Seed Fate

Predation, Dispersal and Seedling Establishment

Dedication

We dedicate this volume to Daniel Janzen, whose many ideas germinated, took root and bore fruit, including this book

Seed Fate

Predation, Dispersal and Seedling Establishment

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Preface

Since the pioneering work of Janzen (1969, 1970, 1971), a large number of ecologists have become interested in analysing seed fate, whether seeds are preyed on or secondarily dispersed by either invertebrates or vertebrates. This growing interest in seed ecology was particularly obvious for both tropical and temperate habitats during the Third Symposium-Workshop on Frugivory and Seed Dispersal that took place in São Pedro, Brazil (see Silva *et al.*, 2000; Levey *et al.*, 2002) and where the four editors and many of the authors of this book met and interacted, especially during a workshop on 'Methods Used to Study Seed Fate and Removal' chaired by P.-M. Forget. During this meeting, it was evident that there is continued interest in the topic of post-dispersal seed fate among the international community, with new findings in the tropics (Forget and Vander Wall, 2001). A number of the papers included in this book were presented during another Symposium on 'Post-Primary Seed Fate: Predation and Secondary Dispersal' that took place at the annual conference of the Association for Tropical Biology and Conservation (ATBC) in Panama City, a meeting jointly organized by the Smithsonian Tropical Research Institute and the ATBC. During this symposium, our goal was to move a step forward beyond previous symposia on frugivores and seed dispersal (Estrada and Fleming, 1986; Fleming and Estrada, 1993), with original talks presenting and evaluating recently collected data on the roles that tropical animals, both invertebrate and vertebrate, play while preying on and/or secondarily moving seeds that have been transported by other means, mostly primary seed dispersers. None the less, the philosophy of this book was comparable to that of previous cited ones related to frugivory and seed dispersal; that is to offer students and scholars in the field an updated review of our current knowledge of seed ecology focusing on the destiny of seeds before or after being released or removed from the parent plant.

The purpose of this book is thus to present and to evaluate the most recent data on seed fate in diverse geographical regions around the world. This has been achieved by inviting leading scientists involved in research on seed ecology and, most particularly, animal–plant interactions from the perspective of predation and primary and secondary seed dispersal. The goal was also to evaluate questions relating to seed fate at several scales: temperate/tropical, continental, regional and smaller, within-site comparisons. In addition to a broad geographic assessment, we aimed to evaluate the impact of a variety of animal taxa on seed fate: from small invertebrates to medium- and large-bodied mammals. Finally, we wanted to evaluate these interactions and their influence on plant and animal strategies at both ecological and evolutionary scales. We aimed for a worldwide review of this topic with chapters dealing with organisms from a diversity of habitats in the tropics, i.e. from savanna to lowland tropical, montane cloud and subtropical forests in Brazil, Costa Rica, French

Guiana, Mexico, Panama, Peru, Venezuela, and the North American continent as a whole, central Africa and eastern Africa, Malaysia, China and Queensland in Australia, and from a diversity of habitat types in temperate and boreal ecosystems from mountain to arid desert habitats in northern China, Europe, Japan, North America and South Africa. The preface of Levey *et al*. (2002) ended with: 'We hope the ideas expressed in this book will disperse, take root and grow!'. Today, we may add that not only these ideas established and developed in the community, but they are now fruiting on its branches. This book is one of these fruit, and we hope its seeds will disperse, again and again, and successfully establish in many fields. We also hope those reviews will help students in many regions to start research and will continue to fill that gap of knowledge regarding seed fate and the events occurring between plant and offspring.

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Acknowledgements

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1 Seed Fate Pathways: Filling the Gap between Parent and Offspring

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Introduction

Seeds are mature ovules containing an embryo and stored nutrients inside a protective seed coat. Seeds are the products of sexual reproduction in most vascular plants (i.e. gymnosperms and angiosperms) and are the means by which plants produce genetically diverse offspring capable of surviving in variable and changing environments. Mature seeds remain dormant (*sensu lato*) for days to many years, and in this state they are able to tolerate adverse conditions and stressful environments (e.g. intense cold, heat, drought, darkness) that could not be endured by most plants (Baskin and Baskin, 1998). The particulate nature and small size of seeds relative to mature, seed-bearing plants lend mobility and also make it possible for a plant to produce large numbers of seeds during its life. Seeds are the principal means by which plants move across landscapes. The biotic and abiotic factors that affect seeds have unparalleled importance in the demography and evolution of plants.

