

- McComb, J.A. and Andrews, R. (1974) Sequential softening of hard seeds in burrs of annual medics. *Australian Journal of Experimental Agriculture and Animal Husbandry* 14, 68-75.
- McCullough, J.M. and Shropshire, W., Jr (1970) Physiological predetermination of germination responses in *Arbidopsis thaliana* (L.) Heyn. *Plant Cell Physiology* 11, 139-148.
- Maun, P.A. and Payne, A.M. (1989) Fruit and seed polymorphism and its relation to seedling growth in the genus *Cakile*. *Canadian Journal of Botany* 67, 2743-2750.
- Negh, M. and Tamari, B. (1963) Germination of chlorophyllous and achlorophyllous seeds of *Salsola volkensis* and *Aelentia aubruni*. *Kornel Journal of Botany* 12, 124-135.
- Okuneva, O.T. and Unger, I.A. (1963) The effects of time of seed production on the germination response of *Spergularia maritima*. *Physiologia Plantarum* 59, 335-342.
- Philippelid, J. and Unger, I.A. (1984) The effect of seed polymorphism on the germination and survival of *Salicornia europaea* L. populations. *American Journal of Botany* 71, 542-549.
- Platt, S. and Larter, E.N. (1986) Influence of maturation temperature and stage of kernel development in sprouting tolerance of wheat and triticale. *Crop Science* 26, 804-807.
- Pourat, Y. and Jacques, R. (1975) The influence of photoperiodic conditions received by the mother plant on morphological and physiological characteristics of *Chenopodium polysperum* L. seeds. *Plant Science Letters* 4, 273-279.
- Raach, D.A. and Wulff, R.D. (1987) Maternal effects in plants. *Annual Review of Ecology and Systematics* 18, 209-235.
- Rolz, L. (1989) Sexual strategies in some gynodioecious and gynomonocious plants. PhD thesis, Tel-Aviv University, Tel-Aviv.
- Takano, K. and Yamaguchi, H. (1991) Diversity in seed germination behavior in relation to heterocarpy in *Salsola komarovii* Iljin. *Botanical Magazine of Tokyo* 104, 207-215.
- Thomas, T.H., Biddington, N.L. and O'Toole, D.F. (1979) Relationship between position on the parent plant and dormancy characteristics of seed of three cultivars of celery (*Apium graveolens*). *Physiologia Plantarum* 45, 482-496.
- Unger, I.A. (1979) Seed dimorphism in *Salicornia europaea* L. *Botanical Gazette* 140, 102-108.
- Vander Veem, R. (1970) The importance of the red-far red antagonism in photoblastic seeds. *Acta Botanica Neerlandica* 19, 809-812.
- van Klasee van Oudshoorn, K. and van Rooyen, M.W. (1989) *Dispersal Biology of Desert Plants: Adaptations of Desert Organisms*. Springer, Berlin, 242 pp.
- Weinland, M.J. (1965) The effect of photoperiod on the seed dormancy of *Chenopodium album*. PhD thesis, University of Wisconsin-Madison.
- Werker, E. and Mary, T. (1974) Heterocarpy and its ontogeny in *Aelentia aubruni* (Post) Zoh: light and electron-microscope study. *Israel Journal of Botany* 23, 132-144.
- Wurzbarger, J. and Koller, D. (1976) Differential effects of the parental photothermal environment on development of dormancy in caryopses of *Aegilops kotschy*. *Journal of Experimental Botany* 27, 43-48.
- Yamaguchi, H., Ichihara, K., Takano, K., Hori, Y. and Saito, T. (1990) Diversities in morphological characteristics and seed germination behavior in fruits of *Salsola komarovii* Iljin. *Botanical Magazine of Tokyo* 103, 177-190.
- Zaewart, J.A.D. (1966) Reduction of the gibberellin content of pharbitis seeds by CCC and after-effects in the progeny. *Plant Physiology* 41, 856-862.
- Zohary, M. (1937) Die Verbreitungskologische Verhältnisse der Flora Palästinas. *Beihfte zum Botanischen Zentralblatt* 56(1), 1-155.
- Zohary, M. (1966) *Flora Palaestina, Part I - Text*. Israel Academy of Sciences and Humanities, Jerusalem, 364 pp.
- Zohary, M. (1972) *Flora Palaestina, Part II - Text*. Israel Academy of Sciences and Humanities, Jerusalem, 489 pp.

Seeds: the ecology of regeneration in plant communities. 2nd ed. Fenner, M. CAB, 2004. (2000)

The Ecology of Seed Dispersal

Chapter 4

Mary F. Willson¹ and Anna Traveset²

¹ 5230 Terrace Place, Juneau, Alaska, USA; ² Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Esporles, Balearic Islands, Spain

Introduction

Seed dispersal has long been a topic of interest to naturalists, but it has not been until the last three decades that the ecology of dispersal has received much rigorous scientific attention. Many theoretical and empirical advances have recently been made, although important lacunae in our understanding still need to be filled before dispersal ecology becomes a coherent body of knowledge. A major goal of this chapter is to review the existing literature on seed dispersal, highlighting these essential but missing kinds of information.

This review is divided into two sections, the first dealing with the evolution of dispersal mechanisms and the second with the consequences of dispersal at population and community levels. Dispersal can occur in both space and time, but only the former will be treated here, except where some relationship between the two axes is known (Venable and Brown, 1988; Leck *et al.*, 1989; Eriksson and Ehrlén, 1998a; see also Murdoch and Ellis, Chapter 8, this volume).

The seed shadow

The spatial distribution of dispersed seeds around their source is called a 'seed

shadow' (Janzen, 1971). The term is most commonly (and perhaps properly) used in reference to the postdispersal distribution of seed around the maternal parent, but it can also be used to refer to the distribution of seeds around a source composed of multiple parents. Although the unit of dispersal may be technically a fruit or a group of fruits and, thus, the generic label should be disperse or propagule, we shall continue to use the more euphonious term of seed shadow, with the intent of conceptually including all disperses of any morphological and genetic derivation.

Seed shadows exist in two horizontal dimensions for most seed plants (a salient exception is found in epiphytic plants, in which the third, vertical, dimension is presumably well developed). The shape of the seed distribution in the horizontal plane may be asymmetric with respect to the source (if, for example, the wind carries most seeds in a downwind direction). This simple descriptor of shape is generally augmented by information on seed density, such that the seed shadow resembles a topographic map, with peaks of high seed density. Two factors, then, can be used to describe seed shadows - the relationship of seed numbers or density to distance from the source and the directionality with respect to the source.

