

3 The Fate of Seed Banks: Factors influencing Seed Survival for Light-demanding Species in Moist Tropical Forests

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Introduction

Seed mass in species-rich moist tropical forests often varies over six or more orders of magnitude (Foster, 1982; Foster and Janson, 1985; Hammond and Brown, 1995). Most of these species, including some with the minutest seeds (Metcalf, 1996; Metcalfe and Grubb, 1997), can be classified as 'shade-tolerant' with the ability to establish beneath a closed canopy. Seeds of the shade-tolerators vary widely in morphology and physiology, but many are recalcitrant, and most germinate within a few months of dispersal (Hall and Swaine, 1980; Ng, 1980; Hopkins and Graham 1983; Garwood 1983).

This chapter concerns the approximately 10–20% of tree species in moist tropical forests that can be classified as 'light-demanding' or 'gap-dependent' (Dalling *et al.*, 1998a; Molino and Sabatier, 2001). These species require higher levels of irradiance than are found in closed forest understories for successful seedling establishment. Variation in seed mass, morphology and physiology among these species can be as great or greater than that of shade tolerators (Hammond and Brown,

1995). Establishment of light-demanding species occurs when seeds are dispersed directly to canopy openings, or perhaps more frequently, when disturbance cues the germination of seeds present in the soil seed bank (e.g. Putz and Appanah, 1987; Lawton and Putz, 1988; Dalling and Hubbell, 2002). Successful recruitment from a persistent seed bank depends on surviving an array of predators on the soil surface, remaining buried or being returned to shallow soil depths that permit seedling emergence, and avoiding predation or infection by soil invertebrates and pathogenic microbes.

The additional interactions that seeds encounter during their stay in the soil set apart studies of seed fate for light-demanding species from those of rapidly germinating shade-tolerant species in tropical forests. Greater duration of the seed stage of the regeneration cycle might also imply that sources of seed mortality play a more important role as a demographic filter influencing population growth and niche partitioning for these species. Despite this, however, seed fate in the soil remains poorly explored, with most studies restricted to relatively simple experimental assays of seed survival (e.g. Hopkins and Graham,

1987; Dalling *et al.*, 1998b; Murray and Garcia, 2002).

This chapter reviews the potential fates of small-seeded (< 100 mg) light-demanding species from dispersal to seedling emergence. It emphasizes the experimental and observational approaches necessary to uncover the interactions between seeds and soil macrofauna, and highlights the near absence of studies examining microbial interactions with seeds. Finally, studies of seed fate underscore the need to take an integrated life-history approach to the interpretation of seed traits. Light-demanding species exhibit remarkable diversity in seed characteristics, including seed mass variation over four orders of magnitude, adoption of varied dispersal mechanisms, and capacities for seed persistence ranging from weeks to decades (Dalling *et al.*, 1997, 2002; Murray and Garcia, 2002). Different combinations of seed traits may contribute to species coexistence by influencing the size of canopy gaps that can be detected by the seed and the seasonality of seedling emergence (Dalling *et al.*, 1997; Pearson *et al.*, 2002). However, many potential combinations of seed traits may be essentially equivalent, resulting in similar recruitment success despite the manifold fates that seeds can experience.

Effects of Dispersal Mode on Post-dispersal Seed Fate

Dispersal mode is one of the strongest determinants of the subsequent fate of seeds. Seeds dispersed by vertebrate frugivores may retain residual fruit pulp, or aril tissue, or faecal matter that attracts secondary seed dispersers and predators to the site of seed deposition. Experimental arrays of small seeds placed on the soil surface as intact drupes (Dalling *et al.*, 1998b), intact arilate seeds (Horvitz and Schemske, 1986, 1994; see Pizo *et al.*, Chapter 19, this volume), bird droppings (e.g. Kaspari, 1993; Byrne and Levey, 1993), and primate defecations (Estrada and Coates-Estrada, 1991) are typically removed by ants and beetles (see

Andresen and Feer, Chapter 20, this volume) within a few hours. Similarly, many ballistically dispersed seeds frequently carry eliaosomes (food bodies attached to the seed), which attract ants that subsequently carry seeds (see Mayer *et al.*, Chapter 10, this volume) to the nest site (Passos and Ferreira, 1996). In contrast, wind-dispersed seeds lack these attractants.