The problem of seedling recruitment from the plant's perspective is that the environment is hostile and most points on the landscape are unsuitable for seedling establishment. Many organisms attempt to obtain the nutrients within seeds for their own purposes and kill the embryo in the process (Janzen, 1971; Hulme and Benkman, 2002). These risks are often intensified near the parent (Janzen, 1970; Connell, 1971), so effective dispersal usually must move seeds well beyond the influence of the parent plant (Howe and Smallwood, 1982; Herrera, 2002). Common modes of dispersal include abiotic forces (e.g. wind or rain splash), ballistic actions (e.g. as projectiles from exploding capsules), inadvertently by animals (e.g. within vertebrate guts, inside the cheek pouches of primates, or attached to the outer surface of animals), or purposely by animals (i.e. by seed-storing corvids, rodents or ants). These varied means of dispersal are associated with adaptations of fruit (the mature ovary wall and associated structures of angiosperms) that facilitate dispersal. Despite the diversity of dispersal mechanisms, most seeds move at random

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with respect to suitable establishment sites, and few seeds arrive at microsites conducive to seedling establishment. Janzen (1986) likened the task of a plant having its seeds reach a safe site for seedling establishment to a blind hunter trying to shoot a moving buffalo on an undulating plain. The hunter's success is likely to be low but depends on the amount of ammunition, size of the ammunition and the number of buffalo. Like the hunter's bullets, most seeds miss their target and fall on inhospitable ground (Schupp *et al.*, 1989; Schupp, 1993). What has not been appreciated until recently is that some seeds get to take two or more shots at the target (i.e. if they miss a suitable habitat or microsite after primary dispersal, secondary dispersal may eventually move them to a favourable site).

Interest in the ecology and function of seeds has a long history (Ridley, 1930). However, it is only since the mid-1970s that scientists have begun to tease apart the dynamic role seeds play in plant demography. Historically, interest focused primarily on seeds on or beneath plants. Most attention was directed towards pre-dispersal seed mortality, how seeds are morphologically adapted for dispersal, and the behaviour of animals that removed seeds and fruits from plants. When dispersal was studied, the focus was usually on the initial stage of dispersal such as the consumption of fruits by frugivores (Sutton, 1951; Rick and Bowman, 1961) or the frequency of occurrence of wind-dispersed seeds in seed traps located at varying distance from a seed source (Cremer, 1965; Greene and Johnson, 1989). Moreover, many important seed dispersing taxa (e.g. primates and caviomorph rodents; Forget, 1990; Lambert, 1999) received comparatively little attention relative to other, more conspicuous frugivores such as birds (Snow, 1971). Although seed dispersal has always been viewed as an important process (e.g. Ridley, 1930; van der Pijl, 1969; Thoreau, 1993), it was seldom studied from start to finish (e.g. Wang and Smith, 2002). Instead, the general patterns of dispersal were surmised from traits of propagules and, where relevant, the behaviour of animals that handled seeds. The latter stages of dispersal were inferred from the patterns of seedling establishment. The occurrence of plants on oceanic islands, the establishment of seedlings outside the local distribution of conspecifics, and evidence for plant migration from fossils and pollen records all bore testament to the efficacy of seed dispersal mechanisms. But nearly all of the early studies on seed dispersal were incomplete in the sense that they failed to provide a full accounting of the diverse fates and various pathways that a population of seeds might follow between production and germination.