Although directionality is clearly

significant for many ecological questions, it is common to discuss seed distributions chiefly in terms of distance from the source. Conventional wisdom describes the seed number/distance relationship as leptokurtic (with a higher peak and longer tail than a normal distribution); from the peak outward, seed numbers are generally considered to decrease monotonically, fitting a negative exponential curve (or sometimes a negative power function: Okube and Levin, 1989; Fig. 4.1). Most measured seed shadows conform to this expectation (Fig. 4.2; Willson, 1993a). The nature of the source (single or multiple individuals) can influence the location of the peak of the curve, and the use of seed density rather than numbers can change the overall shape of the curve, including the proximity of the peak to the source (Peart, 1985; Greene and Johnson, 1996).

Deviations from the conventional seed shadow shape can result from patchiness of habitat structure (Hoppe, 1988; Debussche and Lepart, 1992; Debussche and Isenmann, 1994; Kollmann and Pirl, 1995; Aguiar and Sala, 1997) and other

ecological factors, including behaviour patterns of the seed vectors that lead to nucleation processes (Willson and Crome, 1989; McClanahan and Wolfe, 1993; Verdú and García-Fayos, 1996, 1998; Julliot, 1997). For species with polymorphic seeds (i.e. with and without dispersal devices, or with two or more different kinds of dispersal devices), the shape of the seed shadow for each seed type may differ, such that the combined seed shadow for a given parent may have a very unconventional shape.

Many factors can alter the location of the peak and the slope and shape of the tail of the seed shadow for particular species and individuals (e.g. Rabinowitz and Rapp, 1981; Johnson, 1988; Debussche and Lepart, 1992; Verdú and García-Fayos, 1996, 1998; Julliot, 1997). Some factors are, from the plant's perspective, strictly environmental and thus outside the control of the plant (e.g. the strength and direction of the wind, the social behaviour of animal dispersal agents, the patterns of rainfall and relative humidity). Other factors, such as plant height, have a strong environmental component (Greene and Johnson, 1996)

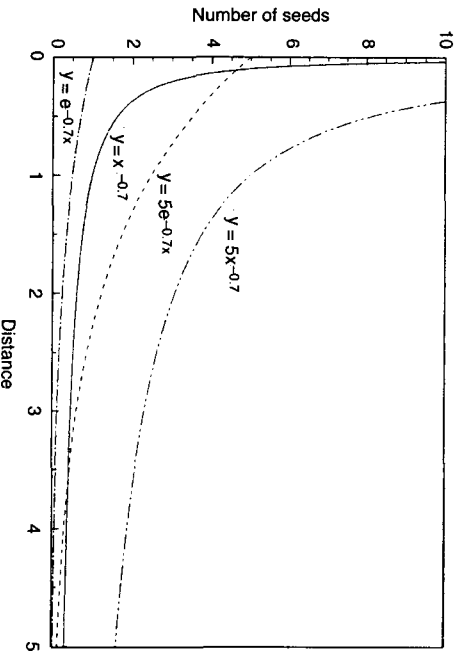


Fig. 4.1. Idealized curves commonly used to describe the distribution of seeds at increasing distances (arbitrary units) from the seed source. Real seed shadows often peak at some distance from the source; in that case, the curves refer to the part of the seed distribution from the peak outward. For a given set of coefficients, the negative exponential curve ($Y = ax^{-m}$) drops less steeply than the negative power function ($Y = ax^{-m}$); it is converted to a straight line on a semilogarithmic scale. (From Okube and Levin, 1989.)

but may also have a genetic component. Still others are probably controlled both by environment and the genetic constitution of the parent plant, the balance depending on the species and circumstances (e.g. fruit size, seed size, ease of dehiscence or abscission). All such factors can contribute to variation in the size and shape of the

seed shadow among species and among conspecific individuals.

Few data yet exist, either from the tropics or from the temperate zone, for on-pare seed shadows generated by different dispersal modes (but see Gorshov *et al.*, 1993; Portnoy and Willson, 1993; Willson, 1993a). Even less is known about how the

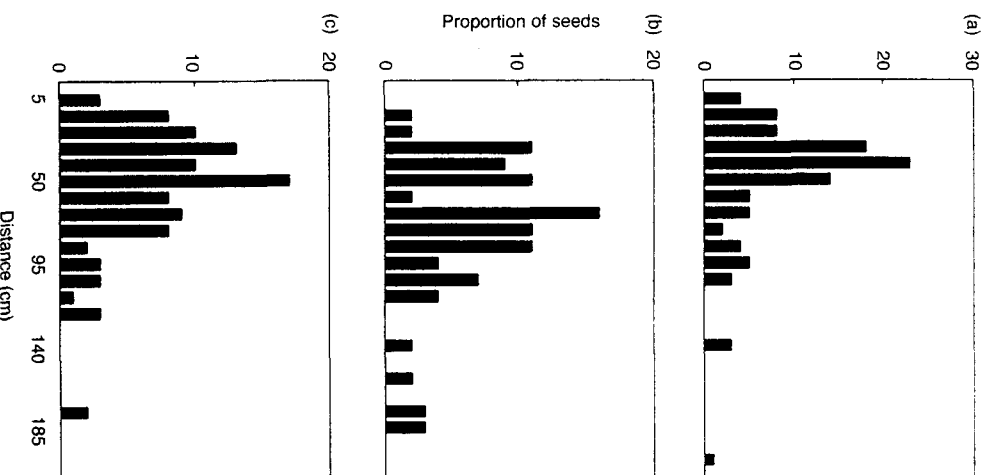


Fig. 4.2. Seed shadows of three individuals of *Lithospermum carolinense*. The tails of all three seed shadows fit a negative exponential curve, but the slope of that curve (on a semilog plot) varies from -1.47 to -1.72 , and the location of the peak differs. (From Westelaken and Maun, 1985.)

loss or the addition of a dispersal agent alters the seed shadow of a plant. Moreover, we cannot yet make any generalization about the relative ecological importance of different portions of the seed shadow for the evolutionary ecology of plants.

