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A DAY IN THE LIFE OF A SEED: Movements and Fates of Seeds and Their Implications for Natural and Managed Systems

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Abstract

We develop a model that outlines the movements and fates of seeds after they leave the parent plant, and then we examine the relative influences of abiotic and biotic factors on those movements and fates. Phase I dispersal is movement of a seed from the parent to a surface, while Phase II dispersal includes subsequent horizontal or vertical movements. Although less studied, Phase II dispersal is more likely to account for the patterning of plants in communities and ecosystems and is the focus of this review. Abiotic factors influence Phase II dispersal—the distance and type of movement depend on seed morphology, surface attributes, and the nature of the physical forces. Biotic factors (animals) move seeds to new sites passively either on body surfaces or by ingestion, or actively by consuming fruits or hoarding seeds. Animals also influence the movements of seeds through digging and burrowing activities. Arrival at microsites suitable for germination and establishment is critical and is affected not only by abiotic and biotic factors but also by seed morphology and germination responses. We emphasize that seed banks are much more dynamic than they are usually portrayed. Although often poorly quantified, seed mor-

tality can occur at any point in the model. Sufficient differences exist among biomes that certain generalizations can be made regarding seed dynamics. Knowledge of seed movements and fates is essential for ecosystem restoration and conservation efforts and for the control of alien species in all biomes.

The consequence of all this activity of the animals and of the elements in transporting seeds is that almost every part of the earth's surface is filled with seeds or vivacious roots of seedlings of various kinds, and in some cases probably seeds are dug up from far below the surface which still retain their vitality. The very earth itself is a granary and a seminary, so that to some minds its surface is regarded as the cuticle of one great living creature.

HD Thoreau (140, p. 151)

INTRODUCTION

Thoreau's view of the abundance of seeds in nature as forming a veritable granary is true in terms of the large number of seeds that often occur in nature, yet few of these "potential" plants survive to produce seeds themselves. This abundance of seeds and their importance in nature has spawned a plethora of studies that treat nearly every conceivable aspect of seed biology from the chemistry of individual seeds (56) to the accumulation of seeds in the seed pools of a variety of communities (41, 80). Few of these studies consider the day-to-day movements and fates of seeds in nature. In a very real sense we do not have a balance sheet, in space or time, that permits us to account for the seeds that a plant produces.

To organize our thinking we use a conceptual model (Figure 1) that outlines the pathways that seeds follow after leaving the parent plant, the states in which they reside, and some of the biotic and abiotic factors that influence them. We present a compilation of the extant literature to give a sense of the significance of the various factors that influence the movements and fates of seeds in nature. We then examine some basic differences among biomes and infer ways that knowledge of seed movements and fates can be used for the management of ecosystems and their components.

The Model

The model (Figure 1) begins with a cohort of potentially germinable seeds on a plant. Although we use the term seeds throughout, we are actually referring to diaspores, i.e. the seed and any investing structures. Seeds are treated as free-living, immature plants that are tracked until they germinate and become seedlings. Germinable seeds are subject to death from biotic or abiotic factors at any point in the model. Seed mortality resulting from consumption, weather, or other factors moves seeds to a sink because they have lost their potential to become plants. The movement of germinable seeds from the plant to a

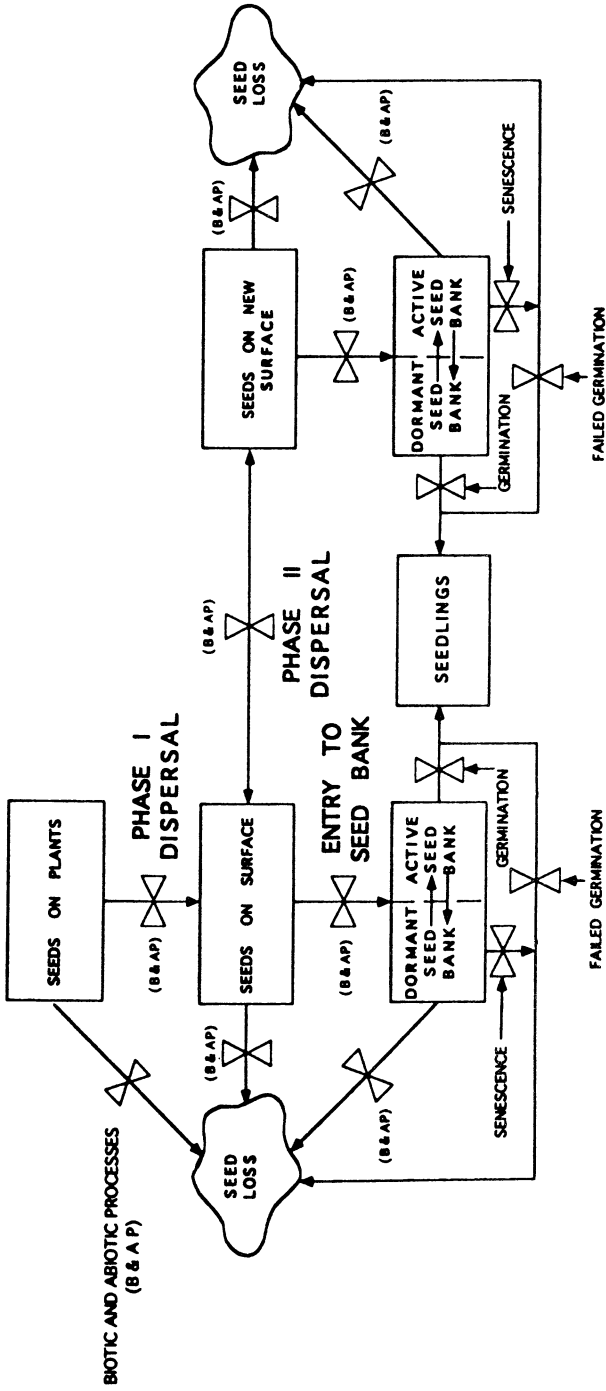


Figure 1 A conceptual model of the movements and fates of seeds. The germ of this model derives from consideration of Figure 4/1 of Harper (57), Figure 1 of Simpson et al. (131) and the dispersal phases of Watkinson (151). The model is explained in the Introduction.