The lack of empirical studies of the intimate details regarding seed dispersal processes is a consequence of at least four factors. First, most seeds are small, and once they leave the parent plant they can be exceedingly difficult to find, let alone follow. Second, the relatively long dormancy of most seeds (ranging from several weeks to many years), especially in the temperate zone, greatly complicates the problem of following seeds until they germinate. Third, many scientists believed that it was not necessary to understand seed fate dynamics. Plants produced so many seeds over their lifespan and so few seeds survived to produce seedlings that it was generally believed that survival of seeds and the arrival of seeds at safe sites was essentially a stochastic process. The realization in the 1960s (Harper, 1967; Janzen, 1969) that natural selection is a factor during all stages of a plant's life cycle, including post-dispersal seed predation and microsite conditions at germination sites, increased our need to understand better the fate of seeds during the interval between seed production and germination. In addition, conceptual advances (e.g. Price and Jenkins, 1986) helped to point out the need for more detailed studies of seed fates. Fourth, and perhaps most importantly, there were few techniques for following seeds after they left the parent plant. The study of seed movement was limited to direct observation (e.g. Cahalane, 1942; Howe, 1977; Darley-Hill and Johnson, 1981; Forget and Wenny, Chapter 23, this volume). The technical difficulty of following small seeds over long periods of time contributed to an impression that seeds became nearly invisible between the time they left the parent and when the seeds germinated.

Things began to change with the emergence of methods that permitted researchers to follow seeds. These methods include the use of gamma-emitting radionuclides to label seeds and detect them with Geiger counters (Lawrence and Rediske, 1959; Radvanyi, 1966; Abbott and Quink, 1970), the use of metal objects in or on large seeds allowing them to be located using a metal detector (Stapanian and Smith, 1978; Sork, 1984), the use of string with an attached label or spool-and-line methods (Hallwachs, 1986; Forget, 1990; Yasuda *et al.*, 1991), fluorescent dyes (Longland and Clements, 1995), and, for some very large seeds, radiotransmitters implanted inside seeds (Tamura, 1994; Soné and Kohno, 1996). Following these pioneering studies (discussed in more detail in Forget and Wenny, Chapter 23, this volume), detailed investigations of seed fates have proliferated. Coupled with these new methods for following seeds, it was realized that more rapid progress can be made in understanding seed demography if seeds are individually marked (e.g. numbered) for repeated observation. It is apparent from these studies that the pathways that seeds follow are often longer and more complex than previously assumed (Chambers and MacMahon, 1994; Vander Wall and Longland, Chapter 18, this volume). Prior to the availability of these methods, it was generally assumed that the dispersal of most seeds was a rather simple, direct process. Seeds move away from the parent plant, land or get deposited at a point on the landscape, and then either die or germinate at some later time. The view that has emerged since the early 1990s is that seed dispersal is a far more dynamic process, often involving multiple steps by two or more distinctly different mechanisms (e.g. Forget and Milleron, 1991; Kaufmann *et al.*, 1991; Bohning-Gaese *et al.*, 1999; Vander Wall, 2003). In earlier studies, when dispersed seeds disappeared it was often assumed that the seeds had been found by a predator and eaten. We have learned that this is often not the case. Instead, disappearance of a seed may simply indicate that a new stage in the dispersal process has begun.

With a growing realization that the pathways that seeds follow to favourable germination sites are diverse and often complicated, it is becoming increasingly important to have a detailed understanding of seed fates. A central element of any study that attempts to account for seed fates is a means of tracking seeds as they move from site to site. Additionally, a number of related studies need to be conducted in conjunction with studies of seed movement. Such studies might include, for example, measures of seed production, observational studies of the behaviour and effects of seed predators and dispersers, measurements of seed removal rates, the dynamics of soil seed banks, germination experiments under a range of environmental conditions that simulate possible deposition sites, and studies of post-germination seedling survivorship. Studies that have done this effectively include Holthuijzen *et al.* (1987), Kjellsson (1991), Hughes and Westoby (1992), Vander Wall (1994), Feer *et al.* (2001) and Lambert (2002). In addition, one might incorporate modelling studies and simulations into analyses of seed fates (e.g. Alvarez-Buylla and Martinez-Ramos, 1990; Alvarez-Buylla and Garcia-Barrios, 1991; Kalisz and McPeek, 1992; Charles-Dominique *et al.*, 2003). By understanding questions such as when and where seed mortality occurs, how animals assist and/or hinder seed survival, and where germination is occurring but seedling establishment is failing, we will gain a fuller understanding of the selective forces that shape fruiting phenology, seed and fruit morphology, seed chemistry, dormancy schedules and other characteristics of seeds. The goal of this series of essays is to take stock of what we have learned about seed fates from studies throughout the world and to point out directions for future research.

