

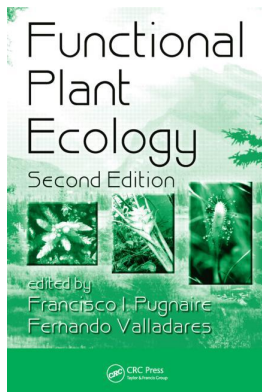
This article was downloaded by: 10.3.97.143

On: 05 Dec 2023

Access details: *subscription number*

Publisher: *CRC Press*

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: 5 Howick Place, London SW1P 1WG, UK



## **Functiona Plant Ecology**

Francisco I. Pugnaire, Fernando Valladares

## **Seed and Seedling Ecology**

Publication details

<https://www.routledgehandbooks.com/doi/10.1201/9781420007626.ch18>

Kaoru Kitajima

**Published online on: 20 Jun 2007**

**How to cite :-** Kaoru Kitajima. 20 Jun 2007, *Seed and Seedling Ecology from: Functiona Plant Ecology* CRC Press

Accessed on: 05 Dec 2023

<https://www.routledgehandbooks.com/doi/10.1201/9781420007626.ch18>

**PLEASE SCROLL DOWN FOR DOCUMENT**

Full terms and conditions of use: <https://www.routledgehandbooks.com/legal-notices/terms>

This Document PDF may be used for research, teaching and private study purposes. Any substantial or systematic reproductions, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The publisher shall not be liable for an loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

# 18 Seed and Seedling Ecology

*Kaoru Kitajima*

## CONTENTS

Introduction .....	549
Seed Size and Its Correlates .....	549
Natural Enemies .....	553
Dispersal.....	556
Dormancy and Germination .....	558
Seedling Recruitment.....	560
Seedling Growth and Survival.....	562
Conclusion.....	566
Acknowledgments .....	566
References .....	566

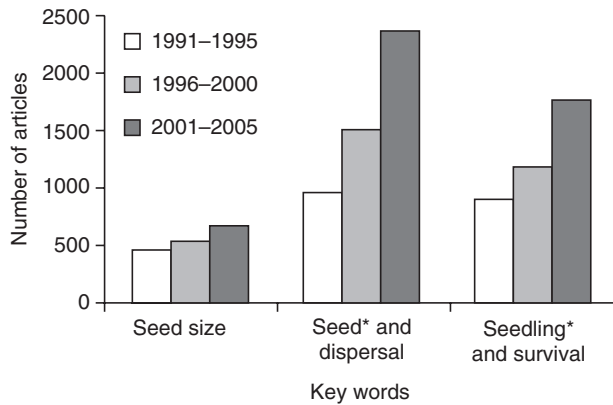
## INTRODUCTION

Many features of plant communities are strongly influenced by events surrounding reproduction by seeds. Characteristics such as the relative abundance of the species, their annual fluctuation in number, and their spatial pattern are all influenced by the ability of each species to reproduce. The diversity and dynamics of plant communities hinge on the ability of species to regenerate successfully, resist local extinction, as well as disperse from neighboring communities. Grubb (1977) suggests that the coexistence of so many plant species that appear to have indistinguishable niches as adults can be explained by their distinct requirements in early stages of their life histories.

The goal of this chapter is to demonstrate how species-specific traits of seeds and seedlings are related to life history traits and regeneration strategies of species. The importance of seed and seedling ecology has been increasingly recognized both in basic and applied research during the last few decades as is evident in a literature search (Figure 18.1). Within the limited space here, only a limited number of important new perspectives can be discussed in addition to the key processes summarized in the previous version prepared with Michael Fenner in 1997. Those interested in further details should consult books that provide a more comprehensive coverage (Baskin and Baskin 1998, Fenner 2002, Fenner and Thompson 2005). The following sections follow largely chronological order of events surrounding regeneration from seeds. The take-home message, however, is that each step of seedling regeneration is intimately linked to other events surrounding reproduction, as well as to the overall life history of the species.

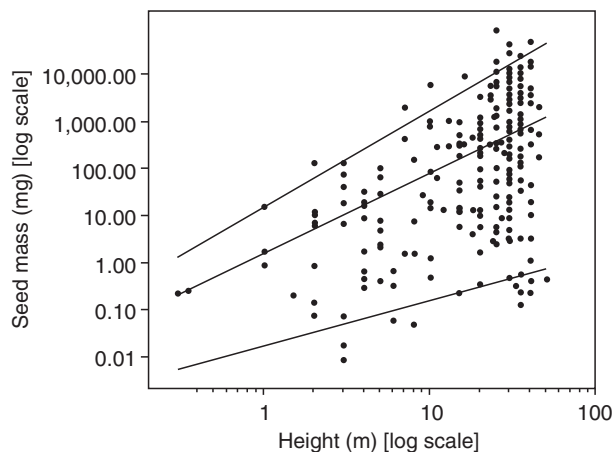
## SEED SIZE AND ITS CORRELATES

Seed size is a key trait that has evolved in association with a multitude of other species-specific traits (Moles and Westoby 2006). Among present-day seed plants, seed size varies over



**FIGURE 18.1** Number of journal articles indexed by Web of Science search engine for three key words, “seed size,” “seed\* and dispersal,” and “seedling\* and survival” for three 5 year periods, 1991–1995, 1996–2000, and 2001–2005. The asterisk allows searching of both plural and singular forms. The number during the 8 year period since the original preparation of this review (1998–2005) was 989, 3329, and 2498 in each of these topic areas, respectively.