In order to understand the ecological and evolutionary consequences of variation in the length and shape of the seed shadow, we need to experimentally modify seed distributions and monitor the fitness of recruits in different parts of the distribution, for a variety of species and circumstances (Portnoy and Willson, 1993). The tail of the distribution may be at least as important as the modal portion of the curve, although little theoretical effort has been devoted to this question (but see, for instance, Cain *et al.*, 1998). Propagules in the distribution's tail potentially spread the parental genes more widely, and plant traits that affect the behaviour of such tails can be subject to selection. The examination of 68 data sets has shown a lack of association between tail shape and dispersal mode, suggesting that, in most circumstances, selection for tail behaviour contributes little to the evolution of the dispersal mode itself (Portnoy and Willson, 1993).

The evolution of dispersal

Why are seeds dispersed?

If the dispersal of offspring increases the fitness of a parent, we should expect that dispersed offspring survive and reproduce better than undispersed offspring, either because they avoid detrimental conditions near the parent or because they reach better conditions farther away (which amounts to the same thing, from a different perspective). If seeds fall directly beneath the canopy of a parent, the physical separation hardly constitutes real dispersal, but fallen seeds are normally treated as part of the seed shadow, for purposes of comparing seed fates. Van der Pijl (1982) actually treats simple seed fall as a separate mode

of dispersal for species that have no evident special means. The principal factors that favour dispersal are avoidance of natural enemies or sibling interactions and the probability of finding a physically suitable establishment site.

1. Some natural enemies of seeds and seedlings respond to density and/or distance from the parent (or other conspecific). Pathogens, postdispersal seed predators, parasites and herbivores often concentrate their activities where their resources are common, and more distant seeds/seedlings may survive better than those close to the parent (e.g. Howe and Smallwood, 1982; Augspurger, 1983a, b; Augspurger and Kelly, 1984; Howe, 1993; Peres *et al.*, 1997; Hulme, 1998); the magnitude of this effect varies among species (Augspurger, 1984; Howe, 1993). The impact of such consumers depends, in part, on their specificity to genotype or to species of resource – some attackers may specialize in the offspring of particular parents or in particular taxa. The density or proximity of other genotypes or species of seed would have little impact on the availability of suitable resources for such specialists, and thus the effect of density- and distance-responsive enemies must often vary with their specificity.

The ability of natural enemies to depress seed and seedling density also depends, of course, on other factors limiting their abundance and activity. These will vary among consumers, and even among populations of the same species of consumer. Thus although numerous cases of density- and distance-responsive attackers have been reported, we do not yet have a general picture of which plant species are subject to such attacks and in what circumstances (e.g. habitat, season, geographical region, adult densities).

2. Because the seeds and seedlings of any one parent are genetically related (at least half-sibs), they are subject, potentially, to sibling competition. Conventional wisdom suggests that sib competition may often be more severe than competition with non-sib conspecifics, because their patterns of resource use are probably more similar (see

references in Ellstrand and Antonovics, 1985; see also McCall *et al.*, 1989). However, in a number of cases, sib competition does not have a detectably different outcome from that of non-sib competition, and sibs may even profit, at some early stages of the life history, from the proximity of genetic relatives (Smith, 1977; Williams *et al.*, 1983; Willson *et al.*, 1987; Kelley, 1989; McCall *et al.*, 1989). Furthermore, self-fertilized seeds disperse less well than outcrossed seeds in *Impatiens capensis* and *Amphicarpa bracteata* (Schmitt and Ehrhardt, 1987; Trapp, 1988), which is the opposite of what would be expected if dispersal were an adaptation to reduce sib competition. Also, if sib competition were critical, genetically variable offspring should have higher fitness than clonal progeny where sib densities are high, but this was not the case in *Anthoxanthum odoratum* (Kelley *et al.*, 1988).

Another potential disadvantage of high sibling densities is the possibility of inbreeding when (and if) the offspring reach adulthood (Chiselin, 1974). The relative effects of extreme inbreeding and outcrossing on the genetic variance of offspring are not predictable in any simple way, because they depend on many aspects of the genetic system, as well as past episodes of inbreeding (McCall *et al.*, 1989). As a result, the degree of offspring similarity and the intensity of potential sib competition are likewise difficult to predict. A degree of inbreeding may be advantageous under certain circumstances (e.g. Shields, 1982; Jarne and Charlesworth, 1993). Furthermore, even if inbreeding is disadvantageous, there are other ways for plants to reduce inbreeding (e.g. through changes in the floral biology and mating system), so it is difficult to assess the importance of inbreeding avoidance as a factor that selects for offspring dispersal. Moreover, dispersal has its own costs (e.g. Cohen and Motro, 1989), which may outweigh the costs of some inbreeding (Waser *et al.*, 1986); the benefit/cost ratio is likely to vary among species (e.g. Augspurger, 1986).

Attacks by parasites and pathogens may be more devastating when sibs grow in close proximity to each other (see Alexander and Hoi (1998) for a recent review on the interaction between plant competition and disease). Just as conspecifics growing in a monoculture are often more heavily hit by pests than the are when growing in a mixed stand, so also are the genetic monocultures of closely related individuals sometimes more heavily hit by certain kinds of pests than stands of mixed percentage (e.g. Parker, 1987; Burdon, 1987). To the extent that a species is subject to such attacks on particular genetic lineages, there may be selection for dispersal, which lowers the concentration of any one lineage in a given area (Fig. 4.3).

3. Some species have special physical requirements for germination and establishment that are met only in scattered locations, such as fallen logs, tree-fall gaps or badger mounds. In the absence of well developed dormancies and the ability to wait for suitable conditions to arrive, selection may favour dispersal in order to increase the probability of finding the necessary kind of location (Platt and Weibull, 1985; Reid, 1989; Sargent, 1995). Even with good dormancy mechanisms, dispersal should enhance the probability that waiting seed will eventually encounter the right conditions for establishment. Theoretically, dispersal generally enhances the likelihood that at least some offspring reach appropriate sites (Hamilton and May, 1977; Comins *et al.*, 1980). These theoretical expectations need to be examined for a variety of particular cases. If the seed shadow is adapted to the distribution of safe sites, species with widespread seed shadows should have more far-flung establishment sites than species with restricted seed shadows (Green, 1983; see also Cease *et al.*, 1984; Horvitz and Le Corff, 1993).