surface is Phase I dispersal. We specifically use the terms “seeds on a surface” because many seeds arrive on surfaces other than soil, e.g. seeds of mistletoes, some bromeliads and orchids, are specifically adapted to disperse to tree branches or trunks (118). Phase I dispersal is the subject of a significant portion of the current seed literature. In part this emphasis is due to the fact that the movement of seeds from the plant to their first site of repose is amenable to direct observation and experimentation, including detailed aerodynamic studies and modeling (17, 49, 105). In contrast, we know much less about the fates of seeds once they land on a surface. Their size, mobility, and the fact that many are lost to animals or buried out of view makes them intractable objects of observation and experimentation. Consequently, the movements of seeds after initial dispersal from the parent plant are not well documented. In the model, Phase II dispersal includes both secondary horizontal and vertical movements of seeds. Thus, the model has an additional spatial component that is usually ignored. The point of entry into the seed bank depends on the plant species. Most seeds enter the seed bank after arrival on a surface, but in plant families characteristic of fire-prone habitats, e.g. Myrtaceae, Proteaceae, and Casuarinaceae, many species form aboveground seed banks (11). Seeds entering the seed bank may be in either an active or a dormant state. Physiologically active or nondormant seeds may germinate immediately, remain nondormant in the seed bank until the proper environmental conditions occur, or become dormant (8). We emphasize that seeds in seed banks are more dynamic than they are often portrayed. Seeds in seed banks may be moved by animals, wind, or other physical forces, lost to consumption by animals or attack by pathogens, change physiological status, or lose their germination potential because of senescence, but they are not static. As we detail below, the result of Phase I dispersal is often the arrival of a seed at a site close to the parent. The dispersal movements that account for the patterning of plants in communities and ecosystems is much more likely the result of Phase II than of Phase I dispersal, yet this is the area of our greatest knowledge gap. Although we examine all aspects of the model, our primary focus is on Phase II dispersal and its consequences.

PHASE I DISPERSAL

Phase I dispersal involves any mechanism by which a seed moves or is transported from the parent plant to a surface. Most plant seeds move only short distances from the parent (129). The resulting patterns of seed deposition are usually skewed, with a distribution represented either by a negative exponential function or by a curve that peaks a short distance from the plant and then shows a negative exponential decrease (154). Variation in this pattern results from factors such as habitat patchiness, seed vector behavior, or chance.

Details of the spatial result (seed shadows) of Phase I dispersal are well studied for a variety of individual species (155). Studies of Phase I dispersal for entire natural communities are much less common (20, 114).

Abiotic Influences

Abiotic dispersal may involve only gravity—seeds may simply fall beneath the parent. It may, however, involve specialized morphology for wind transport, such as samaras or plumes, or ballistic mechanisms in which seeds are ejected when hit by rain drops or when enveloping structures dry. When wind is the only agent, the height of plant, characteristics of surrounding vegetation, details of seed weight, size, and wind conditions during dispersal are normally sufficient data to predict patterns of seed deposition (49, 105). Recent models of wind-dispersed seeds have examined the effects of variations in meteorological conditions, seed mass, or form (49, 105). Models for other types of abiotic Phase I dispersal are more difficult to develop and are less common.

Biotic Influences

More attention has been devoted to biotic than abiotic dispersal, and several recent reviews discuss animal dispersal (62, 63, 136), frugivory (42, 70, 153), adhesion (133), and food hoarding and its dispersal consequences (113, 144). Biotic dispersal is described in terms of the method of seed acquisition and dispersal by the animal (136). Seed acquisition is categorized as passive when seeds or fruits are transported, by accident, on body surfaces (passive external) or consumed incidentally with other foods (passive internal). Active acquisition occurs when animals select seeds or fruits. Specific morphological characteristics of seeds and fruits facilitate the plant-animal interaction, whether during active or passive acquisition. Many seeds have adhesive properties such as hooks, barbs, or viscid surfaces for passive animal dispersal; these may result in longer dispersal than active dispersal by animals or wind dispersal (133). Actively acquired seeds are often attractive to animals because of fruit or seed color, odors, or the presence of a food reward such as investing pericarps or eliasomes on ant-dispersed seeds (136). The degree to which seeds are acquired while they are still attached to the parent plant or after they arrive on the soil surface depends on the life form and life history attributes of the plant species and on the behavioral characteristics of the animal. Animals that disperse seeds include birds, mammals, and ants as the main dispersers, but there are instances of dispersal by earthworms, beetles, Amazonian forest fish, tortoises, some herbivorous lizards, and even a frog (135, 136). Although not as common as for abiotic dispersal, models of biotic dispersal do exist. Murray (99) developed a simulation model that estimates reproductive output and relative “fitness” of neotropical gap-species from data on the seed shadows produced by different avian dispersers, germination requirements, and forest dynamics.

It is important that many studies fail to distinguish between Phase I and Phase II dispersal. Studies that quantify both Phase I and II dispersal and their relative effects on the various aspects of plant establishment are the most likely to lead to an understanding of plant population processes and community dynamics. Although many dispersal studies associate animals with plants as agents of dispersal only in the space dimension, many animal activities, e.g. hoarding, are equally important for dispersing plants in the time dimension—a function seldom quantified.

PHASE II DISPERSAL

Once a seed has arrived on a surface, it can remain where it initially came to rest, it can move to a new location (horizontal movement), or it can be incorporated into the soil (vertical movement). The probability of redistribution is determined by the nature of the abiotic or biotic factors that act on the seed, the characteristics of the site where the seed rests, and the interactions of the seed with abiotic or biotic factors.

Abiotic Influences

Relationships between a seed's physical dimensions, e.g. mass, length, width, and depth, and surface characteristics influence the horizontal and vertical movement of seeds after they have reached a surface. The type of movement and the distance moved depend on the nature of the physical forces. In steep terrain, gravity can move seeds downslope. The slope characteristics influence both the distance and direction of seed dispersal (152). Obviously, gravity facilitates entry into seed banks, but the amount of movement depends upon soil pore size and the physical dimensions and surface characteristics of the seeds (23). Wind contributes to the horizontal or surface movement of seeds in many environments, especially those where vegetation is sparse or low in structure (i.e. deserts and tundra). Wind is often a dominant dispersal agent for severely disturbed sites, e.g. Mount St. Helens (32). Wind has less effect on vertical movement of seeds, except for seed burial or reexposure along with wind-blown soil fines and litter (159). Horizontal transport of diaspores in rain wash can occur in any environment where the intensity and amount of precipitation is sufficient to result in overland flows, and such transport has been observed in a variety of ecosystems, including rain forests (122) and deserts (117). Precipitation also moves seeds vertically through the soil column (143). The duration and intensity of individual storm events and surface characteristics affect the vertical and horizontal movement of seeds. Several soil characteristics, including type, structure, and the amount of clay and colloid material, affect vertical movement of water, small soil particles, and, presumably, seeds. Precipitation and cryoturbation alter the structure of surface soils (128, 159)

and, consequently, susceptibility of soils and seeds to later movement by wind or water. Cryoturbation alters the vertical distribution of seeds, moving seeds both upward and downward (143) and, in the case of solifluction lobes, may result in deep burial (94).