Potential Seed Fates

Figure 1.1 is a generalized seed fate diagram, showing the most likely alternative

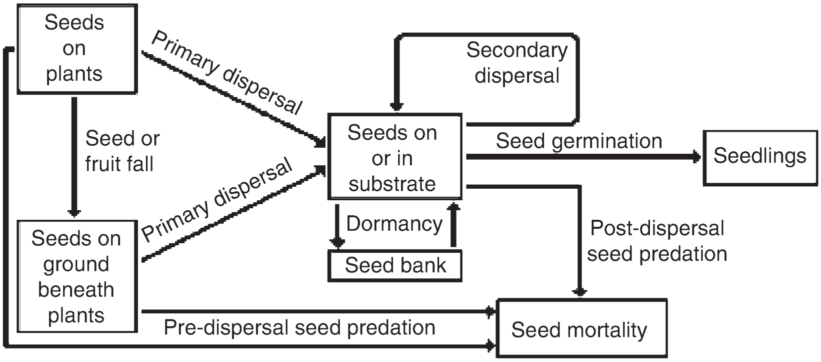

Fig. 1.1. A generalized seed fate diagram. Rectangles represent seed states and arrows between rectangles indicate movement or transition between states. See text for an explanation.

pathways that a seed might follow. Plants produce seeds within fruits, but here we focus on the seeds. Seeds on plants can be dispersed via a variety of primary dispersal mechanisms, including abiotic factors, like wind or ballistic projection, or biotic factors, like fruit-eating birds. Because of the diversity of fruit and seed types and the variety of dispersal processes, defining what constitutes primary dispersal can be complicated. Some seeds fall to the ground surface beneath the parent plant. Whether this should be viewed as primary seed dispersal depends on the structure of the fruit and how the seeds are typically dispersed. Consider two situations: first, some seeds are adapted for dispersal by ground-foraging animals, and falling to the ground is part of the adaptive syndrome of plants to get seeds to dispersers. The clearest example of this is nut fall by trees (e.g. walnuts, hickories, chestnuts, oaks, Brazil nuts, Carapa) that are dispersed by nut-caching animals (Boucher and Sork, 1979; Lewis, 1982; Forget, 1996; Peres and Baider, 1997). In these cases, nut fall beneath the tree is best viewed as nut presentation, not dispersal. Similarly, overripe fruits adapted for dispersal by ground-foraging vertebrates can fall beneath the parent plant. As long as the fruits remain below the parent, we view fruit fall as non-dispersal. However, if topography (e.g. steep slopes) assists fruits or nuts to move beyond the canopy of the parent (e.g. Grinnell, 1936; Forget, 1992), then these longer movements should be viewed as primary seed dispersal. For animal-dispersed diaspores, whether the seed is taken from a plant canopy or the ground beneath a plant, we consider the animal-mediated movement of the seed to be primary dispersal. Second, if the fruit or seed is adapted for some means of dispersal (e.g. ballistic projection, wind, or fruit-eating animal) that typically carries seeds beyond the canopy of the parent, but the seed falls below the parent because of a failure of the dispersal mechanism, then we view this as primary dispersal. For example, a ballistically dispersed seed may hit an obstruction and fall below the parent (Hanzawa *et al*., 1988; Forget, 1989; Espadaler and Gomez, 1996), a wind-dispersed maple (*Acer*) samara or pine (*Pinus*) seed could fall below the parent on a windless day (Guries and Nordheim, 1984; Nathan *et al*., 2000), or animal-dispersed tropical seed may be spat out underneath a parent tree by cercopithecine primates (Lambert, 1999, 2001). In these cases, primary seed dispersal has occurred despite the poor quality of that dispersal.

Whether on a plant or on the ground beneath a plant, many seeds die before they can be dispersed. Animals that attack seeds before dispersal can occur are known as pre-dispersal seed predators (Janzen, 1971; Hulme and Benkman, 2002). These animals are often specialized seed predators that are attracted to chemical cues emanating from the parent plant and/or fruit. The most prominent of these organisms include bruchid beetles, weevils, moth larvae, seed bugs and wasps (Janzen, 1971; Hulme and Benkman, 2002). Birds and mammals, including some potential dispersers like seed-caching rodents, pitheciine primates and corvids, also kill numerous seeds before they are dispersed. Yet other seeds are killed or made unacceptable to dispersers by microbes that attack fruit.