In a comparative study of secondary removal rates of seeds of six light demanding species in Panama, Fornara and Dalling (2004, unpublished results) placed arrays of seeds of four vertebrate dispersed, and two wind dispersed species on microscope slides on the soil surface in five lowland and lower montane forests in Panama. Removal rates were remarkably similar among sites. Overall, 45% of seeds of the four vertebrate-dispersed species (*Miconia argentea* Melastomataceae 0.08 mg; *Cecropia peltata* Cecropiaceae 0.5 mg, *Trema micrantha* Celtidaceae 1.3 mg; *Apeiba aspera* Tiliaceae 14.2 mg) were removed over 2 days, primarily by ants. In contrast, only 2% of seeds of the wind-dispersed species (*Luehea seemanii* Tiliaceae 1.9 mg; *Jacaranda copaia* Bignoniaceae 4.7 mg) were removed. The explanation for the differential attractiveness of wind versus vertebrate dispersed seeds remains unclear. Residual fruit pulp on vertebrate-dispersed seeds that might have attracted ants was washed off prior to the experiment, while removal of the large samara attached to *Luehea* seeds did not influence their removal rate. Future work with a larger number of species will be needed to determine whether primary seed dispersal mode is indeed a predictor of subsequent seed fate. One possibility is that invertebrate seed predators may discriminate against wind dispersed seeds based on their lower seed moisture content (Augspurger, 1988).

Dispersal mode may also indirectly affect seed fate by influencing the spatial pattern of seed dispersal. For large-seeded species, the number and density of seeds deposited, and the distance seeds are moved from reproductive conspecifics can affect the probability that seeds are encountered by predators and that predators will be

satiated by seed resources (e.g. Augspurger and Kitajima, 1992; Burkey, 1994); similar patterns might also be expected for small-seeded species. For vertebrate dispersed seeds, the number of seeds deposited in each dropping is likely to scale with body size. Large bodied primates such as howler monkeys, and Capuchin monkeys and ungulates, such as tapirs in the neotropics may deposit several thousand small seeds in a single defecation (Janzen, 1982; Andresen, 1999; Wehncke *et al.*, 2003) contributing to locally aggregated dispersal patterns. Furthermore, physiology and behaviour of vertebrate frugivores may also determine seed fate. For example, in neotropical forests, howler and spider monkeys defecate at infrequent intervals depositing seeds in large clumps at feeding roosts, latrines and sleeping roosts (Milton, 1984; Fragoso, 1997; Julliot, 1997). In contrast, Capuchin monkeys defecate frequently through the day producing small dung piles that result in significantly lower rodent seed predation rates than dung piles left by howler monkeys (Zhang and Wang, 1995; Wehncke *et al.*, 2004).

Mechanisms of Seed Incorporation into the Soil

In temperate forest and grassland communities seed size and morphology are important determinants of the rate of incorporation of seeds into the soil (Peart, 1984; Thompson *et al.*, 1993). Larger seeds, and seeds with appendages for wind dispersal, are less likely to become embedded in soil particles or fall between soil aggregates, and as a consequence, are more conspicuous to seed predators that are primarily active on the soil surface (Thompson, 1987). Biophysical constraints on seed burial rates can therefore strongly influence the survival of dispersed seeds and may provide an explanation for the negative relationships found between seed size or shape (variance is seed dimensions), and seed persistence (Thompson and Grime, 1979; Rees, 1993; Bekker *et al.*, 1998; Funes *et al.*, 1999; but see Moles *et al.*, 2000).

Similar relationships between size and persistence may exist for wind-dispersed species in tropical forests. In wet forests, passive seed burial may occur when rain splash covers seeds with fine soil particles, but frequent rain storms also block the spaces between soil aggregates limiting opportunities for small seeds to percolate through soil pores (Pearson *et al.*, 2003). In more seasonal forests, subjected to repeated wetting and drying cycles, soil particles form larger aggregates of up to a few centimetres in size with larger pores between them (Marshall *et al.*, 1996). In strongly seasonal forests, soil cracks may appear in the dry season that extend tens of centimetres into the soil permitting seeds to be deeply buried during the dry season (Garwood, 1989).