The type and intensity of the physical forces that act on seeds and the sites of deposition are largely determined by ecosystem characteristics. The vertical and horizontal structure of the vegetation, precipitation and temperature regimes, and the importance of wind vary significantly among ecosystems. Because of the importance of abiotic seed dispersal in systems with extreme environmental regimes, these environments have received the most study. In arid shrublands and woodlands where individual shrubs or trees are widely spaced, wind-blown or water-transported soil and litter accumulate under the long-lived shrubs or trees, resulting in a highly heterogeneous surface environment (88). Interspaces are often sparsely vegetated and characterized by a high percentage of bare ground. Wind velocities in interspaces are as much as four times greater than under shrubs (107). Consequently, interspaces serve as avenues of seed transport, with seed entrapment occurring primarily in soil cracks and crevices or under the litter-strewn canopies of shrubs or trees (74, 102, 117). The highest seed densities and greatest species richness in pinyon-juniper woodland are found at the interface between interspaces and the dense litter underneath the tree (79).

Within a given ecosystem, seeds dispersed from the parent plant can land within dense vegetation, on sites covered with litter, on exposed soils, on snow or ice, or even on other plants. The surfaces that seeds land upon are primary determinants of subsequent movement. Seeds that fall within dense vegetation generally have shorter secondary dispersal distances and are often more concentrated than seeds that land within open vegetation or on exposed soils (151). Within chalk grasslands, seed accumulation commonly occurs in patches of bryophytes (143). Plant litter also traps seeds. Seeds of *Bromus tectorum* are more likely to remain in place on natural or artificially littered microsites than on bare soil microsites (74).

Exposed soil can comprise most of the surface cover in extreme environments like deserts and tundras, in agronomic situations, or on sites disturbed by human activities. In many natural systems, soils exposed by small-scale disturbances serve as important sites of recruitment. Soil properties, climate, and disturbance characteristics determine the physical attributes and microtopography of exposed soils. In turn, these soil attributes influence both the horizontal and vertical movement of seeds. Wind-blown seeds often move farthest on smooth soils and remain in position, trapped in crevices, in rough soils (57, 102). A study of wind movement of four asymmetric samaras on four surface roughnesses (a smooth board, 250 μm , 50 μm and 2.0 mm particle size soil) showed that seeds remained in place longer on rougher surfaces

because the threshold wind velocity was greater and the return time for that velocity was longer (69). Heavy seeds moved less frequently than light seeds. On exposed soils in a windy alpine environment, it was possible to develop predictive models of the vertical and horizontal movements of seeds with varying morphology over a range of soil particle sizes (23). In smaller particle size soils, smaller seeds tend to remain trapped in position and to reach greater depths in the soil column, while seeds that are longer or have higher eccentricity (length/width ratios) move horizontally over the soil and are not trapped. In larger particle size soils, both small and large seeds are trapped, but smaller seeds reach greater depths. For these alpine species, patterns of seedling emergence in the field could be explained largely by relationships between seed attributes and surface characteristics (22, 23). Depressions in the soil or obstructions serve as accumulation sites for seeds that move over the soil surface (117) by generating eddies or wind shadows and trapping seeds moved by overland flows. For artificially created depressions in Sonoran Desert soils, depression features such as perimeter, volume, depth, and surface area were significantly correlated ($R^2 = 0.9$ to 0.91) with longest seed dimension and density of seeds trapped in the depression (116). Obstructions or mounds frequently result from small mammal burrowing and tunneling. Such digging can expose surface and near-surface soils that act as catchments. In aspen woodlands, more seeds were found on pocket gopher mounds than in equivalent columns of adjacent topsoil (92).

Soil crusting and compaction occur on many types of exposed soils and can preclude seed entrapment and hinder seedling emergence (128). Soil crusts form when clods are broken down by raindrop impact and the dispersed finer particles are washed into the pores of the surface soil, resulting in a cemented seal (68). On crusted soils, seedling emergence (and presumably seed entrapment) most frequently occurs in soil cracks (34, 37, 58, 128). Similarly, for soils covered with cryptogamic crusts, seed entrapment and germination are highest in cracks in the crust (18). Soil compaction can result from vehicle passage and animal trampling as well as raindrop impact (59). Both seed incorporation and seedling emergence are lower on compacted than on non-compacted soils (128). Soil crusting, cracking, and compaction change over the growing season (159) owing to cyclical wetting and drying of soils and the effects of freezing and thawing.

Seeds of certain species can be wind-dispersed over snow-covered surfaces. Winter dispersal favors species whose inflorescences are located above the snow surface or that grow on exposed sites. Small, light seeds are transported the farthest. Sorting occurs, depending upon seed morphology and their associated aerodynamic properties, and distinct zones of debris accumulation, including seeds, occur on snowbeds in arctic and alpine tundras (47). For a gap colonizing tree, *Betula lenta*, secondary dispersal across a snow surface

resulted in a distribution area 3.3 times greater than that covered by aerial dispersal alone (90). Seeds of *B. lenta* accumulated in shallow depressions in the snow at the bases of uprooted trees, resulting in aggregated seed distributions which increased the chances of successful regeneration.

Biotic Influences

Phase II dispersal by animals has multiple effects on seed fates. Seeds with morphological adaptations for abiotic or biotic primary dispersal or that apparently lack adaptations for dispersal can be secondarily dispersed by animals. Secondary dispersers often transport seeds farther than they are dispersed by primary mechanisms. For example, pine species that produce winged seeds typical of many wind-dispersed plants are often scatter-hoarded by rodents. In the Sierra Nevadas, animals had the capacity to harvest most of the naturally-produced seed of several pines (*Pinus jeffreyi*, *Pinus ponderosa*, and *Pinus contorta*) during the two-month period between seedfall and winter (146, 148). While wind-dispersed seeds of *Pinus jeffreyi* were distributed primarily within 12 m of source trees, chipmunk caches were found 2–69 m from trees (146). In some cases different animal species are responsible for Phase I and Phase II dispersal in the same plant species, and both animals may have mutualistic associations with the plant. In a Costa Rican Forest, ants harvest a high percentage of the seeds in bird defecations and cache them in their nests in partially decomposed twigs or deposit them on refuse piles (81). Similarly, for some species of figs a two-phase system exists that involves both birds and ants (71).

Many animals have direct or indirect effects on the vertical movement of seeds. Animal digging, burrowing, and tunneling can bury surface seeds or resurrect buried seeds. Large terrestrial mammals (armadillos, coatis, porcupines) and smaller animals (arthropods, caecilians, terrestrial crabs) dig holes that can influence seed movement (45). Estimates of the amount of soil moved by pocket gophers, through their tunnelling activities, range from 1 to 8.5 kg m⁻² yr⁻¹ (1). This soil churning affects seed entrapment patterns, the microsites of establishment, and in the long term, plant community composition (66). Following the volcanic eruption of Mount St. Helens, the activities of surviving pocket gophers in bringing soil and propagules to the surface of ubiquitous and deep tephra deposits facilitated plant establishment (2).