$10^{11}$ -fold, but within a given local community, the range is typically  $10^6$  excluding extremes such as the dust-sized seeds of orchids and the double-coconuts that weigh 20 kg (Moles et al. 2005). The size adopted by a particular species is partly determined by phylogenetic influences; big (or small) seeds run in families. Flowering plant species of the early Cretaceous had small seeds and fruits, but their eventual dominance in closed forest vegetation was apparently conducive for the evolution of larger seeds and fruits (Eriksson et al. 2000). A recent analysis of seed size evolution in seed plants reveals that the largest divergence occurred as an overall reduction of seed size from gymnosperms to angiosperms (Moles et al. 2005). The same analysis also confirms a widely observed pattern found in a range of floras that seed size is associated with growth form and height of parents (Leishman et al. 1995, Poorter and Rose 2005). Daisies cannot produce seeds the size of coconuts; adult height and terminal twig diameter set an upper limit on seed size (Grubb et al. 2005) (Figure 18.2). This may be the main reason for the latitudinal gradient of seed



**FIGURE 18.2** The relationship between mean seed dry mass and mature plant height for 226 species in tropical lowland rainforest in Australia. (Adapted from Figure 1 of Grubb, P.J., Metcalfe, D.J., and Coomes, D., *Science* 310, 783A, 2005. With permission.)

size, as tropical communities dominated by trees should have larger seed size on average than temperate communities represented proportionally more by herbaceous species. Across latitudes, mean seed mass decreases by 10-fold for every *c.* 23° moved toward the poles (Moles and Westoby 2003). An obvious question to functional ecologists, then, is how seed size variation among species is associated with their differences in life history and habitat preferences within and across plant communities.

Within the constraints of the genetic makeup and size of the plants, the characteristic seed size of each species is presumed to be the result of natural selection. There is usually some variation in mass among and within populations, and within the progeny of individual plants. However, the variation within a species is generally much less than that of the vegetative parts (Harper 1977). The selection pressures influencing seed size are likely to have been numerous, often operating in opposite directions, resulting in a size that may represent the best compromise.

Seed size should be viewed in relation to the overall reproductive strategy and life history of the species. For a given allocation of resources to reproduction, the plant can either invest in a small number of large seeds or a large number of small ones, or at some intermediate combination of number and size. The compromise size adopted is conventionally thought to represent the conflicting requirements of dispersal (favoring small seeds) and establishment (favoring large seeds). Seed size variation is often interpreted in terms of a trade-off between dispersability and establishment (Ganeshiah and Uma 1991, Geritz 1995, Ezoe 1998). Short-lived early colonizers of disturbed sites and open ground typically produce numerous light, easily dispersed seeds; long-lived species of less-disturbed sites tend to have larger, less widely dispersed seeds. Seed augmentation experiments demonstrate that dispersal poses a greater constraint for colonization in large-seeded species than in small-seeded species (Leishman 2001, Makana and Thomas 2004, McEuen and Curran 2004). Large-seeded species tend to be more competitive, and depend less on disturbance for seedling establishment than small-seeded species in grasslands (Reader 1993, Burke and Grime 1996, Lindsay et al. 2004). Improved seedling establishment associated with large seed size helps compensate for dispersal limitation, but it does not appear sufficient to overcome the average reduction of fecundity per unit crown area associated with increase in seed size (Moles and Westoby 2004).

Numerous additional life history correlates, such as long-term survival of established seedlings, time to reach reproductive maturity, and life-time seed production, must be taken into account to understand the seed number–size trade-offs. Furthermore, residual variation among species arises from the methods of dispersal adopted, influence of particular species of animals as seed dispersers and predators, establishment conditions (degree of shade, drought, nutrient level), formation of persistent seed banks, cotyledon functional morphologies, and adoption of a parasitic or hemi-parasitic way of life (Leishman et al. 1995).

Ecologists have long identified the advantage of large seeds for successful seedling establishment in shade (Salisbury 1942, Grime and Jeffrey 1965). Recent meta-analyses confirm this pattern for temperate and tropical species (Hewitt 1998, Hodkinson et al. 1998, Moles and Westoby 2004, Poorter and Rose 2005). Across and within many taxa, seed size is correlated with the ability to survive and establish in shade (Osunkoya et al. 1994, Saverimuttu and Westoby 1996, Paz and Martinez-Ramos 2003), although there are exceptions of small-seeded shade-tolerant species and large-seeded light-demanders (Augsburger 1984b, Metcalfe and Grubb 1995). There are three possible ways in which large seed size may contribute to seedling establishment in shade (Westoby et al. 1992). First, a large seed can create a large seedling that can successfully display leaves above litter (Molofsky and Augspurger 1992). Second, a significant fraction of resources in a large seed may remain in storage instead of being used for immediate seedling development (Garwood 1996, Green and Juniper 2004). Third, the advantage of a large seed may be indirect via association of seed size with seedling morphology, development types, and growth rates

(Hladik and Miquel 1990, Kitajima 1996). Across many floras, large-seeded species tend to have storage cotyledons, whereas small-seeded species tend to have thin photosynthetic cotyledons (Ibarra-Manriquez et al. 2001, Zanne et al. 2005). Phylogeny exerts a strong influence on both seed size and cotyledon functional morphology, which have diverged in concert (Wright et al. 2000, Zanne et al. 2005). The three pathways for large-seed advantage are not mutually exclusive, and the relative importance of these mechanisms must be evaluated experimentally.

All else being equal, the greater the seed reserve mass, the greater the initial seedling mass. As a rule of thumb, seed reserves alone appear sufficient to construct the seedling up to development of the first photosynthetic organs (cotyledons or leaves, depending on the species). Certainly, within a species, bigger seeds produce larger seedlings initially (Stanton 1984, Wulff 1986, Gonzalez 1993). When different species are compared, lipid content in seeds is a small modifier to this rule; a unit mass of oil-rich seed is converted to a greater mass of seedling than a unit mass of starchy seed (Penning de Vries and Van Laar 1977, Kitajima 1992a). Yet, interspecific variation in seedling size due to variation in seed lipid content (up to twofold) is completely dwarfed by the variation due to seed mass (typically up to  $10^6$ -fold). Other factors, such as whether the seedling sets aside a part of its seed reserves in storage, or what type of seedling tissue is created, appear to be greater modifiers of the relationship between seed size and seedling size.