For seeds dispersed by frugivores, however, secondary dispersal and predation seem more likely fates than passive incorporation into the soil. In lowland forests, an array of ant species are attracted to defecated, regurgitated or fallen seeds. These seed-harvesting ants are remarkably abundant and diverse (e.g. 44 seed harvesting ant species, and > 300 *Pheidole* ants/m² at La Selva, Costa Rica; Levey and Byrne, 1993; Kaspari, 1996), and remove seeds varying widely in size (0.5–15 mg; Kaspari, 1996; Fornara and Dalling, 2003, unpublished results). Ant removal of seeds in the litter is less important in montane forests, however, as ant abundance declines sharply above about 1500 m (McCoy, 1990; Olson, 1994; Samson *et al.*, 1997; Brühl *et al.*, 1999).

The fate of ant-harvested seeds remains somewhat unclear, but a detailed study by Levey and Byrne (1993) of *Pheidole* ants at La Selva has begun to reveal the complexity of the ant–seed interaction. *Pheidole* are small ants (minor workers < 2 mm) with small colony sizes (< 100 individuals) that forage in the litter and on the soil surface removing seeds from frugivore faeces and caching them in nests consisting of partially decomposed twigs. Most small seeds of Melastomataceae removed by *Pheidole* are consumed in the nest, but a small fraction (6%) of seeds are deposited in refuse piles or abandoned as nests are periodically

relocated to new twigs (Levey and Byrne, 1993). Thus, removal by litter ants permits some seeds to become incorporated in the litter/soil seed bank, and may result in some dispersal of seeds to nutrient-rich microhabitats (refuse piles) more favourable for seedling growth than the original site of deposition (see Pizo *et al.*, Chapter 19, this volume).

However, not all seeds harvested by ants remain close to the soil surface. Larger seeds and fruit (5–50 mg) are harvested by larger ants that nest in the soil and may be cached a few centimetres to metres below the soil surface, or concentrated in large refuse piles by leaf-cutter ants. On Barro Colorado Island (BCI), Panama, large numbers of *Miconia argentea* (Melastomataceae) fruit (20–100 mg) containing numerous tiny seeds are collected from the canopy and soil surface by leaf-cutter ants (*Atta* spp.) to provision their fungus gardens. Densities of > 1000 viable seeds/g are subsequently deposited in refuse piles on the soil surface by *A. colombica* and in underground chambers by *A. cephalotes* (Dalling and Wirth, 1998), where they can remain viable for several months (Farji-Brenner and Medina, 2000). In addition to *Miconia* fruits, larger individual seeds (> 10 mg) may also be removed by larger ponerine litter ants such as *Ectatomma ruidum* and carried to nests below the surface (J. Dalling, personal observation). It remains unclear, however, whether these larger seeds are actually predated by ants as their seed coats may be too thick for ants to penetrate (as is the case for some desert annuals, O'Dowd and Hay, 1980).

In addition to ants, seeds defecated by mammals may also be secondarily dispersed by dung beetles. Dung beetles are attracted to clumps of faeces which they bury at depths of 0.5–12 cm and use as a food source for their larvae (Estrada and Coates-Estrada, 1991; Andresen, 2002). Dung is often detected and buried by beetles within a few hours of defecation and seeds are incidentally buried along with it. Rapid burial provides an important escape for seeds from rodents, as predation rates for large seeds remaining in faeces on the soil surface or

within the top centimetre of soil are very high (Estrada and Coates-Estrada, 1991; Andresen, 1999; Andresen and Feer, Chapter 20, this volume). The extent to which rodents are attracted to the smaller seeds of light-demanding species remains unclear. Small murid mice have been observed eating *Cecropia* seeds < 1 mg seed mass in Amazonian Ecuador (Paula Barriga, Quito, 2003, personal communication), and rodents are reported as seed predators for *Cecropia* in montane forest in Costa Rica (Murray and Garcia, 2002). More generally, if ants and rodents compete for seed resources, as has been shown in desert ecosystems (Brown and Davidson, 1977; Midgley and Anderson, Chapter 11, this volume), then rodents might be predicted to be more important sources of predation in high elevation sites where ant abundance is low.