Earthworms overturn large quantities of soil by burrowing and casting, while termites and ants overturn smaller quantities. Ingestion of seeds by earthworms is important in initial burial and in subsequent return of seeds to the surface in casts. On one temperate grassland area, 70% of the seedlings occurred on worm casts, although they comprised only 24% to 28% of the surface area (48). Similarly, in one year earthworms deposited on the soil surface a quantity of *Cerastium fontanum* seeds almost equal to the entire seed bank of the species

(139). Ingestion is dependent on seed size, and seeds in worm casts are smaller than those in the seed bank as a whole (139), indicating selective effects on seed bank dynamics.

Many animal species, especially those that function as Phase II dispersers, have associations with plants that are both antagonistic (granivory) and mutualistic (dispersal). Many of the seeds that are harvested are killed, but those that survive may exhibit substantial benefit (81, 144, 149). The tendency is often to classify interactions between seeds and animals based on the most common outcome, even though the least common outcome may be of greatest importance to the plant (81). The outcomes of seed movement or handling by animals have been variously defined in terms of efficiency, quality, goodness, and reliability. Schupp (126) defined disperser effectiveness as a product of quantity or the number of seeds dispersed, and quality or the probability that a dispersed seed will produce a new reproductive adult. This approach requires that disperser effectiveness be defined in terms of the contribution that a disperser makes to plant fitness. This is appropriate for examining the fates of seeds, because it defines the best measure of disperser effectiveness as the number of new adult plants that result from the activities of a particular disperser relative to those that result from other dispersers or types of dispersal. Few studies have examined all of the components necessary to determine disperser effectiveness, although some come close (61, 78, 149).

The primary factors that influence disperser effectiveness include animal foraging behavior, seed availability, seed attributes, and seed location. The foraging behavior of animal species and the complement of animal species within a given area determine both the quantity and quality of seed dispersal. Plant species are often dispersed by a suite of unrelated animals that harvest varying numbers of seeds and place these seeds in quite different locations. Assemblages of dispersers may differ among locations, and both the likelihood of seed harvest and the fates of harvested seeds depend on the composition of the local fauna (14, 113, 126). In a chaparral community dominated by the shrub *Dendromecon rigida*, ant species differing in nesting and foraging behavior had varying effects on seed mortality, the microsites of germination, aggregation, and position on the landscape (14). In the Sonoran Desert, ants foraged only on the surface (85% of experimental seeds) while rodents harvested seeds from below the surface as well (96% of experimental seeds) (115).

Seed availability has important effects on the quality and quantity of seeds dispersed by animals. Within well-established populations of myrmecochorous plants with high seed densities, seed dispersal may be ant limited. Removal rates decrease over time, presumably because ants become satiated (132). Seed masting often increases the proportion of seeds that establish through predator

satiation (28). In contrast, given low availability of seed, the animal disperser may consume a large portion of the seed crop, resulting in declines in plant populations (113). Seed availability may exhibit a high degree of stochastic variability, due to climatic and other environmental variability, and these fluctuations can be reflected in plant population densities and rates of expansion attributable to disperser activities (119). Rates of seed acquisition by animals for different plant species are often related to animal seed preferences. Most harvester ants exhibit preferences based on seed size, morphology, and availability (60). Seed use by ants in the Sonoran desert was related to seed size, with the smaller *Pheidole xerophila* specializing on small seeds, and the larger *Pogonomyrmex rugosus* preferring larger seeds (94). For *Pogonomyrmex occidentalis* in shrub steppe, relative seed abundance and size explained 28% of the variation in preference by ants (30). Decreases in the total potentially viable seed pool near the surface were estimated at 9% to 26%, while decreases in preferred species approached 100% (30).

Rodents usually exhibit seed preferences when presented with equally accessible seeds from several species (113). Factors influencing seed preference include the types of energy contained within seeds (carbohydrate vs protein), the presence of secondary compounds, and the ease of handling (144). Because energy gain usually increases with seed size, most rodents prefer large seeds as long as they are not too large to transport (115). Rodents discriminate between edible and inedible seeds using olfactory and, to a lesser degree, visual and tactile cues (144, 147), which result in greater harvesting of viable seeds.

Seed removal by secondary dispersers varies among the microsites in which seeds are located and among species (64). Selective harvest of clumped seeds by animals reduces the spatial patchiness of seeds in the soil (115) or redistributes the clumps through caching. Soil characteristics influence rodent foraging and, thus, seed distributions. Seed harvesting rates increase with seed density and soil density, and the rates decrease with soil particle size (112). Surface litter also influences the efficiency of seed harvesting (100), with the numbers harvested depending upon the seed species, the animal species, and perhaps overall seed availability (125).

The assumption that small size often allows seeds to "escape" seed harvesting by animals (67, 85) needs to be reevaluated in the context of Phase II dispersal. The probability of seed harvest is clearly related to the microsites of seed deposition and the size of the animal. If small seeds land on surfaces that promote incorporation into the soil or decrease seed-harvesting efficiency, then the probability of seed harvest decreases (113). However, if small seeds arrive on readily accessible surfaces or in identifiable depots (e.g. frugivore feces) they may be highly susceptible to harvest by small mammals or ants (14, 81, 113).

ENTRY INTO SEED BANK—SEED/MICROSITE INTERACTIONS

The potential benefits of seed dispersal to plant fitness depend on the microsites to which seeds are dispersed and the interactions of seeds with those microsites. Those microsites to which seeds are dispersed or that promote seed retention are not necessarily the best microsites for seed germination or seedling establishment (127).

Abiotic Factors

Soil surface attributes influence not only the sites of seed retention but also the microenvironment of germinating seeds and establishing seedlings. Larger soil particles increase the number of seeds trapped in soils (23) and result in longer residence times of large seeds and, consequently, higher seed germination (69). However, there is a soil particle size above which seedling establishment is compromised. Larger-particle-size soils seldom have the nutrient retention or water holding capacity of small-particle-size soils and may not provide the close root-soil contact needed for seedling growth and survival. In a seeding experiment on the pumice plains of Mount St. Helens, higher seedling emergence occurred in coarse pumice, while higher seedling survival was observed in fine pumice (158). Although not mentioned by the authors, higher seedling emergence on the coarse pumice was likely due to higher seed entrapment and retention.

Surface microtopography significantly affects the ultimate fates of seeds. Soil depressions or troughs tend to trap high numbers of seeds, and this “clumping” of seeds may result in higher seed predation (117). In arid environments, depressions can result in higher humidity and more favorable soil water relations for seeds and seedlings by trapping snow and accumulating precipitation. One-hundred times higher emergence of *Bromus tectorum* seedlings was reported for seeds sown in 9-mm soil pits than for seeds sown on bare soils (37). In humid environments, increased moisture may result in higher seed loss to pathogens.