Do larger-seeded species depend exclusively on seed reserves for a longer duration than smaller-seeded species? Initially, seedlings depend completely on seed reserves for both supply of energy and mineral nutrients, but gradually following the development of photosynthetic organs and roots, seedlings start utilizing externally supplied resources. Reserves remaining in large-storage cotyledons may be utilized for a rapid recovery from shoot loss to herbivory in very early stages (Dalling et al. 1997a). Logically, this advantage lasts only as long as the reserves last. For example, Saverimuttu and Westoby (1996) found that the large-seed advantage of seedling longevity in shade exists only during the cotyledon stage, but not for seedlings transferred to deep shade after full expansion of leaves. In California tan oak, transfer of energy reserves from storage cotyledons occurs before leaf expansion (Kennedy et al. 2004). After the first leaf expansion, seedlings of five tropical trees experiencing negative carbon balance due to defoliation or shading do not rely on energy reserves in cotyledons, but instead on starch and sugar stored in stems and roots (Myers and Kitajima 2007). However, storage cotyledons that remain attached to the seedling axis may continue to support seedling demands for mineral nutrients (Oladokun 1989, Milberg et al. 1998), even after energy reserves cease to be exported. Functional growth analysis of seedlings raised with and without deprivation of light or nitrogen demonstrates that complete seed reserve dependency lasts longer for nitrogen than for light in all three species tested (Kitajima 2002). Seedling size achievable without external supply of an individual mineral element can also be indicative of the relative duration of seed reserve dependency for that element (Fenner and Lee 1989, Hanley and Fenner 1997).

If prolonged support enabled by large seed size is more important for mineral nutrients than for energy, large seeds should enhance seedling establishment in infertile soils. Interestingly, experimental support for this idea comes largely from fire-prone communities on infertile soils (Jurado and Westoby 1992, Hanley and Fenner 1997, Milberg et al. 1998, Vaughton and Ramsey 1998). Lee et al. (1993) found that among species in the grass genus *Chionochloa*, there is a negative correlation between seed size and soil fertility of the habitats of the species. In contrast, Maranon and Grubb (1993) found that in a selection of 27 Mediterranean annuals, the species with the largest seeds tend to occupy the soils with a richer nutrient supply. A higher seed concentration of a particular mineral element also extends the dependency on seed reserves for that element, as shown for a prolonged nitrogen dependency in a Bignoniaceae species (Kitajima 2002). Concentrating particular mineral

elements in seeds should be preferred to increasing seed size when there is a selective pressure to enhance dispersal. Indeed, there is a negative correlation between seed mass and nitrogen concentration across species (Fenner 1983, Pate et al. 1985, Grubb 1998). However, plants from more infertile habitats do not necessarily have greater mineral nutrient concentrations (Lee et al. 1993, Grubb and Coomes 1998). Yet, it is possible that high concentrations of particular mineral elements in seeds may complement the deficiencies of these elements in the environments (Stock et al. 1990). Perhaps, imbalance of nitrogen and phosphorus supplies in postfire soils may select for fire-dependent species to concentrate nitrogen reserves in seeds.

There is also some evidence that plants from dry habitats tend to have larger seeds. Baker (1972) carried out a survey of 2490 species in California and showed a fairly consistent relationship between seed size and dry conditions. It is thought that greater seed reserves might enable the seedling to establish roots quickly and so exploit a greater volume of soil for moisture than would otherwise be possible. However, in a survey of dunes in Indiana, Mazer (1989) was not able to show any significant relationship between seed size and water availability. Jurado and Westoby (1992) in a test involving Australian species found that seedlings from heavier-seeded species do not (as they hypothesized) allocate a greater proportion of their resources to roots than lighter-seeded species. Glasshouse experiments on seeds of semiarid species by Leishman and Westoby (1994b) indicate an advantage to larger seeds in dry soil, but their field experiments failed to confirm this. Further surveys of the type carried out by Baker (1972), on a range of floras, would help to clarify the relationship between seed size and dry habitats.

There is no doubt that a myriad of complex natural selective pressures have acted on plants resulting in the seed sizes observed in contemporary floras. Many ecological traits at seed and seedling stages discussed in the subsequent sections could not have evolved independent of seed size.

## NATURAL ENEMIES

Seeds and young seedlings represent attractive resources to a broad array of consumers. In general, seed tissue has a much higher concentration of nitrogen, phosphorus, sulfur, and magnesium than other plant tissues, in addition to being a rich source of carbohydrates and, in some cases, oils (Vaughan 1970, Barclay and Earl 1974). It is not surprising therefore to find that in many plant species a large proportion of seed production is lost to predation. Crawley (1992) provides a useful list of examples from the literature of percentage loss of seeds to predators in different plants. The proportion averages at about 45%–50%, but often approaches 100%. Two distinct groups of seed eaters exist. Predispersal seed predators are typically highly specialized sedentary larvae of beetles, flies, moths, or wasps that mature within the seed or seedhead. In contrast, postdispersal seed predators are usually vertebrates, more mobile, less-specialized feeders, although some tropical insect seed predators attack seeds postdispersally. Whole taxa of granivorous birds and mammals have evolved (e.g., finches, rodents) to exploit this rich food source. In the seasonally inundated forests of Amazonia nearly all the seeds that fall into the water are eaten by fish (Kubitzki and Ziburski 1994). In addition, there are many invertebrates that act as predators of dispersed seeds: various species of ants (Gross et al. 1991), earwigs (Lott et al. 1995), slugs (Godnan 1983), and even crabs (O'Dowd and Lake 1991). Soil-borne fungi are also important consumers of seeds after dispersal (Dalling et al. 1998, O'Hanlon-Manners and Kotanen 2004, Schaffer and Kotanen 2004). Many of these organisms also act as predators of young seedlings attracted to their soft and less-defended tissues.

Rather few experimental studies have been carried out to determine the long-term demographic effect of seed predation. In some cases, there is no doubt that seed eaters reduce recruitment. Louda (1982) excluded seed-eating insects from the Californian shrub

*Haplopappus squarrosus* by the use of insecticide, and found that the mean number of seedlings established per adult after 1 year was greater in the treated plots by a factor of 23. Further proof that seed predators can reduce subsequent recruitment (and hence lifetime fitness) is provided by a demographic study in which insecticide was applied to the thistle *Cirsium canescens* by Louda and Potvin (1995). Generally, there are significant increases in recruitment when seeds were protected from predators (Molofsky and Fisher 1993, Terborgh and Wright 1994, Asquith et al. 1997). However, the consequences of seed predation for a plant population depend on whether regeneration is limited by seed numbers or by some other factor such as dispersal and availability of safe sites, which may change from season to season (Edwards and Crawley 1999). Even when seed number is not limiting, predators may still influence the genetic makeup of the plant population by differential selection of the seeds. They can also affect the evolution of the structural defenses of the seeds. Benkman (1995) compared the allocation of putative seed defenses in limber pine (*Pinus flexilis*) in sites where tree squirrels are present (in the Rocky Mountains) with sites where they are absent (in the Great Basin). He found that allocation of energy to cone, resin, and seed coat relative to the kernel is greater by a factor of 2 where the predators are present. This difference in allocation may be a relatively recent evolutionary development since tree squirrels became extinct in the Great Basin only within the last 12,000 years.