Seed Persistence and Seed Dormancy in the Soil

Once in the soil, seeds can remain viable for periods ranging from several weeks to several decades. Experimental burial of seeds in mesh bags in the soil showed that in NE Australia 22 of 25 species of pioneer and early successional species retained > 10% germinability after two years (Hopkins and Graham, 1987), while in Panama 10 of 14 pioneer species retained similar germinability after 18 months (Dalling *et al.*, 1997). These results are consistent with those of a study comparing annual inputs of seed rain with standing soil seed bank densities in a Costa Rican montane forest, which provided evidence of super-annual accumulation of seeds in the soil for 13 of 23 pioneer species (Murray and Garcia, 2002). Thus in general, more than half of pioneer species establish persistent seed banks (*sensu* Baskin and Baskin, 1998).

None of these studies, however, show the negative relationship between seed persistence and seed mass typically found in temperate grassland communities (Thompson and Grime, 1979; Rees, 1993; Thompson *et al.*, 1993; Funes *et al.*, 1999). This suggests

that diverse seed predator communities in tropical forests preclude size-dependent predation. At this stage we can only speculate on the morphological and ecological correlates of seed persistence that might exist in tropical forests.

Seed persistence in the soil may be mediated by either physical or chemical defensive traits, or may possibly be constrained by the availability of seed reserves and the rate of metabolism (Garwood and Lighton, 1990). Within a single genus, reported rates of seed persistence can vary substantially. For example, seeds of *Cecropia insignis*, *C. obtusifolia* and *C. polyphlebia* persist for little more than a year in the soil and rapidly lose viability under dry storage conditions (Alvarez-Buylla and Martínez-Ramos, 1990, Dalling *et al.*, 1998; Murray and Garcia, 2002). In contrast, seeds of *C. sciadophylla* remain viable for > 4 years (Holthuijzen and Boerboom, 1982), perhaps reflecting differences in the chemical composition and thickness of the pericarp among *Cecropia* species (Lobova *et al.*, 2003).

On BCI, Panama, long persistent seed banks appear to be more common among species with larger seed mass (> 3 mg) and with thick seed coats. Small-seeded species, and wind-dispersed species tended to show rapid declines in germinability during the first year of burial (Dalling *et al.*, 1997). Indeed, some species with thick seed coats are capable of extraordinary seed persistence. ¹⁴C dating of seeds extracted from natural seed banks using accelerator mass spectrometry (Moriuchi *et al.*, 2000), has shown that seeds of four pioneer species with seed mass > 3 mg (*Trema micrantha*, *Hyeronima laxiflora*, *Zanthoxylum eckmannii* and *Croton bilbergianus*) buried at depths of < 3 cm can be > 30 years old (J. Dalling and T. Brown, 2003, unpublished results). Similarly, Murray and Garcia (2000) argue that the high densities of thick-seed coated *Phytolacca rivinoides* in the seed bank at Monteverde, Costa Rica, suggests accumulation in the soil over many decades.

The adoption of a hard seed coat may provide a broadly effective defence against predators analogous to quantitative

defensive traits such as lignin and tannins that reduce the palatability of leaves and shoots to a broad array of herbivores (Feeny, 1976). Hard seed coats, however, are only likely to be effective above a minimum thickness, thus constraining the effectiveness of this defence to larger-seeded species. Persistent small seeds are therefore likely to be chemically defended. An additional potential constraint imposed by a hard seed coat is that its impermeability and toughness may impose physical dormancy. All four species on BCI with decade-long seed persistence have been shown to have a very low initial germination rate under favourable conditions of high red : far red ratio irradiance and moisture availability (Dalling *et al.*, 1997; Silvera *et al.*, 2003). For three of these species which are insensitive to light, presumed physical dormancy can be broken with high temperature or scarification (Acuña and Garwood, 1987), but fresh *Trema micrantha* seeds cannot be induced to germinate, perhaps reflecting physiological rather than physical dormancy. How long initial dormancy remains for seeds buried in the soil remains unclear, but presumably the permeability of seeds increases as the seed coat degrades in the soil.

If physical dormancy represents an unavoidable cost associated with the defence against predators, then we might expect that some shade-tolerant species with hard seed coats would also show super-annual seed persistence in the soil. On BCI, at least two species, the palm *Attalea butyracea* (= *Scheelea zonensis*), and the canopy tree *Vantanea occidentalis* (Humiriaceae) with exceptionally thick, hard endocarps, germinate slowly over at least 3 years (Harms and Dalling, 1995). However, the dormancy mechanisms used by these species are unclear, and may be morphological or physiological rather than physical (*sensu* Baskin and Baskin, 1998). Long-term studies of the germination ecology of shade-tolerant tree species are seldom performed in moist tropical forests (but see Garwood, 1983), and prolonged dormancy may therefore be under-reported among these species.

