and hardwoods, Southeast Asian dipterocarps and bamboos, (Gurnell 1993; Kelly 1994; Herrera et al. 1998; Curran & Leighton 2000), further suggest the importance of selection by seed-predators, although in some cases community-wide synchrony might merely reflect the use of the same environmental cue to initiate large reproductive episodes (Norton & Kelly 1988).

Seed-predators in turn have adapted to variable seed crops. At least 70 species of insect seed-predators on conifers (Diptera, Hymenoptera and Lepidoptera) extend their normal winter diapause for one to seven additional years (Turgeon et al. 1994). These insects produce progeny with a mixture of diapause lengths (risk-spreading diapause) or rely on environmental cues to emerge from diapause during a large seed crop (predictive diapause). Some insects and vertebrates move seasonally or yearly from one large seed crop to another. Birds such as crossbills (Benkman 1987) are the most effective at tracking seed fluctuations, especially considering that synchronous seed production among northern conifers can extend 500 or more kilometres (Koenig & Knops 1998). Many seed-predators eat alternative foods, but it is unclear if specialist seed-predators have evolved to become generalists in response to increasing fluctuations in seed availability. Enough is known about the feeding habits of conifer-seed-eating insects (Turgeon et al. 1994) that, given the appropriate phylogeny, one could investigate whether generalists have evolved from specialists.

Reproductive synchrony works well against specialist seed-predators, but the large pulses of seeds (which tend to lack chemical defences (Janzen 1969, 1971)) attract generalist seed predators, which may or may not be swamped (Section 5.3.2). Satiation is less likely with increasing adaptation by seed-predators. This favours even larger seed crops and possibly longer intervals between them (Silvertown 1980). Because of the costs and limitations of resource storage, most of the resources allocated to reproduction might be from current photosynthesis (Koenig & Knops 1998) limiting the size of the seed crop. Eventually asynchronous reproduction and perhaps physical or chemical defences might be favoured. However, in contrast to chemical and physical defences, the benefits of a particular temporal seed-production pattern to a plant is dependent on the temporal seed-production patterns of other plants in the population and even other species (Silvertown 1980; Curran & Leighton 2000). Once periodic and synchronous seed production evolves, selection operates against individuals that deviate (Lalonde & Roitberg 1992). It is an evolutionarily stable strategy (ESS) that cannot be invaded by *individuals* that differ from the rest of the population. It is conceivable, therefore, that with counter-adaptations of seed-predators and perhaps changes in the environment (e.g. deforestation; Curran & Leighton 2000) that periodic and synchronous seed production is no longer a good, let alone the best, strategy. But in contrast to chemical and physical seed defences, which presumably could more easily change in response to selection, periodic and synchronous seed production might remain because it is an ESS. Change might occur only after, for example, plant population density decreases so that movement of seed-predators between plants is reduced, or physical or chemical defences increase. Thus, we should anticipate cases where predators are not satiated.

The seasonal phenology of seed production is thought to have evolved in response to selection by seed-predators, with predator satiation more likely if seeds mature quickly and are available to seed-predators only for brief periods of time (Janzen 1971; Kelly 1994). Yet some plants retain mature seeds from successive seed crops in their canopies. These seeds are held in closed seed-storing structures to be released synchronously when conditions are favourable for germination (e.g. after a fire). This is called serotiny, and is characteristic of woody perennials that occur in habitats having strongly seasonal climates and recurrent fires within the reproductive lifetime of the plant (Lamont et al. 1991). Serotiny is advantageous because it maximizes the quantity of seeds available for recruitment following fire (Lamont et al. 1991) and, like mass seeding, it satiates post-dispersal seed-predators (O'Dowd & Gill 1984). Areas where serotiny is most common are the sclerophyllous shrublands and woodlands of Australia and South Africa, and the coniferous forests of North America (Lamont et al. 1991).