Because seeds have many of the same physical attributes as “litter,” abiotic forces deposit seeds in the same locations as plant litter (39). Animals often bury seeds in litter or under litter-covered surfaces. Relationships between seed morphology and the physical attributes of litter influence seed movement and burial on litter-covered surfaces. Litter facilitates the burial of seeds with hygroscopic awns in wind-blown arid environments (134) but retards burial of awned grass seeds such as *Aristida longiseta* (43). If extremely thick or coarse, litter can act as a physical barrier preventing seed penetration (55). Mortality results if germinating seedlings cannot emerge through the litter (150) or if the roots of seedlings cannot reach the soil (12, 43). In *Bromus*

tectorum, an annual grass, variability in emergence timing may be due largely to variable penetration of both seeds and seedlings through the litter mat (86).

Biotic Factors

The role of animals in placing seeds in sites suitable for germination during Phase II dispersal is highly variable. Seed burial by animals may result in a more suitable physical environment for subsequent germination. However, the effects of seed burial on germination and establishment are highly species specific and are related to both soil conditions and depth of burial. In deciduous forests, seeds of some species such as oaks (50) may fail to germinate if they are not buried. In contrast, germination rates of white oak and pignut hickory are similar for seeds buried 2.5 cm deep or covered only with leaf litter (7). Soil water and temperature regimes influence both germination and decay of buried seeds. In arid areas, burial by animals may increase establishment by decreasing desiccation of the germinating seedling (113). Burial in cool dry soils may promote seed longevity, while burial in cool moist soils may result in natural stratification and increased seed germination. In warm humid areas, burial may increase the rate of seed decomposition and the probability of attack by pathogens.

Burial of seeds by food hoarders decreases the probability that seeds will be located and eaten by seed predators. Harvest rates of large seeds and nuts on the soil surface can be close to 100%, but rates may decrease as depth in the soil or litter increases (147). Not all secondary dispersal by animals results in seed burial. Ants often deposit seeds in refuse piles where they are susceptible to subsequent movement (14).

Animals may deposit seeds in nutrient rich environments, e.g. feces. In some ecosystems soil nutrients, including nitrogen and phosphorus, and soil aeration are significantly higher on ant refuse piles than on the surrounding area (9, 10). This may increase seed bank turnover rates by placing seeds in favorable germination sites and enhance seedling growth and survival (81). Ant nest sites are not always characterized by higher soil nutrients. In Australian sclerophyll vegetation, soil next to emerging seedlings of myrmecochores did not have higher levels of total N or available P than did soil around seedlings of nonmyrmecochors or soil not occupied by seedlings (120).

Seed Morphology and Seed Germination

Many seeds have specific morphological adaptations that influence seed movement into suitable germination microsites. Hygroscopic awns twist and untwist in response to changes in humidity, moving the diaspore over the soil surface and, given the proper surface, drilling the diaspore into the soil (108, 134). The pappuses of some species of Asteraceae collapse irreversibly or collapse and expand in response to humidity (128). This action also moves the diaspore

over the soil surface and pushes it into the soil. Pappuses of other species remain rigid and maintain a constant angle between achene and soil, ensuring contact of the micropyle with the soil surface (128). Seeds of many species, including those with awns and pappuses, have antrorse (backwardly directed) bristles or barbs at the base of the seed that anchor the diaspore firmly in position. This prevents further movement and may produce a counter force to that of the radicle penetrating a compacted soil surface (109). In certain species the hairs on the hypocotyl swell in response to hydration and can raise seeds to a 30–45° angle with the soil surface, causing micropyle contact with the soil (52). The tips of the hairs become mucilaginous and, as they dry, bind to the soil, which helps the seedling to anchor and its roots to penetrate. Other species have mucilaginous seed coats that adhere to the soil surface when wetted (23). Morphological adaptations for primary dispersal do not preclude adaptations for movement on the soil surface. In *Erodium moschatum*, a geranium, seeds that moved on average 56 cm by explosive dispersal later moved another 7 cm over the soil surface through the activity of the hygroscopic awn (134).

Interactions of seeds with their environment can be highly specific, influencing not only the burial of individual seeds, but also the distributions of species. In southeastern Queensland, soils with a relatively high clay content had surfaces that were either loose and crumbly or that cracked on drying (110). Species with hygroscopically awned diaspores predominated, presumably because their diaspores encountered more suitable microsites. Soils with a high sand content had surfaces that were hard setting, had a tendency to form surface crusts, or were loose and single-grained. These surfaces were unsuitable for hygroscopically awned species and were dominated by unawned species.

Seed germination syndromes provide environmental cuing mechanisms that increase the probability of encountering conditions that are favorable for seedling growth and survival, essentially allowing seeds to disperse in time (3). Dormant seeds are those that will not germinate under normal environmental conditions and that must undergo afterripening or embryo maturation or be exposed to the proper environmental stimuli (8). Once seeds become active or nondormant, they must still experience the proper set of environmental conditions (light, temperature, and soil moisture regimes) to germinate. Seeds of many species, annuals and perennials, exhibit secondary dormancy or annual dormancy/nondormancy cycles that vary depending on species life histories and habitat characteristics (6, 8).

Because the seeds of most species require specific environmental conditions to become nondormant and then to germinate, the microsites of dispersal and the secondary movements of seeds are important determinants of seed germination. Small-scale variability in light, temperature, and moisture regimes exist within most communities. These environmental differences are accentuated by

disturbance. Vegetation cover often results in lower soil temperatures, a lower red/far-red photon flux than sunlight and thus a low proportion of the active form of phytochrome, and in areas where growing-season precipitation is limited, lower soil moisture (22, 44). Higher soil temperatures, light fluxes, and soil moisture on disturbed soils or in open areas often favor seed germination (8). Although seldom studied, interactions among seed dispersal patterns and seed dormancy and germination undoubtedly influence seed turnover rates and the apparent spatial distribution of seeds in seed banks.

SEED LOSS

Abiotic Influences

Direct effects of abiotic factors on seed mortality include deep burial, crushing, abrasion, burning, water-logging, etc. As detailed below, the effects of abiotic factors on biotic interactions, senescence, and germination are probably more important for population and community dynamics.

Biotic Factors

Predation on fruits and seeds and its consequences for the plant community have been the subject of over a thousand studies and several reviews (28, 67, 85, 124). Recent papers emphasize the consequences of predation for plant population dynamics and plant community composition (65) and processes such as succession (31). The approach has shifted from investigating how many seeds are taken to determining the distributions and fates of those seeds that escape predation.

Seed predators and predation differ during the different life stages of plants. Predispersal predators are likely to be "small, sedentary, specialized feeders belonging to the insect orders Diptera, Lepidoptera, Coleoptera, Hymenoptera" (28). In addition to selective seed consumption by specialists, many seeds are lost by the consumption of flowers, seed heads, and fruits by large herbivores. Although Crawley (28) lists over 50 studies of predispersal seed predation, few of these demonstrate unambiguously the population or community consequences of predation (but see Louda (84, 85)).