Seed predation by animals may have had an evolutionary influence on seed size. One means by which a plant could reduce loss to predation would be to reduce seed size (with corresponding increase in seed number), thereby increasing the foraging cost/benefit ratio of potential predators. Janzen (1969) cites the case of two groups of Central American legumes, which adopt contrasting means of coping with predation by beetle larvae. The small-seeded group escapes predation by subdivision of their reproductive allocation, whereas the large-seeded group is defended by toxic compounds. A study of predispersal predation of seeds in a number of *Piper* species in Costa Rica found that the large-seeded species lost a much greater proportion of their seeds to insects (Greig 1993). Within a species, the larger seeds may be more vulnerable to attack by predispersal predators. For example, bruchid beetles preferentially oviposit on larger seeds in the sabal palm (Moegenburg 1996). At the same time, extremely large seeds of some tropical trees (seed reserve mass >50 g) appear to have ample reserve to germinate even after consumed by up to eight bruchid larvae (Dalling et al. 1997a). Differential loss is also seen in vertebrate grazers that consume seeds as part of their forage. Among legume seeds likely to be eaten by grazing livestock, small seeds may be at an advantage. Tests with sheep found that small seeds have the highest survival rate after passage through the gut (Russi et al. 1992). Large seeds may thus need to devote more of their resources to structural defense. Fenner (1983) showed a consistent trend among 24 herbaceous Compositae for relatively greater seed coats in larger seeds. The proportion of seed weight allocated to seed coat varies from 15% in *Erigeron canadense* (seed weight 0.072 mg) to 61% in *Tragopogon pratense* (seed weight 10.3 mg). Thus, defense against seed predation may be another factor in determining the balance between seed size and number.

Seed predation (mainly by insects, rodents, or birds) is widely thought to select for masting, that is, bumper crops at irregular intervals with a light seed crop (or total crop failure) in the intervening years (Kelly and Sork 2002). Recently published examples of long-term studies on seed production for individual tree species include rimu (Norton and Kelly 1988), southern beech (Allen and Platt 1990), oak (Crawley and Long 1995), and ash (Tapper 1996). Multiple species may participate in community-level masting by synchronizing to climate cues or simply tracking favorable climate. Because climatic variation is greater in temperate latitudes than in the tropics, Kelly and Sork (2002) hypothesized that masting is more likely in temperate than in tropical forests. In support of this view, interannual variability of seed production is lower in a tropical forest in Panama (Wright et al. 2005) than in a temperate forest in Japan (Shibata et al. 2002). Yet, community-level masting occurs

in the tropics, most famously in the SE Asian forests dominated by Dipterocarpaceae (Janzen 1974, Curran and Leighton 2000). It is hypothesized that masting results in the alternate starvation and satiation of the seed predators; in lean years the predators eat most of the seeds produced, but are overwhelmed by the bounty in bumper years, leaving a surfeit available for regeneration.

Swamping predators may not be easy. Species-specificity, mobility, and generation time of seed predators affect whether they can be successfully satiated or not. Even if species-specific predators are satiated, natural enemies that can attack multiple species, such as damping-off pathogens, may cause greater seed and seedling mortality when seed crop is high. Seed predator populations can respond markedly, at least in some cases, to the level of mast and remove the entire crop in most years (Wolff 1996). Seeds unconsumed by resident predators may be eventually eaten by nomadic animals that become attracted to masting localities (Curran and Webb 2000). There are alternative explanations for the benefits of masting, such as greater pollination efficiency and the need for large-seeded species to accumulate sufficient reserves for reproduction (Fenner 1991, Kelly and Sork 2002). Masting may also be a way to track favorable climate for seed production (Wright et al. 1999) and seedling establishment (Williamson and Ickes 2002). Although it is difficult to exclude these alternative explanations, there is a large body of evidence in support of the general applicability of the predator satiation hypothesis. For example, species most prone to seed predation show masting behavior most strongly (Silvertown 1980a). Seedling establishment can be virtually confined to those following mast years (Jensen 1985, Forget 1997). Rogue individuals that produce seed in a nonmasting year are targeted by seed predators, thus selecting for synchronicity, as found for pinyon pine populations (Ligon 1978), the cycad *Macrozamia* (Ballardie and Whelan 1986), and *Acacia* spp. (Auld 1986). These observations are at least consistent with the predator satiation hypothesis.

In addition to obvious population effects, predators and other natural enemies affect spatial patterns within a community. Janzen (1970) and Connell (1971) put forward the idea that seed predation near trees in tropical rainforests may prevent regeneration of the same species in the immediate vicinity of the parent plant, reducing intraspecific clumping and so promoting diversity. The high mortality near parents may occur either as a direct result of distance to parents (because the parent and its offspring share the same natural enemies) or an indirect result of high density of offspring near parents (because the natural enemies are either attracted to or can spread easily in a dense populations). Because seed density is almost always confounded with distance from the parent plant, an experimental approach is necessary to tease apart whether it is density or distance that is responsible for the observed patterns (Augsburger and Kitajima 1992). This is an important distinction, as modeling studies found that dispersal patterns of not only seeds, but also of natural enemies, affect whether such interactions would yield greater plant species richness (Nathan and Casagrandi 2004, Adler and Muller-Landau 2005). The natural enemies that operate in a density-dependent manner include not only seed predators, but also pathogenic microbes (Augsburger 1983b, Dalling et al 1998, Bell et al. 2006) and leaf-eating herbivores (Sanchez-Hidalgo et al. 1999). Such negative density dependency is observed not only in tropical rain forests but also in less-species rich temperate forests (Packer and Clay 2000). Interestingly, a recent meta-analysis of distance effects on seed and seedling survival using 152 published data sets found a significant effect of distance on seedling survival but not for seed survival (Hyatt et al. 2003).