The disadvantage of serotiny is that seeds are predictably and reliably held, favouring the evolution of specialist pre-dispersal seed predators (Lamont et al. 1991). This in turn has produced strong selection for increased seed defences, which has resulted in the evolution of harder or woodier structures surrounding the seeds (Smith 1970). These well-developed physical barriers also protect the seeds from damage by fire, which may explain why physical rather than chemical defences have been developed. The importance of protection from fire may also explain why monocots, which lack wood, are not serotinous (Kelly 1994). In the following section we will discuss an example of coevolution between a serotinous tree and its specialist pre-dispersal seed-predators.

5.4.5 Case studies in coevolution

Although numerous examples exist of adaptation by plants to seed predation and adaptations of animals to exploit seeds, compelling examples of coevolution between

Figure 5.12 Representative red crossbills (*Loxia curvirostra*) and lodgepole pine (*Pinus contorta*; distribution in black) cones from the northern Rocky Mountains. Lodgepole pine has relatively short and wide cones (lower right) throughout most of its range in response to selection by red squirrels. The crossbill found in these forests (lower right) has an average bill size that approximates the optimum for foraging on these cones. In the South Hills (SH) and Albion Mountains (AM) in southern Idaho red squirrels are absent and crossbills are coevolving with lodgepole pine. Here, lodgepole pine cones are larger and have thicker distal scales in response to selection by crossbills, and crossbills have stouter bills to get seeds out of these cones. This was repeated in the Cypress Hills (CH) in southern Canada; however, squirrels were introduced here in 1950 apparently causing the extinction of this population of crossbills. (From Benkman 1999.)

seeds and seed-predators are rare (Johnson 1990). We discuss two examples of coevolution below. It might not be a coincidence that both represent pre-dispersal seed-predators. For at least four reasons we expect coevolution between seed-predators and seeds to be most obvious in pre-dispersal seed-predators. First, it is easier for a seed-predator to be selective of seeds prior to rather than after dispersal. For example, pre-dispersal seed-predators can more readily avoid seeds from a particularly toxic plant when the seeds are clustered on the plant than after they are scattered on the ground and mixed with seeds from other plants (Janzen 1971). Second, defences associated with dry fruits have fewer constraints than those associated solely with the seed. Third, pre-dispersal seed-predators limit the evolutionary effect of subsequent seed-predators on the subset of remaining seeds. Finally, pre-dispersal seed-predators tend to be more specialized, so that increasing seed defences are more likely to lead to counter-defences than to the predators switching to an alternative food.

5.4.5.1 Wild parsnip and parsnip webworms

The defences of wild parsnip and the counter-measures of the parsnip webworm have already been discussed in Chapter 3. Nevertheless, we would also like to lay claim to this example because seeds are a critical component of the webworm's diet, even though, like many granivores, they also eat the reproductive structure surrounding the seeds. Moreover, no other study of coevolution between insects and plants is as compelling. Rather than repeat the details of this marvellous example, some of which we have already noted, we just want to point out an intriguing dynamic; that is, instead of simply an arms race with escalating defences and counter-defences until tradeoffs result in a stalemate (which also occurs), there are apparently cyclic chase dynamics with different populations at different points in the cycle (Berenbaum & Zangerl 1998). Although it is unclear what exactly causes the cycling, frequency-dependent selection is undoubtedly critical (Berenbaum & Zangerl 1998).

5.4.5.2 Lodgepole pine, squirrels and crossbills

One of the earliest examples of seed and seed-predator coevolution was that between lodgepole pine and pine squirrels in western North America (Smith 1970). This study is a classic in part because Smith was able to identify fire as a variable independent of the interaction between seed and seed-predator, which determined the strength of the coevolutionary interaction. Where fire was frequent lodgepole pine evolved serotinous cones that accumulated on the tree until the next fire. This allowed for a more stable population of seed-predators, which resulted in strong selection for increased defences. The serotinous cones are so well defended (seeds represent about 1% of total cone mass) that only two seed-predators, pine squirrels and red crossbills, commonly consume seeds before the cone scales open wide and seeds are released.