Predation following Phase I dispersal is the common topic of seed predation studies. Here generalist and specialist vertebrates increase in importance. So long as the seed has not reached a safe site (often used synonymously with seed bank), it is subject to discovery and consumption. Even in the seed bank, seeds are not safe from pathogens and larger predators, especially vertebrates (some birds and mammals) that can find buried seeds. The consequences of predation range from effects on recruitment and distribution within a population of a single species to changes in composition of plant communities

mediated directly by seed predation (85) or indirectly by changing the competitive balance between two seed consumers and subsequently between plants.

In contrast to animal predation, few ecological studies have addressed the effects of pathogens on seeds, especially those occurring in seed banks. Surface-contaminating fungi or bacteria can cause seed death directly through necrotic action or indirectly via production of toxic metabolic wastes (15, 16). In contrast, internally borne pathogens (some fungi and many viruses) often increase seed metabolic activity thus accelerating senescence (15, 16). In addition to seed death, fungal pathogens can decrease or stimulate germination (24) and may result in altered seedling survival following germination (29). Susceptibility to pathogen attack may be higher for physiologically active seeds than dormant seeds and may also increase as seeds age and membrane structure deteriorates (15, 16). Estimates of the effects of pathogens on soil seed dynamics are rare. In shrub steppe, overwinter seed decomposition and attack by fungi decreased the viable seed banks of common species by about 56% (29). In contrast, fungicide applications reduced seed loss of an invasive tropical shrub, *Mimosa pigra*, by only 10–16% over the seven month dry season, indicating that pathogens may have greater effects on germinating than on dormant seeds in this species (83).

Senescence

Environmental characteristics of the site and location in the seed bank determine the moisture and temperature regimes that seeds are exposed to and also can influence respiration and aging. Seed longevity is promoted under either extremely cold or dry conditions, and viability loss is increased under warm and moist conditions (98). The loss of seed viability over time can often be described with a negative exponential model, although a rectangular hyperbola sometimes provides a better fit to the data (98). While the relationship between seed longevity and temperature does not appear to vary among species, the relationship between longevity and soil moisture does (33).

The spatial and temporal effects of varying environmental conditions among the microsites of seed entrapment on seed longevity are largely unexplored. Most estimates of seed longevity come from studies in which seeds are buried under close-to-natural field conditions and retrieved over time (98). Because seeds are usually buried in soil under somewhat protected conditions, longevity of the seed population as a whole may be grossly overestimated. Such experiments often exclude seed harvesters and pathogens and thus fail to consider the effects of seed handling or pathogenic interactions on longevity. In addition, they restrict secondary seed movements and thus neglect the effects that exposure to varying environmental conditions may have on seed longevity.

Large differences in seed longevity exist among individual species in all ecosystems—tundra (19) to rain forest (45, 150). Two common generalizations

regarding differences in species longevity are that there is a tendency for early seral or arable weed seeds to exhibit greater longevity than late seral species, and that small seed size is related to seed longevity. There is considerable evidence for the first generalization (51), but it is the second that is important for Phase II dispersal. An examination of nine species in the British flora showed that small seed size (mass) and low variance of seed or fruit dimensions (length, width, and depth) were related to greater seed longevity and either short-term (1–5 yr) or long-term (> 5 yr) persistence in the seed bank (138). Persistence of small and compact seeds in the seed bank is undoubtedly increased by a higher probability of seed burial. Short-lived seeds are usually larger and either flattened or elongate (138). Small and compact seeds exhibit higher soil incorporation than large seeds (23). Seed size is not a universal predictor of seed longevity, and seed morphological characteristics influence lifespans. While the large, hard-coated seeds of the Leguminosae are usually long-lived, the tiny, soft-coated seeds of *Salix* species live only a few weeks.

Failed Germination

Failed germination constitutes seed death soon after germination. We distinguish between failed germination and seedling death because seedling death is usually evaluated only after seedling emergence. This potentially ignores the death of numerous germinated seeds and underestimates seed bank losses. Antecedent conditions such as the effects of fungi (24) or handling by animal dispersers (147) increase mortality of germinating seeds. Consumption of germinating seeds by pathogens, predators, or granivores also reduces survivorship. Highly variable environmental conditions or unusual weather events can cause high mortality of germinating seeds (27). Unusual weather conditions can also “miscue” germination so that the timing of germination is inappropriate. Finally, seeds may arrive at microsites that provide the necessary conditions for germination but that are inadequate for growth and survival (127).

COMPARISONS AMONG BIOMES

Our presentation of the model provided examples from a variety of ecosystems to show the generality of our comments. This approach masks specific climatic or vegetational relationships that may exist and obscures some potentially interesting ecological differences. Here, we look for such general trends at the biome level of organization, of sufficient scale that the nuance of local variation can be ignored.

Desert

Among the world’s deserts, a lack of specific adaptations for long-range dispersal is common, and species often have characteristics that hinder long-

range dispersal (35). Many species have adaptations for short-range dispersal such as ballistic seeds. Wind dispersal varies in importance (35, 142). Abiotic redistribution of seeds on the soil surface by wind (74, 102) or overland flows (117) can be significant. In many deserts seed harvesting by ants and caching and hoarding by small mammals, particularly heteromyid rodents in North American deserts (113), influence seed distributions and plant establishment patterns. The importance of granivory by small mammals differs significantly among the world's deserts. Only in North America, Australia, and the Afro-Asian desert belt are there small bipedal desert mammals that specialize on seeds—other small desert mammals are opportunistic foragers on insects and vegetation (89). Predation by birds and ants is an important agent of mortality in all deserts. Additional seed losses due to fungi and other pathogens (29), as well as failed germination, can be significant.

Correspondence between the seed bank and current vegetation depends upon species composition. Few long-lived desert perennials have persistent seed banks, while persistence of annual species ranges from highly stable to transient (76). In the Sonoran and other hot deserts, high seasonal and annual variability in the seed bank indicates a lack of persistence or stability of the seed bank as a whole (76). Seed distributions in desert systems are highly clumped—a 10-fold variation in the numbers of seeds exists among various Sonoran desert microhabitats (117).

Tundra

In tundra ecosystems, seeds are often small, and few species invest in adaptations for seed dispersal. Adaptations for dispersal are primarily for wind, although alpine grasslands have small numbers of species with adaptations for ant, vertebrate, adhesive, or ballistic dispersal (157). Redistribution is strongly influenced by wind, with relationships between soil surface characteristics and seed attributes determining the horizontal and vertical movement of seeds (22, 23). Phase II seed dispersal by animals is rare. Seed-eating birds (horned larks and rosy finches) and insects (e.g. bruchid beetles) can be abundant in North American alpine tundra, and the potential for seed predation is high, although rates have not been measured (21). Low heat budgets and cold soils result in slow decomposition and may promote seed longevity relative to more temperate biomes (93). Deep burial of seeds can occur in solifluction lobes resulting in the long-term (300+ yr) preservation of genetic material (94).