Biotic Constraints on Seed Survival in the Soil

Whereas seeds on the soil surface and in the litter interact with ants, beetles and rodents, seeds buried in the soil encounter a different, but potentially overlapping suite of potential mortality agents. As yet, however, most studies have only documented survival rates of buried seeds, and little attempt has been made to attribute seed losses to particular taxa. The limited evidence that earthworms and fungi contribute to seed mortality is reviewed here.

Earthworms have been ignored as potential sources of seed dispersal and predation, perhaps because their abundance in tropical forest soils was initially underestimated (Fragoso and Lavelle, 1992). More recent reviews estimate their densities at 10–400 individuals/m², with mean values similar to temperate forests (Fragoso and Lavelle, 1992; González and Zou, 1999). Earthworms can exert important effects on seed bank dynamics as seeds are ingested in the soil mass (primarily in sites with richer soils), or in the litter (primarily in oligotrophic soils; Fragoso and Lavelle, 1992), and are subsequently deposited deep in the soil or in casts on the soil surface (Grant, 1983). Seeds of temperate grassland species vary in their susceptibility to breakdown during gut passage, but seeds of at least a few species are defecated in a viable state (McRill and Sagar, 1973; Willems and Huijsmans, 1994). In temperate grassland, Thompson *et al.* (1994) demonstrated that earthworms can be quite size-selective in the movement of seeds. Species found in surface worm casts were significantly smaller than species found in the soil as a whole, with one species, *Cerastium fontanum*, accounting for > 85% of seeds in surface casts.

Studies of earthworm effects on seed viability and distribution have not been reported in tropical forests. However, experiments in tropical savannas indicate that earthworms there have mutualistic-antagonistic effects. Decaëns *et al.* (2003) found that earthworms transport a subset of seed bank seeds to surface casts, but that viability of seeds from casts was up to 40

times lower than in the surrounding soil. Seeds may therefore be degraded during gut passage or perhaps infected by pathogens dispersed with seeds (Toyota and Kimura, 1994). Standing vegetation in savanna and pastures, however, was more similar in composition to worm casts than to the seed bank as a whole, suggesting that worm casts may provide particularly favourable microsites for seedling recruitment (Decaëns *et al.*, 2003).

Fungal pathogens have frequently been invoked as important sources of mortality for tropical forest plants (Augspurger, 1984; Clark and Clark, 1984; Khan and Tripathi, 1991; Gilbert, 2002), with most work focusing on the infection of seedlings (e.g. Alexander and Mihail, 2000; Gilbert *et al.*, 2001). Fungi have been similarly implicated as sources of mortality for seeds in the soil, particularly for light-demanding species whose small seeds fill the forest seedbank (Alvarez-Buyulla and Martinez-Ramos, 1990; Dalling *et al.*, 1998a,b). Despite their implied importance however, direct evidence that fungi account for seed losses in the soil is remarkably scarce (Baskin and Baskin, 1998), and information on the taxonomic identity, diversity, host affinity, and ecological importance of seed-infecting fungi represents a 'major lacuna in research' (Gilbert, 2002).

Very few studies have linked seed mortality in the soil to fungi. Crist and Friese (1993) and Masaki *et al.* (1998) attributed 30% of the mortality of five shrub-steppe species, and 20% of the mortality of the warm-temperate tree *contraversa* to pathogenic and decomposer fungi based on evidence of necrosis of seeds extracted from the soil. Application of fungicide to buried seeds has shown modest increases in seed survival. Lonsdale *et al.* (1993) found that the fungicide Benlate reduced mortality of seeds of the exotic shrub *Mimosa pigra* in northern Australia by 10–16%, while Blaney and Kotanen (2002) found that the fungicide Captan significantly increased survival of seeds 39 species of native and alien grasses and forbs in a Canadian old field site, but only by 5–10%. Finally, Leishman *et al.* (2000) showed that a cocktail of fungicides

was able to increase survival of *Medicago lupulina* seeds by 30% in a British grassland.