What portion of the seed shadow is most effective in yielding successful offspring and how does this vary with species and conditions? The peak portion of seed shadow, where the most seeds deposited, often receives the most attention from ecologists. Although the peak ma-

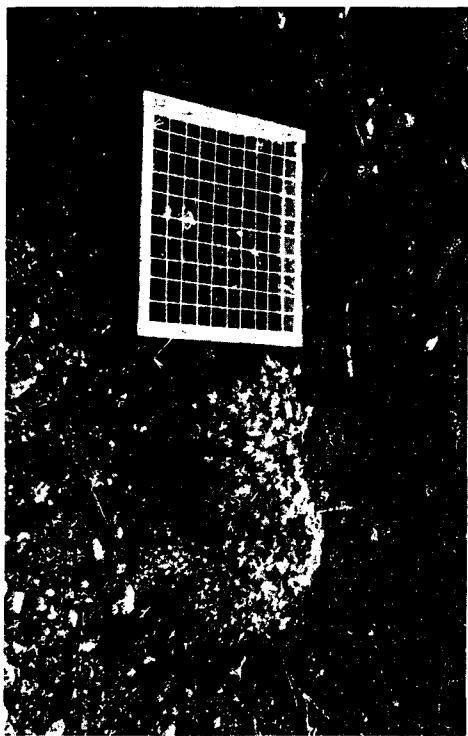


Fig. 4.3. A 'bear garden' – seedlings of *Ribes bracteosum* growing from a faecal deposit of an Alaskan brown bear. The small squares in the grid beside the garden are 3 cm on a side. Both sib and non-sib competition must be intense, predation by rodents can be severe and survivorship may ultimately be low. Some bear deposits contain seeds of two or three species, and germination may occur a month to a year or more after deposition. (Photo by J. Zasada.)

ecologically important as a source of food for seed predators and other consumers, we seldom know if it is the most important in terms of parental fitness. In part because consumers or intense competition can level the peak and in part because rare events can be ecologically important, it seems essential that the tail of the distribution should receive more attention in the future. Moreover, we need to know if there are any patterns (among species, for instance) in the relative importance of the distributional tail. A number of studies have shown that seed and seedling survival increases with distance from the parent (see above), or that more distantly dispersing seeds are more likely to reach good sites (Platt and Weis, 1985). However, a few studies have shown that seeds at the end of the seed shadow often do poorly (Horvitz and Schenske, 1986; Augspurger and Kitajima, 1992) and some authors have argued (without experimental documentation, however) that selection may actually

show that patterns of initial seed-fall density are more affected by distance from a seed source than by the physical structure of the microhabitat, at least for wind-dispersed plants. On the other hand, investigations by Donohue (1997, 1998), who has decoupled the fitness effects of density and distance from the 'home site', have shown that selection on dispersion patterns is likely to be through density rather than distance effects. This author has also investigated the maternal environment effects on seed dispersal within an evolutionary context. Although maternal characters (e.g. fruit and seed traits, architectural traits, plant size, fruit production) are known to influence seed dispersal, only a few studies address the evolution of dispersal within the context of maternal character evolution (see also Thiede and Augspurger, 1996).

How are seeds dispersed?

If dispersal is advantageous, we would expect to find that diaspores have adaptations that enhance dispersal (Ridley, 1930; van der Pijl, 1982). Morphological devices

that enhance dispersal are often quite readily evident and interpretable (Kerner, 1898; Ridley, 1930; van der Pijl, 1982), although some dispersal-enhancing traits (such as buoyancy of seeds dispersed by water) are less immediately obvious. Wind-borne diaspores often have wings or plumes that increase air resistance and slow the rate of fall. Diaspores carried by animal consumers commonly have edible appendages or coverings that are consumed by animals that later eject the seeds (Fig. 4.4): in some cases, the seeds themselves are harvested and either eaten (killed) or cached and sometimes abandoned by the harvester (Sork, 1983; Price and Jenkins, 1986). Other animal-dispersed diaspores travel by means of hooks or sticky coatings that adhere to the exteriors of the animal vectors. Some plants disperse their offspring ballistically, by the explosive opening of the fruits or the springing of a trip-lever. Seeds of certain plant species combine two

or even three modes of dispersal (Weinhold and Rice, 1981; Clifford and Monteith, 1989; Stamp and Lucas, 1990; Arnone and Wilcock, 1994; Traveset and Willson, 1997), as in some *Viola* (ballistic plus ants) *Disporum*, *Rhamnus*, *Myrtus*, *Smilax* (bird-plus ants) and *Petalostigma pubescens* (birds plus ballistic plus ants); a great number of species are dispersed by both birds and mammals (e.g. Herrera, 1989b; Willson, 1993b; Traveset and Willson, 1997).

The dispersal potential of the different modes of dispersal varies greatly. Both wind and vertebrates can potentially carry seeds far from the parent plant, but ant and ballistic mechanisms typically generate shorter seed shadows. A preliminary survey (Willson, 1993a) for herbaceous species indicates that peak and maximum dispersal distances are greater, and the slope of the tail of the seed distribution is less steep, for wind and ballistic dispers-



Fig. 4.4. Ants (*Formica podzolica*) picking up seeds of *Viola nuttallii*. The seed bears an attractive and edible appendage. Ants carry the entire seed back to their nest, eat the appendage and discard the seed. Dispersal of seeds by ants is very common in some floras, but the advantage of ant dispersal may vary greatly among species or regions (e.g. escape from predators or other destructive agents, or deposition in especially favourable site for germination and growth). (From Beattie, 1965, p. 74.)

than for species with no special devices on the disperse. Maximum distances are greater for wind-dispersed than for ballistically dispersed seeds of herbs, although peak distances and slopes are similar. Such results indicate that, on average, dispersal devices seem to work. But variation around the averages was great, and both sampling methods and environmental conditions of dispersal affect the outcome. A much better database is needed to make good comparisons of the seed shadows produced in different ways.

Of course, there is also great variation in the dispersal potential within each general mode of dispersal. The relative size of seed and wing or plume can have enormous effects on the seed shadow of wind-borne seeds (Augspurger and Franson, 1987; Sacchi, 1987; Benkman, 1995). The size and chemistry of the edible appendage on ant-dispersed seeds may influence the rate of seed removal (Gunter and Lanza, 1989; Corb and Corb, 1995; Mark and Olesen, 1996); the array of dispersing ant species and the eventual fate of the seeds. Dispersal of fleshy fruits by ground-foraging vertebrates generates different seed shadows from those produced by flying fruit-eaters. Nuts favoured by scatter-hoarding squirrels may be spread more widely than less favoured species of nuts (Stapanian and Smith, 1984), but jays carry acorns much further than squirrels carry any nuts (Johnson and Webb, 1989). Seeds dispersed by frugivorous lizards also show different patterns of deposition from those dispersed by mammals (Traveset, 1995). By contrasting dispersal syndromes in a family (*Marantaceae*) of tropical understorey herbs, Horvitz and Le Corff (1993) found that bird-dispersed species went further than ant-dispersed species; however, dispersion patterns did not vary among types of dispersal, most species having a clumped spatial patterning.