Tundra florae are characterized by low numbers of species, and species identities in the seed bank and current vegetation are often similar (20, 93). Relative species abundances in the aboveground vegetation, seed rain, and seed bank depend upon species life histories and disturbance regimes (21). Both seed rain and seed banks are spatially and temporally variable, with seed banks exhibiting greater consistency than seed rain (20).

Grasslands

Important dispersal mechanisms in grasslands include wind, animals, and ballistic seeds. Seed production is often highly variable from year to year (121). Seed predation by ants, small mammals, or birds can be significant.

For many perennial grasslands, significant differences exist between the composition of the seed bank flora and the aboveground plant community. Depending upon the length of time since disturbance and the magnitude of disturbance, an abundance of both early seral natives and exotics may persist in the seed bank (121). Perennial species abundant in the standing vegetation may be absent from the seed bank, due to short-lived seeds (25) or heavy grazing and inflorescence removal (104). Highly variable seed production from year to year, combined with low seed longevity of late seral perennial grasses, can result in temporal variability in the seed bank. Spatial variability can occur as a result of individual species dispersal patterns interacting with small-scale topographic features (77).

Coniferous Forests

Coniferous forests tend to be characterized by trees that are dispersed either by wind or by cache-hoarding mammals and birds (40) or trees that exhibit no apparent adaptations for dispersal (157). Seed production often exhibits high periodicity (masting). Phase II dispersal of seeds adapted for Phase I dispersal by wind or animals can be significant (146). Early seral species exhibit a variety of dispersal mechanisms, but redistribution can be facilitated by rodents and ants. Both pre- and post-dispersal predation by insects can be high (4), and seed harvest by rodents can approach 100% (146, 148). Coniferous forests occur over a wide range of environments with varying rates of decomposition, but in warm or humid environments the potential for seed mortality due to pathogens is high.

Low correspondence between the composition of the seed bank and that of the vegetation exists (4). Many late seral species have low seed longevity, and early seral species are as abundant in the seed bank as late seral species in all stages of succession (4). Seed input and seed bank densities decline with time since disturbance, primarily due to differences in reproductive strategies among seral stages (73). Large-scale spatial variability can exist that is related to time since disturbance. Following disturbance, reestablishment of late seral trees may depend on residual plants within the area or chance seedling establishment (4).

Deciduous Forest

In deciduous forests, species are dispersed by wind or vertebrates, or they exhibit no specific dispersal mechanism (157). Masting by late seral species

is common. Large-seeded species occur primarily in later seres because of the ability of seedlings to emerge through dense litter and to tolerate dense shade in mature forests (137). For certain forest herbs such as *Erythronium* and *Viola* species, Phase II dispersal is by ants (9). Rodents assume an important role as both predators and dispersers of many larger-seeded late seral species, as do some birds (146).

The composition of the seed bank in mature forests may be poorly correlated with that of the standing vegetation, and seeds of early seral species often have the highest abundance (111). Most seeds in persistent seed banks are small, possibly due to their ease in penetrating litter. The rarity of very large seeds in forest seed banks may relate to the selection value of masting and predator satiation, which are inconsistent with seed longevity (28, 130). Following disturbance, seed bank richness and density increase for about 30 to 100 years, after which both decline (101). Seed bank similarity to the standing vegetation is often highest in recently disturbed gaps or abandoned fields (111). Increased opening of gaps in the canopy as forests age (106) results in increased richness of seed banks of old growth forests and high spatial heterogeneity on the larger scale (111).

Rain Forest

In rain forests, birds and mammals are usually more important dispersal agents than wind (46). Brief longevity and rapid germination following dispersal are common in tropical rainforest seeds, but many species do exhibit delayed germination (45, 150). Plants often have a suite of dispersers that affect the germinability and longevity of seeds arriving at the soil surface (135). Important secondary dispersers include ants (81, 123), scatter-hoarding rodents (53), and dung beetles (36). Secondary seed movement can also be attributed to heavy rainfall or run-off. Seed longevity in tropical forests may be shorter than in more temperate areas due to warm, moist conditions and the abundance of pathogens and predators (45, 150).

Correspondence between the seed bank and aboveground vegetation in tropical forest is often related to successional stage. In the seed banks of both mature forests and regrowth sites, pioneer species usually dominate while primary species are poorly represented (45). However, forest seed banks are dominated by pioneer trees, while regrowth/farm sites are characterized by herbs. Older regrowth (30–50 yr) has higher numbers of trees and shrubs. The seed bank density of mature tropical forests is often lower than in young secondary regrowth and farms (45). Multiple factors influence the rate at which the seed bank returns to predisturbance size; these factors include degree of isolation, size, and severity of disturbance, and the regeneration strategies of colonizing species. Large-scale spatial variability in seed banks can be attributed to disturbance regime and gap characteristics. Smaller scale variability is

high, and many species exhibit clumped distributions. This may be related to patterns of seed dispersal, abundance of predators, local edaphic conditions, or other factors (45).

MANAGEMENT IMPLICATIONS

Restoration and Conservation

Understanding the fates of seeds is a critical aspect of successfully restoring disturbed ecosystems or conserving endangered species. By using our knowledge of seed fates, it is possible to structure restoration or conservation processes to maximize establishment and persistence of desired species (87). The differences between restoration and conservation, in terms of seed dynamics, are a matter of scale; restoration reestablishes entire communities, while conservation maintains individual species. Because of this similarity, we consider restoration and conservation together.

Both restoration and conservation require knowledge of the influences on Phase II dispersal, seed germination, and seedling establishment. Because seed morphology and soil surface characteristics determine the vertical and horizontal movement of seeds in soils (23, 58, 110, 128), planting schemes can be devised or soil surfaces can be structured to maximize the entrapment and retention of seeds with varying morphology. Some seed attributes have fairly universal implications for establishment. Seeds that are small and lack morphological adaptations for dispersal are trapped after contacting the soil surface over a wide range of soil particle sizes (23). Thus, specialized soil surface treatments are unnecessary for entrapment, although the secondary erosion of seeds along with surface fines can be a problem. Because small seeds have low nutrient reserves, they must arrive at sites that are near the soil surface, but that have the necessary conditions for germination and establishment. Larger seeds are more likely to be moved over the soil surface after they arrive on the soil surface, and sites of deposition depend upon surface attributes (23). Because larger seeds have higher nutrient reserves, they can be seeded beneath the soil surface, placing the seeds in microsites where seed predation is less likely (113, 147), and where conditions for germination, such as higher soil moisture, are met.