Testing the Janzen–Connell hypothesis requires two steps: (1) demonstration of distance or density dependency of juvenile survival, and (2) demonstration that such effects promote species diversity. From comparison of community-wide analysis of seeds collected in traps and seedlings in plots adjacent to these traps, Harms et al. (2000) conclude that density-dependent natural enemies increase species diversity between seed and seedling stage. It is important to remember, however, that the overall level of seed mortality is determined by



interactions of multiple predators that often exhibit contrasting functional responses to seed density. A given seed density may be high enough to satiate one predator species, but may promote consumption by another. Furthermore, the availability of alternative food sources, phenologies, clumping of adult trees, and other environmental factors affect the spatial patterns of seed predation (Forget et al. 1997, Hammond and Brown 1998, Kwit et al. 2004). Nevertheless, the net result is negative density dependency for many coexisting tree species in terms of seedling recruitment from seeds (Harms et al. 2000, Wright et al. 2005) and seedling survival (Webb and Peart 1999).

## DISPERSAL

Seed dispersal is important for avoiding competition from the parent, escape from localized natural enemies, arrival in safe sites, successful colonization of other communities to avoid extinction, and so determining plant diversity and distribution at both local and regional scales (Wang and Smith 2002, Vormisto et al. 2004, Muller-Landau and Hardesty 2005). Some of these processes clearly hinge on rare long-distance dispersal events that are important but hard to quantify (Cain et al. 2000). Understanding seed dispersal is also important for conservation of endangered species and management of invasive exotic species. A species may be absent at a given locality simply because seeds do not arrive there (dispersal limitation) or because it is not a safe site for seedling establishment (establishment limitation). The relative importance of these processes can be evaluated experimentally by planting seeds to overcome dispersal limitation. Dispersal limitation appears ubiquitous across biomes (e.g., Tilman 1997, Maron and Gardner 2000, Dalling et al. 2002, Makana and Thomas 2004, McEuen and Curran 2004, Svenning and Wright 2005) and is considered important for species coexistence (Tilman 1994, Hubbell et al. 1999).

The means by which seeds are transported varies from species to species. Many appear to have no particular adaptation for dispersal. They may be carried in mud on the feet of animals and birds, as was shown in experiments by Darwin (1859), or eaten as part of the forage of grazers and survive passage through the gut and deposition some distance from their source (Janzen 1984, Sevilla et al. 1996). The seed itself may be the reward in many scatter-hoarded species, such as oaks and many tropical tree species with fruits and seeds that lack any apparent dispersal appendages. Other plant species provide an attractive reward for their dispersers in the form of a fleshy fruit (or aril) in which the seeds are imbedded. Another large group exploits the wind as a means of transport, with wings or feathers that decrease the rate of descent, thereby increasing the horizontal distance traveled in a given time (Augsburger 1986). The distance traveled is also a function of the height of release. Techniques for quantifying the rate of descent of seeds under standardized conditions allow comparisons of dispersal potentials among species (Askew et al. 1997).

The interaction of dispersers with a species results in a characteristic spatial pattern of distribution of its seeds, called its seed shadow or dispersal kernel. Much progress has been made in statistical techniques to describe seed shadows in recent years (Okubo and Levin 1989, Clark et al. 1999, Nathan and Muller-Landau 2000, Levin et al. 2003, Greene et al. 2004). Yet, how to model the tail of dispersal shadows, that is dispersal beyond 100 m from the parent, continues to pose an important challenge to ecologists (Cain et al. 2003). Genetic methods are increasingly recognized to be useful for quantification of long-distance dispersal events (Cain et al. 2000, Wang and Smith 2002, Jones et al. 2005, Hardesty et al. 2006). Regardless of the methods employed, spatial patterns of seed dispersal are easier to model for wind-dispersed species than for animal-dispersed species. Wind-dispersal is usually skewed toward the down-wind direction, often peaking at a short distance from the source (Augsburger 1983a). Steep slopes can also influence the skewness (Lee et al. 1993). Animal-dispersed seeds tend to be more clumped because they are deposited beneath roosting sites (by birds and bats,

Russo and Augspurger 2004), in caches (by rodents, Howe 1989, Forget 1990, Willson 1993), or in latrines (by tapirs, Fragoso et al. 2003). Some dispersal agents not only help seeds escape negative density dependency in the vicinity of the parent, but also help deliver seeds to specific safe sites, such as treefall gaps (directed dispersal, Wenny 2001). Examples include bellbirds in tropical cloud forests (Wenny and Levey 1998), ants in lowland tropical forests (Horvitz and Schemske 1994), and mice in temperate forests (Seiwa et al. 2002). Even wind may preferentially deliver seeds into treefall gaps by their interaction with canopy roughness (Augspurger and Franson 1988, but see Jones et al. 2005). Effectiveness of dispersal not only depends on the identity of the dispersers, but also their interaction with fruit and seed size (Seiwa et al. 2002, Alcantara and Rey 2003, Jansen et al. 2004). Loss of effective dispersal animals due to hunting and habitat fragmentations are likely to result in a large proportion of seeds undispersed near parents, all of which may be killed by density-dependent natural enemies (Wright and Duber 2001, Chapman et al. 2003).

The range of animals involved in seed dispersal is very wide. The most important groups are birds and mammals, but cases of seed dispersal by other vertebrates are known, for example, fish (Goulding 1980, Horn 1997), amphibians (Silva et al. 1989), and reptiles (Hnatiuk 1978). Seed dispersal by earthworms has also been recorded (McRill and Sagar 1973, Pearce et al. 1994). Some seeds may be dispersed more than once: first deposited by birds, monkeys, and bats, and then removed by secondary dispersers such as ants (Hughes and Westoby 1992, Levey and Byrne 1993), dung beetles (Chapman et al. 2003), and scatterhoarding rodents (Forget and Milleron 1991). Survival of seeds may be negligible if they remain in clumps under bat or bird roosts. Ants are the only invertebrate group that disperses seeds in any appreciable number (Stiles 2000). Dispersal by ants (myrmecochory) is especially prevalent in warm dry climates and on infertile soils (Beattie and Culver 1982, Westoby et al. 1991). Ant-dispersed seeds are typically provided with an oil body (elaiosome), which the ants eat. They retrieve the seed from the ground, carry them off to their nests, remove the elaiosome, and deposit the seed in a refuse heap. Not all seeds survive ant transport, and in some cases a proportion of the seeds are eaten as well (Hughes and Westoby 1992, Levey and Byrne 1993). The advantages to the plant are thought to be (a) dispersal, though usually only within a few meters of the source; (b) protection from rodents by being buried out of sight; (c) protection from fire; and (d) deposition in a favorable microsite for germination and establishment (Bennet and Krebs 1987). Not all of these features may be equally important in all cases. The importance of the mutualism for the plant can be seen in cases where native ants have been replaced by less well adapted invaders, as in the case of fynbos species in South Africa pushed out by the Argentine ant (Bond and Slingby 1984) and native ants in North America pushed out by fire ants (Zettler et al. 2001).