Pine squirrels are the most important selective agents on the cones of lodgepole pine throughout most of its range. Squirrels preferentially harvest cones that are relatively narrow at the base and have more seeds because this maximizes both feeding rates and the mass of kernel cached per cone (Smith 1970). This results in the evolution of wider (and harder) cones (especially at the base)

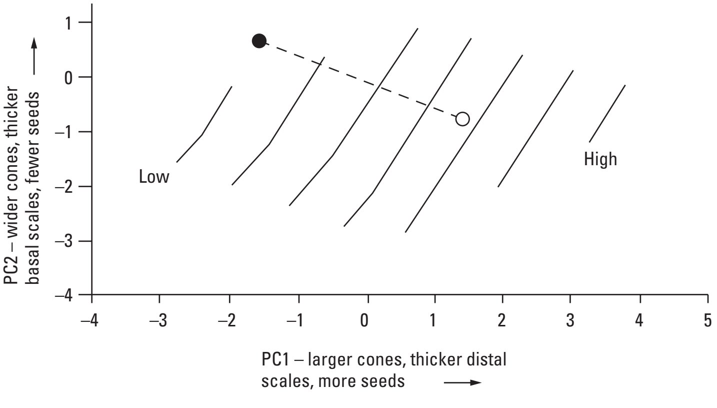


Figure 5.13 The estimated contours (solid lines) for the benefit-to-cost ratio to the tree in relation to the first two principal components of seven lodgepole pine cone and seed traits. The filled circle represents the overall mean values for four sites from the Rocky Mountains, and the open circle represents the overall mean values for South Hills/Albion Mountains and the Cypress Hills, where pine squirrels are absent and crossbills are resident. (From Benkman 1993.) If pines were evolving so as to increase the benefit-to-cost ratio of their defences, they should evolve down and to the right (to high benefit-to-cost ratios). That is what was found.

with fewer seeds (Fig. 5.11; Smith 1970; Benkman 1999). Pine squirrels, in turn, have evolved various adaptations for efficiently exploiting these cones (Smith 1970). By harvesting and caching tremendous numbers of cones soon after the seeds mature (Smith 1970), pine squirrels are effective pre-emptive competitors so that red crossbills are uncommon and apparently have little impact on cone evolution (Benkman 1999). Here crossbills have adapted to the average lodgepole pine cone (Fig. 5.12).

In two sets of mountains east and west of the Rockies crossbills have evolved in the absence of pine squirrels for the past 6000 to 10 000 years (Fig. 5.12). Here crossbills are over 20 times more abundant. Crossbills also select cones providing the highest kernel intake rates (Benkman 1987), but in contrast to squirrels, the mass of kernel per cone is not important, in part because crossbills do not remove cones from the tree. The most striking features of cones in these 'crossbill' ranges are their large size and the increased thickness of the distal scales. Cones are larger because with relaxation of selection by pine squirrels, the number of seeds per cone has increased and selection by crossbills favours larger, thicker scales (Benkman et al. unpublished). Larger, thicker distal scales make sense because the time required to extract a seed increases with increasing scale thickness (Benkman et al. 2001) and most of the seeds are located at the distal end. Not surprisingly, the composite evolution of the cones is most accurately predicted when both the benefits of the defence, in terms of time per seed for a crossbill, and the costs of the defence, in terms of cone mass relative to seed mass, are considered. In response to selection by crossbills, lodgepole pine has increased the ratio of benefits to costs of its defences (Fig. 5.13). Crossbills in turn have adapted to these enhanced defences by evolving deeper and more strongly decurved bills (Fig. 5.12).

The interaction between wild parsnip, lodgepole pine and their seed-predators illustrates many principles common to seed and seed-predator interactions. We would like to end by emphasizing three points. First, the changes in response to selection by seed-predators can be accounted for only when both the benefits and the costs of defences are taken into consideration. Second, geographical variation in seed-predator assemblages (e.g. the presence and absence of pine squirrels), the physical environment (e.g. fire frequency) and perhaps cyclic chase dynamics (e.g. webworms and parsnip) will commonly cause divergent selection between populations and lead to a geographic mosaic of coevolution (Chapter 9). Finally, we suspect that coevolution occurs fairly commonly between plants and seed-predators. However, until we carry out careful studies testing specific models of coevolution this will remain only an opinion, which is unfortunately the basis of many conclusions concerning coevolution between plants and seed-predators.