Seed retention and seedling establishment of all types of seeds can be facilitated with several types of soil surface treatments. In areas where surface erosion due to wind or water is not a problem and there is adequate soil moisture for establishment, small seeds can be broadcast onto the soil surface and pressed into the soil surface either mechanically or by hand. In areas where erosion is a problem, surface mulches can hold both soil and seed in place. Organic and gravel mulches often have a similar function, and both trap

naturally dispersed seeds. In northern climates, snow fences can trap wind-blown seeds and snow thus providing a more favorable environment for spring establishment. In arid areas, surface gouges trap seeds (115) and create moister microenvironments for germination and survival (159).

The importance of seed germination characteristics in restoration and conservation efforts is becoming increasingly clear. Seeds of a variety of species from western North America exhibit large differences in germination response that vary among populations and that are habitat correlated (96, 97), emphasizing the importance of using seeds from local or adapted populations. In Western Australia, seeds from local populations combined with detailed knowledge of seed germination responses are used to restore entire communities following mining (11). These communities conform to the initial floristics model of succession (*sensu* Connell & Slatyer (26)), and the goal is to return as many species as possible in the first post-mining rainy season (11). Various seeding techniques are used that promote germination and establishment of the highly diverse species, including quickly returning topsoil with soil-borne seeds and appropriate mycorrhizal fungi, adding heat-shock responsive seed that have been collected by hand and pretreated by boiling, and mulching with the plant canopies of the original species to provide seed of serotinous species (11). In other highly diverse areas, such as the humid tropics, lack of information on seed germination responses impedes both restoration and conservation efforts (150).

Seed banks can be used to accelerate restoration or conservation of many species. As indicated above, direct replacement of topsoil that contains seeds of desired species and the appropriate fungal or bacterial symbionts promotes community or individual species reestablishment on disturbed sites (11). In some aquatic/semiaquatic systems, water-level management, augmentation of seed banks, and other techniques can be used to develop seed banks comprised of desirable species in the appropriate proportions (141). In some terrestrial systems, such as those disturbed by fire and grazing, management can produce desirable seed bank species mixes (72). Despite their importance for restoring or conserving certain life history groups, seed banks will not be useful tools for restoration or conservation of many late-successional species in closed habitats. These species seldom have long-lived seeds and, thus, do not form persistent seed banks (51, 111, 137). Because it is often difficult to manage seed banks for conservation purposes, the usual practice is to generate an artificial seed bank, *i.e.* a stored seed facility, to help preserve the biological and genetic diversity of certain species. Temperate species store best, and cryogenesis is an effective means of storage, if mutagenesis does not occur (13). Potential problems with this approach may include a reduction in overall genetic variation of the species and the introduction of genotypes with low relative fitness into the desired habitats (54).

In certain situations, it may be necessary to manage the animal component of the system to increase seedling establishment. In areas where seed predator densities are high, it may be possible to use economical, commercially available seed with high preference values, such as millet, to satiate the predators and minimize mortality of desired species (75). Seed-dispersing animals actively transport seeds into disturbed areas, thus expanding native populations into these areas (82). In areas with high densities of seed-dispersing animals such as heteromyid rodents, it may be possible to manage these animals actively to promote establishment of desirable native plant species. Bird dispersal to disturbed sites can be enhanced by bird-attracting structures such as snags or perches, increasing the abundance and diversity of bird-dispersed seeds (91). For plants that require dispersers but that do not form tightly coupled relationships with particular animals (many fleshy fruited species (156)), generalist animals within the area may be adequate dispersers. If a mutualism exists between a threatened plant and an animal, then both the specific animal population and the plant population must be managed.

Invasion of Undesirable Species

Invasion of new areas by alien plants can be caused by unusual long-distance migration events, either abiotic or biotic in nature. Alternatively, invasion may occur accidentally in impure seed crops, in soil or on nursery plants, on domestic livestock, or by allowing plants introduced as "useful" species to escape (5). Introductions are often short-lived if the plant species requires a disperser and no appropriate animal species is available. In contrast, some introduced species are relished by generalist, native animals that readily disperse the alien. The spread of the Brazilian pepper (*Schinus terebinthifolius*) in South Florida was facilitated by American robins (*Turdus migratorius*) and an introduced bird, the red-whiskered bulbul (*Pyononotus jocosus*) (38). Detailed understanding of the fates of seeds is very useful in the control of such aliens. Noble & Weiss (103) successfully modelled the movement of buried seeds (seed bank dynamics) of an invasive perennial (*Chrysanthemoides monilifera*) to determine the efficacy of biological control techniques that depended on pre-dispersal mortality of seeds. The model indicated that in addition to a pre-dispersal consumer, they needed a post-dispersal seed predator. This being unlikely, they suggested the possible use of an abiotic factor, fire, as a post-dispersal mortality agent. This was a good use of knowledge of the processes associated with seed fates.

SUMMARY

Phase I and Phase II dispersal are different phenomena, but workers have often failed to distinguish between them. Natural history type observations, many

almost anecdotal, dominate the seed literature. Recent papers develop generalizations about the abiotic forces of dispersal, the influence of animal activities on plant populations and communities, and the effects of seed bank composition on subsequent vegetation and of vegetation on seed banks. Few studies quantitatively treat phase II dispersal, for either abiotic or biotic forces. Fewer studies treat the dynamics of seed banks, other than their composition. Virtually no study follows the fates of individual seeds. Instead, seed fates are determined from samples where the histories of individual seeds are not known (but see 74). General knowledge of the effects of abiotic factors on seed movements exists, but this type of information is uncommon and has seldom been used to explain plant establishment patterns and species distributions (but see 110). Some generalization can be made about the influences of particular animals on seed banks and the differential roles of animal-mediated dispersal as opposed to consumption. Multiple species interactions and interactions between abiotic factors and animals, likely to be extremely common in nature, are seldom documented and almost never quantified. The influence of redistribution of seeds via Phase II dispersal and the importance of seed morphology on both the spatial distributions of seeds in seed banks and on species turnover rates is becoming increasingly clear (e.g. 138, 139). Disturbance has long been recognized as an important force influencing seed bank dynamics, but the roles of seed morphology and of seed germination responses are still poorly understood. Seed loss from seed banks, especially due to pathogens, is undoubtedly significant but has received little study. Some generalization can be made about seed dynamics at the biome level. Knowledge of seed movements and fates is facilitating restoration and conservation efforts and has the potential for use in controlling the invasion of many undesirable species.

Fortunately, recent work is mechanistically oriented and treats a variety of processes and organisms simultaneously rather than cuing on a species or single species-species interactions. There is every indication that generalizations fitting the model we propose are possible and that they are important to both academic and applied ecology. Only after we accumulate more field observations and perform clever experiments can we understand what really happens during a day in the life of a seed.

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