Long-distance dispersal is clearly important for movement of plants after major climate changes, migration to oceanic islands and fragmented habitats, and invasion by exotic species (Cain et al. 2000, 2003). Yet, there are selective pressures against long-distance dispersal, because a seed transported to very long distances is likely to face a risk of removal from its natural habitat, which may be patchily distributed. Comparisons between related plants on mainlands and islands show that dispersability of wind-dispersed species is often reduced on islands, presumably because of selective survival of the less-mobile seeds (Cody and Overton 1996). Remote islands are more likely to be colonized by seeds carried by birds than by wind or sea drift, as in the case of the Pacific Islands (Carlquist 1965). In contrast to the random action of wind and sea, bird movement is from island to island, often on migration routes, and so targeting the islands effectively with seeds deposited in feces and preened from feathers. Birds are also important in dispersing seeds to other types of islands including forest fragments (Johnson and Adkisson 1985) and isolated trees in the middle of pastures (Holl 1999, Zahawi and Augspurger 1999, Slocum and Horvitz 2000).

Variety of traits that influence dispersal patterns must have evolved in relation to life history and regeneration strategies of the species. For example, wind-dispersed species tend to be smaller and more common among pioneer species. Animal-dispersed species that are dispersed in clumps may be selected to have greater resistance against fungal pathogens, which can cause density-dependent mortalities. Thus, dispersal affects distribution and abundance of seedlings not only in terms of the initial spatial pattern, but also through its relationship with functional traits that modify seed and seedling survival after dispersal.

## DORMANCY AND GERMINATION

Another strategy for escaping from the parental plant is the formation of long-lived reservoirs of seeds in the soil, thus undergoing dispersal in time rather than space. This is an effective strategy especially in environments in which likelihood of seedling establishment varies greatly from year to year (Chesson 1985) or season to season (Baskin and Baskin 1998). Persistent seed banks consist of buried seeds that have the ability to remain viable for at least several years. They will only germinate if they are brought to the surface by some chance disturbance such as a tree-fall, an animal digging, or a farmer plowing. Although viable seed populations have patchy distribution and show large seasonal fluctuations (Thompson and Grime 1979, Thompson 1986, Dessaint et al. 1991, Dalling et al. 1997b), rough generalizations can be made for typical seed bank sizes across biomes: 20,000–40,000 m<sup>-2</sup> in arable fields, typically below 1000 m<sup>-2</sup> in mature tropical forests, and only 10–100 m<sup>-2</sup> in subarctic forests (Leck et al. 1989, Fenner 1995). Persistent seed banks are the most characteristic of habitats that are prone to frequent but unpredictable disturbance such as cultivation, fire, and floods. Examples of plant communities with large soil seed banks are agricultural fields, heathlands, chaparral, and disturbed wetlands (Thompson and Mason 1977, Leck et al. 1989). However, in many less-disturbed communities, those species that are characteristic of the early stages of succession and habitually the first colonizers of gaps, also form persistent seed banks. Although these species often dominate the seed bank, they usually form only a very small part of the current aboveground vegetation (e.g., Kitajima and Tilman 1996, Dalling and Denslow 1998). They represent both the past and the potential future species composition of the community (Fenner 1995). Within each species, genetic makeup of a soil seed population must be the result of selection in different years over a period of time, and the appearance of old gene combinations may put a damper on genetic change in the population (Templeton and Levin 1979, Brown and Venable 1986).

Survival of seeds in soil differs greatly among species and biotic and abiotic environments. Some temperate weeds are known to survive in soil for decades (Roberts and Feast 1973, Kivilaan and Bandurski 1981). Among tropical pioneer tree species, persistence of buried seeds range widely from species dying within a few months to species that do not exhibit any detectable mortality over a few years (Dalling et al. 1997b). Buried dormant seeds may suffer high mortality from fungal pathogens (Crist and Fruesem 1993, Dalling et al. 1998). All else being equal, the greater the depth of burial, the better the survival (Toole 1946, Roberts and Feast 1972, Dalling et al. 1997b), as attack from pathogens may be more active in shallow well-oxygenated soil. Small, round, smooth seeds can infiltrate more easily to greater depths in the soil by percolating into crevices. In contrast, large, elongated seeds with appendages such as awns or hairs would need an external agent to be buried. For a range of British grasses, species that form persistent soil seed banks mostly possess smooth and round seeds less than 0.3 mg, whereas those that do not form soil seed banks tend to have elongated bigger seeds with appendages (Thompson et al. 1993). Bekker et al. (1998) extend these generalizations, indicating that seed size and shape can be used in a predictive way as a guide to probable persistence. However, the same trend does not exist in Australia, possibly because of differences in burial regimes and disturbance (Leishman and Westoby 1998).

Dormancy prevents seeds from germinating at times, which would be unfavorable for growth and establishment. Some seeds possess absolute dormancy and do not germinate until certain developmental processes (such as after-ripening) have occurred. However, dormancy can often be a matter of degree. A dormant seed may be induced to germinate, but only under a very restricted set of conditions. The narrower the required conditions, the greater the level of dormancy. This is well illustrated by the cyclical changes in the level of dormancy, which occur in the seeds of many annual species (Baskin and Baskin 1985). During summer and autumn months, the seeds of summer annuals in the soil are fully dormant. However, the seeds are gradually released from dormancy by the chilling temperatures experienced during winter (Washitani and Masuda 1990). This is shown by the fact that if the seeds are taken from the field and tested for germinability in the laboratory, they germinate over an increasingly wider range of temperatures as spring approaches. As spring then advances into summer, the range of permitted germination temperatures narrows, eventually resulting in complete dormancy again. This mechanism of cyclical dormancy thus ensures that the seeds germinate only in spring, the most favorable germination for plants to complete their life cycle in a temperate environment. A similar mechanism ensures that winter annuals germinate only in autumn, in this case with seeds that require high temperatures to release them from dormancy (Vegis 1964, Baskin and Baskin 1980, Bouwmeester 1990). It is important to note that in these examples there is a clear distinction between the conditions required to overcome dormancy and the conditions needed for germination.