Our own studies suggest that fungi are responsible for most seed losses of common pioneer species in the soil seed bank. At BCI, Panama, we found that mortality of seeds of two common pioneer tree species (*Miconia argentea* and *Cecropia insignis*) buried in mesh bags for 6 months was reduced from 90–95% for untreated seeds to 50% for seeds treated with the broad-spectrum fungicide Captan (Dalling *et al.*, 1998a). Similar studies conducted in the growing house at La Selva, Costa Rica, using Benomyl fungicide are consistent with this pattern (Fig. 3.1).

Given the great scarcity of experimental and taxonomic work on seed associated fungi, the major questions regarding their ecological importance remain unanswered. If pathogens show strong host preferences

and are patchily distributed in the soil, then they may contribute strongly to the maintenance of diversity by locally reducing the density of seed banks of susceptible hosts. In contrast, if fungi are broad host-generalists and are uniformly distributed through space, then they may have a more neutral effect by limiting community-wide recruitment. Preliminary studies focused on one host tree, *Cecropia insignis*, suggest limited opportunity for escape from pathogens. Seeds of this species buried at BCI at below maternal crown sites, below conspecific males, and at a range of distances ≤ 50 m from conspecifics showed broadly similar mortality rates (Dalling *et al.*, 1998b; R. Gallery and J. Dalling, 2003, unpublished results).

Initial attempts to isolate fungi from *Cecropia* seeds incubated in the soil have revealed 32 distinct morphotypes emerging in culture from 250 seeds, with seven fungal morphotypes accounting for 72% of the total isolates (R. Gallery and J. Dalling, 2003, unpublished results). The absolute diversity of seed infecting fungi, however, is likely to be substantially higher as many seed-infecting fungi may be unculturable (e.g. Bridge and Spooner, 2001). Molecular analyses of the seven most abundant fungal morphotypes collected from *C. insignis* seeds indicate that they comprise representatives of several orders of Ascomycota, including species of *Fusarium*, *Chaetomium*, *Dictyochoaeta*, *Glionectria* and *Colletotrichum* (A.E. Arnold, North Carolina, 2003, personal communication). Intriguingly, several of these taxa have high sequence affinity with known endophytic fungi that have been isolated from tropical foliage (Arnold *et al.*, 2000; A.E. Arnold, North Carolina, 2003, personal communication). This suggests that some fungi might be vertically transmitted from the maternal host during seed development rather than infecting seeds in the soil (e.g. Kirkpatrick and Bazzaz, 1979). Further possibilities are that some seed-infecting fungi may act as benevolent mutualists rather than deleterious pathogens, or may switch from endophytes to pathogens according to the ontogenetic stage or identity of the host.

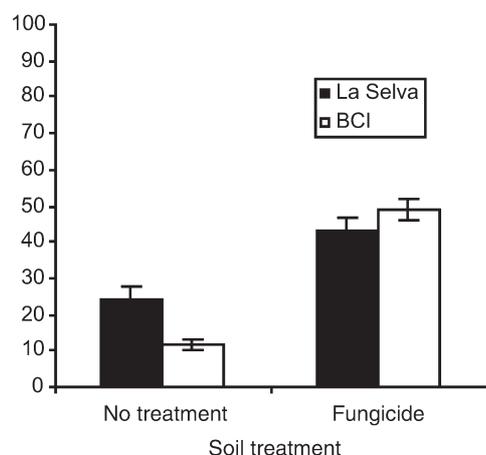


Fig. 3.1. Effect of fungicide treatment on seed germination in *Cecropia insignis*. Shaded bars show results from an experiment conducted at La Selva, Costa Rica, in which seeds were buried for 5 months in soil cores maintained in a shaded growing house. Monthly treatment of cores with Benomyl fungicide had a significant effect on germination, compared with untreated controls ($F = 12.4$, $df = 1.33$, $P < 0.01$; Gallery and Dalling, 2004, unpublished data). Open bars show similar results from an experiment conducted at Barro Colorado Island, Panama, for seeds buried for five months beneath *Cecropia* tree crowns and treated monthly with Captan fungicide ($F = 29.6$, $df = 1.36$, $P < 0.01$; Dalling *et al.*, 1998).