For vertebrate-dispersed species, it has been hypothesized that plants can exert some kind of control over seed shadows produced by frugivores, by specific laxative and/or constipative chemicals in the fruit pulp, which affect seed retention time in

the dispersers' guts (Murray *et al.*, 1994; Cipollini and Levey, 1997; Wahaj *et al.*, 1998). In turn, seed retention time inside the disperser, together with other factors (reviewed in Traveset, 1998), can affect the germinability, the rate of germination, or both, in certain species.

Although many species exhibit the morphological devices that are presumed to enhance dispersal, large numbers of species lack any evident dispersal device (Ridley, 1930; Willson *et al.*, 1990a; Willson, 1993a; Cain *et al.*, 1998). The seeds of some of these species are so small that they are easily wind-borne without special devices (e.g. orchids). Others have small, hard seeds that are consumed by herbivorous vertebrates along with the foliage and dispersed after passing through the animal's gut, but whether or not this constitutes an 'evolutionary design' can be debated (Janzen, 1984; Collins and Uno, 1985; Dinerstein, 1989). Still other species have small, round seeds that are shaken out of the fruit when the plant is stirred by a passing breeze or animal (e.g. *Pappaver*); this is considered to be a special mechanism for dispersal by some (van der Pijl, 1982). Yet many species remain that lack any apparent device for dispersal in space and that also appear to have little capacity for dispersal in time (Willson, 1993a). Although some of these species may be discovered to be dispersed by one of the major modes, it is reasonable to ask why so many species seem to lack dispersal devices. How do such species achieve effective dispersal? Or is dispersal less advantageous in these species?

Variation in dispersal devices is often evident, both within species and among closely related species. Examples of within-species variation are provided by many *Asteraceae* (seeds with and without a device for wind dispersal) and amphicarpic species, which have both above-ground seeds, which may be dispersed by any of the normal vectors, and below-ground seeds, which may not disperse at all or may be harvested and cached by rodents (van der Pijl, 1982). Examples of variation among related species are many,



Fig. 4.5. Variations on a theme - *Acacia* seeds apparently adapted for dispersal by ants (above) and by birds (below). The food reward in the appendage on the seed is larger and usually more colourful (red, orange, yellow versus white) in bird-dispersed species. (Photo courtesy of D.J. O'Dowd.)

one of the most striking being found in the *Acacia* genus, which is widespread through Latin America, Australia, Asia and Africa. Most Australian acacias exhibit morphological adaptations for dispersal by ants or birds (Fig. 4.5); the American species are dispersed by birds or large mammals (O'Dowd and Gill, 1986); the African species are dispersed by large mammals and, reportedly, by wind (Coe and Coe, 1987). Different populations of *Acacia ligulata* in Australia seem to be adapted to dispersal by ants or birds (Davidson and Morton, 1984). Even if this enormous genus is eventually split into several new genera, the basic observation of diversity of dispersal within a set of related species remains valid. In the genus *Pinus*, seed mass is associated with the mode of dispersal: pine seeds weighing less than about 100 mg are wind-dispersed, while heavier seeds usually have adaptations for bird dispersal (Benkman, 1995). In lineages where long-distance seed dispersal predominates, clonal propagation has evolved on frequent occasions, possibly to make genet fitness less dependent on local dispersal by seed (Eriksson, 1992).

The model(s) of dispersal of any plant species must reflect many different pressures and constraints. Because natural selection must work with existing variation and many plants have very long generation times, there are inevitable phylogenetic constraints. Entire families or genera sometimes exhibit only slight variations on a single mode of dispersal. However, extensive variation within families (e.g. *Liliaceae*), genera (e.g. *Acacia*, *Pinus*) and species (e.g. *Spergularia marina*, *Heterotheca latifolia*) demonstrates that such constraints are neither universal nor totally confining.

Constraints on the evolution of dispersal also emerge from the many, sometimes potentially conflicting, selection pressures that impinge on diasporic design (e.g. Ellner and Schmid, 1981; Benkman *et al.*, 1984; Westoby *et al.*, 1991; Armstrong and Westoby, 1993; Leishman and Westoby, 1994a, b; Kelly, 1995; Winn and Miller, 1995; see also Leishman *et al.*, Chapter 2, this volume). For example, seeds must be endowed with adequate resources to accomplish germination and establishment if these processes must take

place in sites where the seedling can initially generate few resources on its own or sites where intra- or interspecific competition is severe, there can be selection to increase the energy reserves within the seed, often resulting in a larger seed (e.g. Foster and Janson, 1985; Wilm and Miller, 1995). Large seeds are generally harder to disperse than small ones—they need larger animals, stronger winds or more powerful propulsion (Kelly, 1995). Thus, selection for large seed size may bring with it selection for altered dispersal devices or may constrain the array of efficacious dispersal agents. Very large seeds cannot go far ballistically or by adhering to animal exteriors, they cannot be carried by small animals (such as ants) and they need very large wings to be successfully wind-dispersed. One option may be dispersal by vertebrates (Willson *et al.*, 1990a), and larger seeds generally require larger vertebrates to carry them (Foster and Janson, 1985; Wheelwright, 1985; Hammond and Brown, 1995). Even the chemical composition of seeds is associated with the dispersal mode: wind- and animal-dispersed species generally have greater proportions of fat and less of protein and carbohydrates than passively dispersed seeds (Lokeshia *et al.*, 1992).

Furthermore, seeds must be protected against the physical environment and from natural enemies (see Chambers and MacMahon, 1994), and the demands of protection may sometimes interfere with dispersal by certain means. Also, fruits are often photosynthetic; selection to enhance the photosynthetic capacity of the fruit could affect fruit size, colour, shape and other design features that influence dispersal. In addition, a long style can increase the intensity of competition among male gametophytes, but it also affects dispersal distance in the ballistically dispersed *Geranium* (M.F. Willson and J. Agren, unpublished). The timing of dispersal affects the probability and pattern of dispersal and the susceptibility to enemies, and hence can affect the selection pressures on diaspore morphology. The physiological costs of the various modes of

dispersal are generally unknown, but they constitute potential constraints on the evolution of dispersal devices.