Another type of dormancy uses physiological mechanisms to ensure germination only in a gap in vegetation and near soil surface. If a seed germinates when buried below a given critical depth, it will not be able to emerge. Some seeds are indeed lost in this way (Fenner and Thompson 2005), but most seeds remain dormant at depth. Exposure of freshly dispersed and imbibed seeds to low red/far red ratio under leaf-canopy is important in inducing secondary dormancy to prevent fatal germination after burial (Washitani 1985). Once they are brought to (or near) the surface, usually by some unpredictable disturbance, it is advantageous for them to ensure that their dormancy is not broken unless they are in a suitable gap in the vegetation.

Some of the responses of seeds to various environmental stimuli may act as gap detection mechanisms. The requirement for light with a high red/far red ratio means that many seeds will not germinate if shaded by other plants (Gorski et al. 1977, Fenner 1980, Silvertown 1980b). The frequent requirement for fluctuating temperatures (Thompson and Mason 1977) or high temperature (Daws et al. 2006) could act as both a gap-detecting and a depth-sensing mechanism. Which of these gap-detection mechanisms is employed must reflect species specializations to different sizes and positions of gaps, as well as seed size (Pearson et al. 2002). Four shrub species within the genus *Piper* in a neotropical forest differ in their sensitivity to red/far red ratios, temperature, and nitrate (Daws et al. 2002a). The positive response to nitrate seen in many species (Hilhorst and Karssen 2000) could also be related to germinating in gaps, where the disturbed soil releases a flush of nitrate (Pons 1989). Some species in fire-prone communities respond to favorable conditions by requirement of high temperature or smoke for breaking dormancy (Keeley 1991, Hanley and Fenner 1998, Keeley and Fotheringham 1998, Brown et al. 2003). These various specific responses likely help seeds to identify favorable sites in which to germinate. Certainly, the seeds of many parasitic species such as *Orobanch*e and *Striga* can detect the presence of their host plant by a root secretion in the soil (Joel et al. 1995). The concept of gap-detection is in principle no different from host-detection, though the latter is considerably more specific.

The opposite of the seed-banking strategy is exhibited by recalcitrant seeds. Recalcitrant seeds completely lack dormancy, and must germinate immediately after they are shed. They also have to be dispersed in rainy months because they do not survive desiccation (Pritchard et al. 2004). The majority of nonpioneer tree species in the tropics, as well as some

large-seeded temperate species, fall into this category (Ng 1978, Hopkins and Graham 1987, Garwood and Lighton 1990, Pammenter and Berjak 2000, Rodriguez et al. 2000). In general, larger seeds tend to be more sensitive to desiccation (Daws et al. 2005). Complex selective pressures may be responsible for evolution of large seeds that lack dormancy. The advantage of large seed size for seedling establishment must be balanced against the risks of seed predation and desiccation. Without burial by scatter-hoarding rodents, the seeds would remain near the soil surface, exposed to a host of pests. Lack of dormancy and fast germination are advantageous to escape seed predators. The smaller surface-to-volume ratios of larger seeds also make them less likely to reabsorb water (Kikuzawa and Koyama 1999). Thus, quick radicle emergence is also advantageous for avoiding the risk of losing water. Yet, some large tropical seeds, including palms and legumes, tolerate dry conditions before radicle emergence. Many such seeds exhibit delayed germination, remaining viable in soil for months and years (Garwood 1983). It remains completely unknown what controls germination timing of such seeds.

## SEEDLING RECRUITMENT

Transformation of a germinating seed to a seedling represents the most vulnerable phase in the life of a plant. Plant species differ greatly in probability to recruit seedlings per capita of seeds shed. In a moist tropical forest in Panama, Wright et al. (2005) counted seeds in 200 traps placed over a 50 ha area weekly, and enumerated seedlings recruited in adjacent plots yearly (in the dry season to count all seedlings that germinated and survived throughout the previous rainy season). The number of seedlings recruited per seed ranged from 0.0003 to 0.15 among 32 species of trees, lianas, and shrubs based on the total sums across the 8 years. These differences among species may reflect their differences in susceptibility to postdispersal seed predation and disease, as well as probability of seed survival in soils, seedling emergence, and early seedling survival. The importance of natural enemies was strongly suggested in this data set, because recruitment probability was negatively dependent on local seed density in all 32 species. Moles and Westoby (2006) demonstrate the significant advantage of large seed size in postdispersal seed survival, survival in soil, and early seedling survival by compiling a large data set mainly from Australia. However, there is a large unexplained variation at a given seed size. This is perhaps not surprising because species show considerable variation within a seed-size category in allocation patterns of seed reserves to construct seedlings, and so suffer differently from different potential causes of mortality.

Young seedlings are susceptible to many hazards including predators attracted to seeds that remain attached to seedlings (Smyth 1978), desiccation (Miles 1972, Maruta 1976, Engelbrecht et al. 2006), pathogens (Augspurger 1983a,b, 1984a,b, Packer and Clay 2000), winter death and grazing (Mack and Pyke 1984), competition from existing vegetation (Fenner 1978, Aguilera and Lauenroth 1993, Tyler and Dantonio 1995, Kolb and Robberecht 1996), and damage caused by litterfall (Clark and Clark 1989, Scariot 2000, Gillman et al. 2004). These hazards may operate sequentially. For example, during the first 2–4 weeks following germination, seedlings of a neotropical tree, *Tachigalia versicolor*, suffer a high mortality rate from mammalian grazers; however, after the fourth week, as hypocotyls become woody and mammalian attack ceases, and pathogens become the main source of mortality (Kitajima and Augspurger 1989). There are many trade-offs that affect evolution of species traits at early seedling stages. Large seeds attract seed-eating animals, but they create large seedlings that emerge above litter and herbaceous vegetation. Small seeds can have better contact with soil to absorb water, but the limited root length of small seedlings makes them more vulnerable to drought. Fast growth and development help reduce the duration of this vulnerable phase, but fast growth also requires soft tissue vulnerable to various natural enemies.