Those seeds that do get dispersed arrive on (or sometimes in) a substrate. This substrate is usually the ground (e.g. soil, rock, plant litter), but it could also be a plant surface (e.g. faeces deposited on leaves or branches for epiphytes, plant parasites or other plants). When the dispersal mechanism moves the seed at random relative to favourable establishment sites, the initial point of deposition may or may not be advantageous to seedling establishment. At this point, the seed can experience one of several fates. First, the seed could be discovered by an animal and eaten. This post-dispersal seed predation is treated separately from pre-dispersal seed predation because both the phase and timing at which the seed is consumed and the organisms that consume it are different (Hulme and Benkman, 2002). These animals, including ants, rodents and birds, often specialize on seeds but forage opportunistically for a wide variety of seed species. Second, the seed could be moved to another site. Any significant movement of seeds after initial dispersal from plants is known as secondary dispersal (e.g. Greene and Johnson, 1997; Bohning-Gaese *et al.*, 1999). In recent years, the importance of secondary dispersal has become increasingly evident (this volume). Secondary seed dispersal falls into two distinct categories: (i) the seed could be moved either by the same general mechanism as that involved in primary dispersal (e.g. dispersal of seeds over snow by wind; Matlack, 1989), or (ii) by a completely different mechanism (e.g. burial of seeds in faeces by dung beetles; Andresen and Feer, Chapter 20, this volume). We refer to the latter form of secondary dispersal as diplochory. We feel that it is important to distinguish between these two possibilities because they have different implications for seeds. Seeds that are moved by a sequence of two or more distinctly different means of dispersal have a much greater chance of arriving at favourable germination sites, a benefit that is not shared with many forms of secondary dispersal involving only one means of dispersal (Vander Wall and Longland, 2004, and Chapter 18, this volume).

If a seed is not consumed or attacked by microbes, and if it lands in a suitable microsite, either as the result of primary or secondary dispersal, it could germinate. The delay from the time that a seed arrives at a substrate until it germinates can vary from a few days to many years (Garwood, 1983). Seeds that do not germinate when conditions appear to be favourable are said to be dormant, and dormant seeds make up the seed bank (Harper, 1977; Bulow-Olsen, 1984; Leck *et al.*, 1989). Most large seeds and nuts germinate within 1 year triggered by seasonal cues (e.g. warm soil in spring, soil moisture in the rainy season). Other seeds can reside in the seed bank until the occurrence of some more unpredictable event (e.g. fire or a change in light levels because of a tree fall). During dormancy, seeds remain susceptible to predators and microbes (see Dalling, Chapter 3, this volume). Most seeds that remain in the seed bank for more than a year or two are small and generally overlooked by potential seed predators.

Our interest in seeds does not end when they germinate. This is because the seed often continues to exert an effect on the seedling for some time. For example, when seeds in a cache germinate, rodents will often excavate the soil around the seedlings to find ungerminated seeds at their base, killing or damaging seedlings in the process. Seedlings often serve as conspicuous ‘flags’ for buried seeds (Vander Wall, 1994; Pyare and Longland, 2000). In species with large nuts, the seed often continues to supply nutrients to the seedling for weeks to months. For woody plants (shrubs and trees), it is usually desirable to follow the fates of seedlings for several years in order to gauge the suitability of establishment sites (e.g. whether shrubs can serve as nurse plants for seedling trees). More generally, it is necessary to evaluate early seedling survival to judge the efficacy of seed dispersal because safe sites for seeds are not always suitable establishment sites for seedlings (Schupp, 1995).

The remainder of this book is divided into three sections (Fig. 1.1). The first section focuses on the sources and consequences of seed predation, including both pre-dispersal and post-dispersal seed losses. The second section covers primary dispersal from the plant and, where relevant, the ground beneath plants to substrates and the subsequent fate of those seeds, including seed germination and seedling establishment. The final section of the book examines the mechanisms and consequences of secondary seed dispersal and how it can influence seed fate at later stages of seed fate pathways. This organization is admittedly artificial, and all chapters contain information that pertains to two or more of these sections.

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