Plant size and growth form show some correlations with dispersal mode, which may affect the evolution of dispersal traits (Thompson and Rabinowitz, 1989; Willson *et al.*, 1990a). For instance, few plants that are dispersed by ants or externally on animals are tall in stature. One reason may be that tall plants typically have large crowns, and ants commonly carry seeds for relatively short distances, such that the seeds of large-crowned, tall plants would seldom be carried beyond the crown of the parent and dispersal would be relatively ineffective. Ant dispersal of small acacia trees in Australia may be the exception that proves the rule and thus worthy of special study. Given that a species has become tall, the range of efficacious modes of dispersal may be limited. Most ballistically dispersed plants are small in stature, but at least a few trees use this mode. Dispersal by wind is frequent among species that are relatively tall within their respective habitats (e.g. trees in forests, tall forbs in fields). Although some understory plants are also dispersed by wind, the common inference is that relatively short stature often renders wind dispersal less advantageous than other modes. Stature and growth form are sometimes correlated with seed size (Foster and Janson, 1985; Willson *et al.*, 1990a; but see Kelly, 1995), which may thus influence dispersal mode indirectly (through growth form), as well as more directly.

Whatever the array of constraints on diaspore evolution may be, it is also necessary to ascertain the occurrence and magnitude of selection on dispersal traits. At least two fundamental approaches are useful.

First, studies explicitly designed to measure selection on dispersal traits are essential. Seemingly small differences in the design of dispersal devices can have profound effects on dispersal ability: on aerodynamic performance by wind-dispersed species (Augsburger and Fanson, 1987; Metlack, 1987; Sacchi, 1987); on capacity for attachment for diaspores car-

ried externally by animals (Bullcock and Pineda, 1977; Carlquist and Pauly, 1985; Sorensen, 1986); on foraging preferences of avian fruit consumers (Howe and van de Kerckhove, 1980; Wheelwright, 1985; Whelan and Willson, 1994; Traveset *et al.*, 1995; Loiselle *et al.*, 1996; Rey *et al.*, 1997; Traveset and Willson, 1998); and on the average distance of seed dispersal in a ballistically dispersed herb (M.F. Willson and J. Agren, unpublished). Furthermore, individual plants often differ in the allocation of resources to dispersal devices on the diaspore (Willson *et al.*, 1990b; Jordano, 1995a), although the extent to which such differences are inheritable is seldom established (but see Wheelwright, 1993). Individual variation in seed shadows has been documented for a few species (Augsburger, 1983a; McCanny and Cavers, 1987; Thiede and Augspurger, 1996; Donohue, 1997, 1998). Such information needs to be brought together, so that we know the extent and pattern of individual variation in dispersal devices: how the variation affects the seed shadows of the respective parents; how the seed shadow affects parental fitness; and how these relationships vary among species and conditions. Several studies have shown that selection by avian dispersal agents may be relatively weak (e.g. Manasse and Howe, 1983; Herrera, 1984c, 1987, 1988; Jordano, 1987, 1993, 1994, 1995a, b; Guitián *et al.*, 1992; Willson and Whelan, 1993; Traveset, 1994; Whelan and Willson, 1994), although, in most cases, fitness is indexed by removal rates rather than by the eventual pattern of offspring dispersion.

Secondly, a less direct but still useful approach is to document patterns of variation in the array of dispersal modes present in plant communities (i.e. the dispersal spectra of those communities). Examination of the pattern can help generate hypotheses about the relative advantage of different dispersal modes in different regions and habitats. A few patterns have begun to emerge, but we seldom know how general they are. One consistent trend is that a high proportion of species in tropical wet forest is dispersed by vertebrate consumers (see

references in Willson *et al.*, 1989), although there are biogeographical differences in the strength of the trend (Karr, 1976; Snow, 1981; Fleming *et al.*, 1987). In temperate zones, forests commonly have more vertebrate-dispersed species than other habitats, and the frequency of fleshy-fruited species is especially high in certain southern-hemisphere forests (Willson *et al.*, 1990a). Vertebrate dispersal apparently increases on moister sites, on fertile soils (in Australia) and in floras dominated by shrubs and/or trees (Willson *et al.*, 1990a). The causal factors for such patterns are not yet clear. In contrast, when comparing the seed dispersal spectra of five different types of communities on the Iberian Peninsula (potential woodland, forest fringe, scrubland, nitrophilic communities and montane communities) between Mediterranean and Eurosiberian regions, no significant differences are found for any type of community, although biotic dispersal appears to be consistently more prevalent at mature stages of succession (Guitián and Sánchez 1992).

A conspicuous and well-documented observation is the extraordinarily high frequency of ant-dispersed species in Australia and South Africa, particularly in sclerophyll vegetation on infertile soils. Several hypotheses (reviewed in Westoby *et al.*, 1991) have been proposed to explain such patterns, although few have been tested thoroughly (Hughes *et al.*, 1993). Seed size, the cost of dispersal structures and the availability of dispersal agents are among the potentially important factors. The availability of potassium and nitrogen in the soil may be limiting for the production of fleshy fruits and elaiosomes, respectively (Hughes *et al.*, 1993). The importance of seed deposition in nutrient-enriched ant mounds is debated (e.g. Bond and Stock, 1989) and may, indeed, vary from place to place. Seed burial may also protect seeds from fire or from surface-foraging seed predators (Bennett and Krebs, 1987). See Stiles (Chapter 5, this volume) for further discussion of myrmecochory.

External dispersal on vertebrates is common in riparian zones in arid parts of

Southern Africa and in disturbed and grazed habitats (Sorensen, 1986; Milton *et al.*, 1990; Willson *et al.*, 1990a; Fischer *et al.*, 1996). This pattern may reflect, in part, the level of activity of terrestrial mammals in such areas (i.e. the availability of dispersal agents).

If dispersal spectra are constructed with some measure of abundance (number of stems, percentage cover) instead of species, quite different trends may appear. For example, ants disperse 29% of the herbaceous species in a North American deciduous forest, but ant-dispersed species constitute 50–60% of the stems (Handel *et al.*, 1981). However, such comparisons are, at present, even rarer than those based on species composition (Frantzen and Bouman, 1989; Willson *et al.*, 1990a; Guitián and Sánchez, 1992). The construction of comparative dispersal spectra based on both species counts and abundances for many vegetation types in diverse regions would be heuristically productive.

When are seeds dispersed?