In addition to fungi, many other microorganisms are seed-borne and are reported as diseases of important agricultural crops, including nematodes, viruses, spiroplasmas and bacteria (reviewed in Agarwal and Sinclair, 1996). Most of these pathogens induce symptoms in developing seedling tissues, with limited effects on seed viability. Bacterial seed rot diseases, however are quite diverse, including *Bacillus*, *Curtobacterium* and *Pseudomonas* (Sinclair, 1978; Agarwal and Sinclair, 1996). More recently developed techniques, including polymerase chain reaction (PCR) technology, are likely to detect many more seed-borne diseases, and shed light on the role of antagonistic relationships between bacteria and fungi that may mediate seed infection in the soil (Kremer, 1987). As yet however, molecular techniques have had only limited application to studies of the microbial seed ecology of non-crop species (e.g. Jacobson *et al.*, 1998).

Seed Germination and Seedling Emergence

Traits that influence seed burial and seed persistence also influence the microsites in which seeds can germinate and the probability that seedlings successfully emerge. Seed mass is correlated with maximal emergence depth in the soil because limits to seed reserves dictate the resources available for the extension of a hypocotyl through the soil (Bond *et al.*, 1999). For the smallest seeded species (seed mass < 0.1 mg), maximal effective burial depths for emergence are < 5 mm (Dalling *et al.*, 1995; Pearson *et al.*, 2002), providing a major constraint on effective seed bank densities.

Seed mass also affects emergence and establishment success by influencing the susceptibility of seedlings to drought. In large canopy gaps, the soil surface may reach temperatures of > 40°C after only a few hours of exposure to direct irradiance, resulting in rapid drying of the top few millimetres of soil even when moisture levels in the bulk soil are close to field

capacity. Dry, clear weather lasting just a few days can be sufficient to cause significant mortality of newly emerging seedlings as soils dry out at a faster rate than roots can grow down through the soil profile (Daws, 2002). This has been shown in large (400 m²) gaps, where the survival of newly emerged seedlings of five small-seeded species was 20–35% higher in irrigated treatments versus non-irrigated controls 10 days after initiating experimental treatments (Engelbrecht *et al.*, 2001).

Finally, seed mass also influences the range of microsites available for seedling establishment through selection on gap detection mechanisms (Fig. 3.2). Small seeded light-demanding species (< 2 mg) have been shown to exhibit photoblastic seed germination (Pearson *et al.*, 2002), which is constrained by the limited penetration of light through the surface few millimetres of moist soil (Tester and Morris, 1987). Photoblastic seeds detect small shifts in the ratio of red : far red irradiance (Smith, 2000) associated with light interception by canopy vegetation or leaf litter on the soil surface (Vázquez-Yanes *et al.*, 1990). Continuous variation in red:far red irradiance allows for the discrimination of a range of disturbance sizes including litter-free microsites, and sites at the edge of gaps that are not exposed to direct irradiance.

Conversely, larger seeded light demanding species (> 2 mg) are capable of emerging from at least 5 cm below the soil surface (Pearson *et al.*, 2002). These species are typically not photoblastic, so must use alternative cues to detect gaps. Four of eight larger seeded species studied on BCI have been shown to respond to temperature fluctuations associated with soil warming during the day in gaps. These diel fluctuations in temperature can be measured at least 10 cm below the soil surface in large gaps and therefore constitute an effective germination cue for species with significant seed reserves (Pearson *et al.*, 2002). A disadvantage, however, of a temperature-based germination cue is that it fails to detect small gaps and gap edge microsites that do not receive sufficient direct irradiance to warm the soil, and therefore potentially limits recruitment