Less seems to be known about the evolutionary ecology of the 'when' of dispersal than of the 'why' and 'how'. Numerous ecological factors may contribute to dispersal phenology. Ideally, seed maturation and dispersal would be timed to match the seasonal availability of good dispersal agents (where required) and the availability of good germination conditions (for seeds lacking dormancy). Constraints on the ideal may derive from selection to avoid seed predators or to shift the flowering time, as well as the length of time required for fruit maturation. In addition, there is environmental variation in the time of fruit maturation and the timing of vector activity in a given area with concomitant differences in rates and quality of dispersal.

A few general patterns in dispersal phenology have been described. Wind-dispersed neotropical trees often mature their seeds during the dry season, when trade winds are strong and trees are leafless (Foster, 1982; Morellato and Leitao, 1996).

This contrasts with the production of fleshy or dry fruits throughout the year (De Lampe *et al.*, 1992). Fleshy-fruited plants in the north temperate zone commonly produce mature fruit crops in late summer and autumn, when avian frugivores are usually abundant, but a little further south, more fruit maturation occurs in winter, when flocks of wintering migrant birds are foraging (Thompson and Willson, 1979; Willson and Thompson, 1982; Herrera, 1984a, 1995; Skeate, 1987; Snow and Snow, 1988). In contrast, ant-dispersed plants in central North America generally mature their seeds in early summer, at a time when avian frugivores are relatively few but ants are very active, given that they bloom in early spring, if they held their fruits until autumn, their low stature would keep the fruits inconspicuous to birds, beneath the foliage of other plants, and the maturing fruits would be exposed to predators all summer long (Thompson, 1981).

As these patterns of phenology in relation to disperser availability have emerged, evidence has appeared that they may not be entirely interpretable as adaptations to dispersal. Fruiting patterns in western Europe tend to match bird phenology at the community level, because abundant species with strictly northern distributions fruit earlier than those with strictly southern distributions, but wide-ranging plant species show no latitudinal shift in fruiting times, as would be expected if their fruiting seasons were adapted to disperser phenology (Fuentes, 1991; French, 1992; Willson and Whelan, 1993). Marked annual variation in the seasonal timing of fruit maturation in temperate plants indicates that events during earlier phases of reproduction can have a large impact on fruit timing and serves as a reminder that compromises may be required between the timing of flowering and the timing of fruit production (see Fenner, 1998).

Eriksson and Ehrlén (1998a) have examined structural and nutritional features of fleshy fruits of temperate plants in relation to phenology, finding that some secondary compounds containing nitrogen

decrease during the season, i.e. are more abundant in early- than in late-fruiting species. Whether this pattern is adaptive remains an open question. In contrast, no phenological trends in lipid or carbohydrate contents were found. The adaptive value of secondary compounds is controversial. Cipollini and Levey (1997, 1998) suggested that they probably have a specific function in the fruits, postulating different adaptive hypotheses, whereas Ehrlén and Eriksson (1993) and Eriksson and Ehrlén (1998b) argue that the distribution patterns of secondary compounds in plant tissues do not call for any adaptive explanation of their presence in the fruits. Another pattern that appears when comparing early- with late-ripening species is in seed number per fruit, which decreases seasonally (Eriksson and Ehrlén, 1998a); assuming trade-offs of numbers and size, this is attributed to developmental constraints imposed by a demand for a long developmental time in large seeds or, alternatively, to a 'better' dissemination of small seeds early in the season.

Future investigation must be directed to unravelling both the ecological causes of seasonal patterns of dispersal and the consequences of variation in dispersal phenology. We know very little about how much variation occurs among individuals in the timing of dispersal and whether this is the result of genetic or site differences in conditions controlling fruit maturation (but see, for instance, Heideman, 1989; see also review in van Schaik *et al.*, 1993). We know even less about the possibility that differences in timing of seed maturation result in accompanying differences in seed dispersal and offspring success. From the perspective of animal dispersal agents, variation in timing and abundance of fruit production can have great effects on consumers, resulting in massive population movements (e.g. Vander Wall and Balda, 1977; Leighton and Leighton, 1983; Ostfeld *et al.*, 1996; Selas, 1997; Hansson, 1996) or catastrophic mortality (see below), and such major effects on the consumer community are likely to have reciprocal, lingering effects on seed dispersal for several years.

For certain, usually long-lived, species, fruits are produced only once every few years in an unpredictable pattern. This phenomenon, called 'masting', has received much attention from ecologists and from evolutionary biologists (Kelly, 1994, and references therein). Three types of masting are distinguished: (i) strict masting, when the population reproduces synchronously and the distribution of seed crop size among years is bimodal (Bambos, *Strobilanthes*); (ii) normal masting, when synchrony is poor and there are many overlapping cohorts (e.g. imperfectly synchronized monocarps and many polycarps; *Fagus*, *Quercus*, *Pinus*); and (iii) putative masting, where variation in seed output is due only to environmental variation, without any evolutionary significance. A number of hypotheses (reviewed in Kelly, 1994) have been postulated to explain this phenomenon, the most widely accepted being related to economy of scale (i.e. larger reproductive efforts are more efficient in terms of successful pollination or seed production and survival) (e.g. Sork, 1993; Tapper, 1996; Kelly and Sullivan, 1997; Shihata *et al.*, 1998). The great variation in fruit production from year to year can have strong effects not only on the recruitment of the plant population itself (e.g. Schupp, 1990; Jones *et al.*, 1994; Crawley and Long, 1995; Shihata and Nakashizuka, 1995; Forget, 1997a), but also on the animal populations that consume their seeds (Ostfeld *et al.*, 1996, and references therein; Selas, 1997; Hansson, 1998; see also Crawley, Chapter 7, this volume).

The usefulness and ecological significance of the masting concept have been questioned by Herrera *et al.* (1998), who argue that a critical re-examination of patterns of annual variability in seed production is necessary, as most species apparently fall along broad continua of interannual variability in seed production, with no indication of multimodality (Kelly, 1994). In reviewing almost 300 data sets, Herrera *et al.* (1998) failed to identify distinct groups of species with contrasting levels of annual variability in seed output, although most polycarpic plants had alter-

ting supra-annual schedules, consisting of either high- or low-reproduction years. Annual variability in seed production appears to be weakly associated with pollination mode (wind versus animal pollination). In contrast, animal-dispersed species are more variable than those dispersed by other invertebrate means or animals that actively act as seed predators (Herrera *et al.*, 1998). These associations certainly deserve further investigation.

Ecological consequences of dispersal

Population structure

Dispersal of offspring away from the natal site is one way that genes move through a population or into new populations. Movement of genes also occurs at pollination in outcrossing species. Paternally inherited genes in outcrossing species move twice in each seed generation, once during pollination and again during seed dispersal; maternally transmitted genes in crosses and all genes in self-fertilized seeds move only once, during seed dispersal. Thus, in any one seed generation, paternally transmitted genes are likely to move farther from their source than maternally transmitted genes. Lloyd (1982) used his observation as a factor favouring the evolution of cosexuality in seed plants. He so noted that the difference in paternal vs. maternal gene movement is less in plants with very effective seed dispersal (e.g. by birds), which might facilitate the evolution of dioecism in bird-dispersed plants.

Gene movement is often limited within a population, such that many plant populations consist of genetic 'neighbourhoods' of more or less related individuals (e.g. Gibson and Wheelwright, 1995). Dispersal by caching animals (Kunler *et al.*, 1987) or by animals that use trapping sites (Julifot, 1997) or that are trapped to infected hosts (e.g. mistletoe dispersers: Larson, 1996) can lead to clusters of related plants within populations, even when the seeds have been carried

long distances. Microdifferentiation of local populations can occur on a very small spatial scale, in response to localized selection and/or very restricted gene flow (e.g. Schemske, 1984; Turkington and Aarssen, 1984; Parker, 1985; Berg and Hamrick, 1995; Linhart and Grant, 1996; Nagy, 1997; Nagy and Rice, 1997). Thus, the dispersal pattern of seeds contributes to the genetic structure of populations and to the potential for both genetic drift and responses to natural selection. Although some correlations of dispersal mode with the degree of local differentiation have emerged, these correlations are not very tight, and other factors must also contribute to observed genetic structuring (Hamrick and Lovell, 1986; Hamrick *et al.*, 1993; and see review in Linhart and Grant, 1996; Schnabel *et al.*, 1998).

On the other hand, the at least occasional passage of genes out of a local neighbourhood or between conspecific populations is important in maintaining the genetic diversity of the recipient population and presumably slows the rate of population differentiation (e.g. Staklin, 1987; Hamrick *et al.*, 1993; Linhart and Grant, 1996). To the extent that outcrossing is advantageous, the most effective outbreeding in populations with neighbourhood structure will occur when genes pass from one neighbourhood to another. Thus, in neighbourhood-structured populations, the 'best' outcrossing is rare, by definition. When neighbourhoods reflect ecotypic differentiation to local conditions, however, the 'best' outcrossing may occur between individuals that are not too close together and yet not too far apart. The concept of 'optimal outcrossing' has been controversial, and the extent to which selection may favour a degree of inbreeding is still unclear (Shields, 1982; Waddington, 1983; Jarne and Charlesworth, 1993, and references therein). Seed dispersal patterns have a clear potential to affect the level of outcrossing achieved.

The demographic and evolutionary consequences of seed dispersal began to receive attention only a few years ago (Houle, 1992, 1995, 1998; Herrera *et al.*,

1994; Horvitz and Schemske, 1994, 1995; Jordano and Herrera, 1995; Schupp, 1995; Schupp and Fuentes, 1995; Shibata and Nakashizuka, 1995; Kollman and Schill, 1996; Forget and Sabatier, 1997; Valverde and Silvertown, 1997; Carlton and Bazzaz, 1998; Dalling *et al.*, 1998). The scarcity of information available on the causes and consequences of spatial patterns of dispersal at a variety of scales from seeds to new adults is certainly a major gap in our knowledge on the ecology of seed dispersal. Most of the studies that consider the multistaged nature of recruitment find no strong and consistent relationships between seed and seedling spatial patterns of abundance. The causes of this 'uncoupling' are mainly attributed to the spatio-temporal variation in the relative importance of mortality factors (e.g. predation, pathogens, competition) for seeds and seedlings (Houle, 1992, 1995, 1998). Seed-seedling conflicts occur, for instance, in those microhabitats where the probability of seed survival is low but seedling survival is high (Jordano and Herrera, 1995). These conflicts probably play an important role in structuring many natural systems, as they appear to be rather common (Schupp, 1995). Plant population dynamics in patchy environments depends not only on stage-specific survival and growth in different patches, but also on the degree of discordance in patch suitability across stages (Kollmann and Pritl, 1995; Schupp, 1995; Schupp and Fuentes, 1995; Kollmann and Schill, 1996; Aguiar and Sala, 1997; Forget, 1997b; Russell and Schupp, 1998). Such discordance can have major impacts on both the quantity and the spatial patterning of recruits. Furthermore, site suitability may not be independent of seed arrival (due to density-dependent mortality factors).

In the case of animal-dispersed plants, the influence of frugivorous animals depends on the extent of coupling of the different stages in the recruitment process, which can vary among sites and populations. Factors acting at the end of the recruitment process can potentially 'screen off' the effects acting at the beginning,

making less predictable the demographic consequences of seed dispersal (Herrera *et al.*, 1994; Schupp, 1995). Intra- and inter-population variation in the composition of disperser assemblages visiting a plant species has been little documented (Snow and Snow, 1986; Reid, 1989; Guitián *et al.*, 1992; Jordano, 1994; Traveset, 1994; Loiselle and Blake, 1999), despite its potential demographic importance. Different species of frugivores generate characteristic seed shadows, depending on foraging behaviour, seed retention times, patterns of fruit selection and response to the vegetation structure (Herrera, 1995; Rey, 1995). In order to evaluate the effect of seed vectors on plant demography we need to know the disperser effectiveness, i.e. the proportion of the seed crop dispersed by a particular species (Schupp, 1993), and to examine how suitable the microsite is where seeds are deposited for germination and establishment. As effectiveness is difficult to estimate in the field, Bustamante and Canals (1995) have proposed a model to estimate it indirectly.

Colonization and plant community structure

Dispersal mode is one factor that affects the ability of a plant species to colonize a new area, especially one at some distance from the seed source. Long-distance dispersal capacity is poorly developed in ballistic and ant-dispersed species and much better developed in wind- and vertebrate-dispersed species. Wind and birds account for the arrival of most species in an isolated cloud forest in Colombia (Stagden, 1982). But wind dispersal is insufficient to result in frequent colonization of extremely distant islands, where many colonists arrive inside avian guts or stuck to the feathers (good numbers also arrive, without special devices, in the mud on birds' feet, and 1974). Birds may have been responsible for post-Pleistocene colonization of habitat islands on mountain-tops in western North America by conifers (Wells, 1983). Many colonists in the island flora of the Great