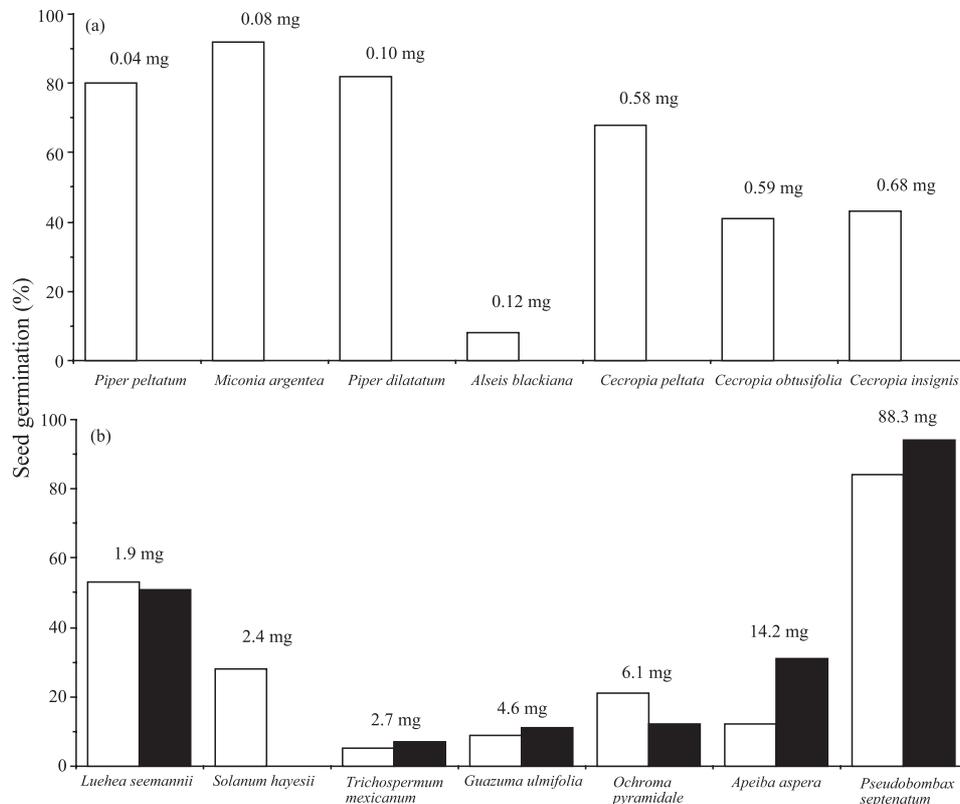


Fig. 3.2. Effect of light conditions on seed germination of pioneer species from Barro Colorado Island, Panama, varying in seed mass. Open bars shown seed germination in the light and filled bars show germination in the dark under constant temperature conditions (30°C). (A) Seven species with seed mass < 1 mg all have significantly higher germination in the light than in the dark (where no germination occurred; G test, $P < 0.01$). (B) For six species with seed mass > 1 mg germination is unaffected by light conditions. One exception is *Solanum hayesii*, where germination is triggered by high red : far red irradiance or by fluctuating temperature in the dark (Pearson *et al.*, 2003). Figure modified from Pearson *et al.* (2002).

of these species to larger canopy disturbances.

Conclusions and Future Work

This review reveals a number of apparently correlated traits that can be sketched out as potential syndromes directing the fate of small seeds present in seed banks (Table 3.1). As yet, however, studies of seed ecology in tropical forests are very incomplete, and these associations are therefore best viewed as hypotheses to be tested from wider comparative studies. Research to date

has been concentrated in the neotropical lowlands, most notably at sites in Panama, Costa Rica and Mexico, and has also focused primarily on a narrow taxonomic group with many studies of vertebrate-dispersed tiny-seeded species in the genus *Cecropia*, and the family Melastomataceae.

A future research priority should be to expand studies of seed ecology in the Old World tropics, and to incorporate greater variation in habitat conditions beyond the moist lowland forest. At present, we have little idea of how gradients in temperature and moisture availability influence seed persistence in the soil, or how shifts in composition and abundance of guilds of

Table 3.1. Suggested linkages among traits influencing the fate of small-seeded light-demanding species in tropical forests according to seed mass.

	Seed mass	
	< 1 mg	> 1 mg
Dispersal mode		No relationship
Probability of seed burial		No relationship
Seed persistence in soil	Mostly short? (< 1 year)	Short–Long (up to 30+ years)
Seed dormancy	Rare	Common
Litter invertebrate predation	Susceptible ^a	Less susceptible
Pathogen infection	Susceptible	Resistant?
Germination cue	Photoblastic	Non-photoblastic

^aLimited evidence suggests that wind-dispersed seeds are less susceptible to predation by litter invertebrates (principally ants).

invertebrate and vertebrate seed predators influence seed fate in the litter and rates of incorporation into the seed bank. Finally, our inferences of how seed morphology and physiology influence fate are potentially biased by a lack of phylogenetic control over interspecific comparisons. Many light-demanding species belong to speciose genera (e.g. *Cecropia*, *Miconia*, *Piper*, *Maca-ranga*) with wide geographic distributions and potentially provide model taxa for investigating how seed traits have radiated in response of environmental variation.

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