Physical and chemical defenses are important for avoiding predation by various grazing animals. Comparing eight tropical tree species, Alvarez-Clare (2005) found that tissue toughness of seedling stems and leaves was positively correlated with their first year survival. High tissue densities (= dry mass per unit volume of stem or leaves) are strongly and positively correlated with tissue toughness, and thus important for defense against not only grazing animals but also pathogenic microbes that cause damping-off disease (Augsburger 1984b). Mollusc grazing kills many seedlings in temperate grasslands (Barker 1989, Hulme 1994, Fenner and Thompson 2005), and may affect number of recruits (Hanley et al. 1995) and eventual species composition (Hanley et al. 1996). Across species, palatability to molluscs is not correlated between adult and seedling leaves, but seedling leaves are always more palatable than adult leaves of the same species (Fenner et al. 1999).

An important determinant of a seedling's likelihood of survival and establishment is whether the seed is deposited in a safe site, defined as a place where the seed is provided with (a) the stimuli for breaking dormancy, (b) the conditions and resources required for germination, and (c) the absence of predators, competitors, pathogens, and toxins (Harper 1977, Fenner and Thompson 2005). Since different species have different requirements and tolerances as seedlings, a safe site for one species may not be safe for another. For example, in a temperate forest in Chile, seedling distribution of small-seeded species is more biased toward elevated microsites, such as logs, than large-seeded species (Lusk and Kelly 2003). Grain size of the substrate affects seedling emergence and establishment in an Alpine environment (Chambers 1995). Flood plain forests cannot be colonized by terra firme species whose seeds are not buoyant (Lopez 2001). Slopes provide microsites free of litter as well as greater moisture availability during the dry season, which are favored by small-seeded species (Daws et al. 2002b). A more common requirement for many seedlings, however, is the absence of competition from larger plants within the immediate vicinity. Closed vegetation provides an inhospitable arena for seedling establishment. Breaks in continuous vegetation cover mean not only higher availability of light, water, and nutrients, but also difference in activity of natural enemies. Mortality due to fungal pathogens is typically lower in gaps than that in the shaded forest understory, possibly because fungi prefer moist and shaded environments in general (Augsburger 1984a, Hood et al. 2004). In contrast, insect herbivores tend to be more abundant and active in gaps (e.g., Chacom and Armesto 2006), but higher photosynthetic income makes it easier for seedlings to tolerate herbivory.

Gaps of different sizes, as well as different positions within a gap, variably affect seedling emergence, growth, and survival. When fates of seedlings are followed in experimental gaps of different sizes, species often differ in their responses in relation to seed size (Gross 1984, McConnaughay and Bazzaz 1987, Bullock et al. 1995, Gray and Spies 1996, Dalling et al. 1999, Pearson et al. 2003). Differential responses of seed emergence in relation to gap size (Daws et al. 2002a) as well as seedling survival (Brokaw 1987) seem to explain species differences in minimum gap size requirements for seedling recruitment. On the other hand, growth rates of 12 tropical pioneer species in large- and small-gap environments are positively correlated, and thus, cannot explain their differences in gap-size preference observed in the field (Dalling et al. 2004). Due to the large environmental gradient from the center to the edge of a given gap (Brown 1993), a seedling's position within a gap may be more important to its survival than gap size per se (Brown and Whitmore 1992). One species may be favored in the center, whereas others survive better near the margins. Gap shape (which determines the ratio of margin to area) may be important for this reason.

There is clearly also a large stochastic element governing regeneration, influenced by unpredictable factors such as the presence of the parent in the vicinity, the absence of grazers, the occurrence of suitable weather conditions, all coinciding at the right place and time. Hence, it is difficult to predict species composition of a given gap, and gaps do not increase species diversity on a per-stem basis (Hubbell et al. 1999, Brokaw and Busing 2000).

Yet, within this haphazard framework, it is still possible to show that certain types of gaps favor the establishment of certain species from seed. A practical example of this is found in forestry management practice in which natural regeneration is encouraged for timber species (Fredericksen and Mostacedo 2000, van Rheezen et al. 2004, Makana and Thomas 2005). Effective treatments to enhance regeneration of timber species, many of which are light demanding as seedlings, include enlargement of logging gaps, soil surface scarification, and maintenance of seed parents near the gaps.

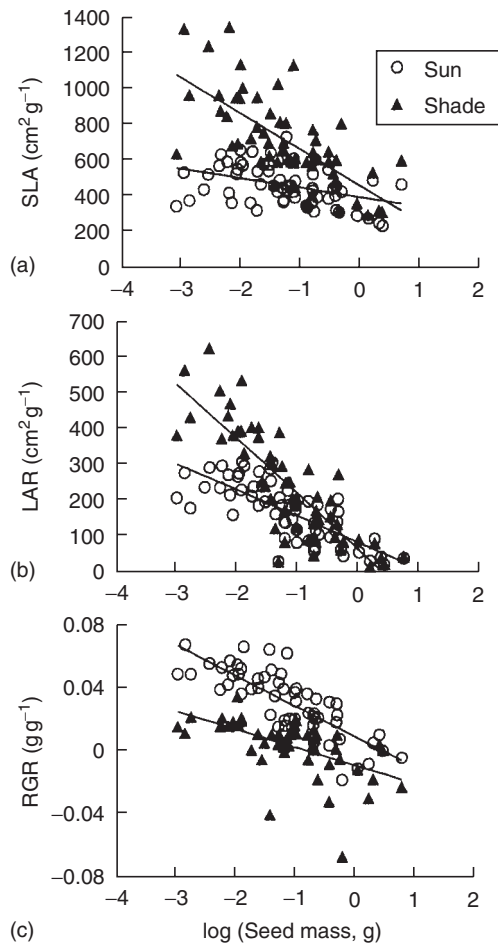
In small gaps or shaded environments, the attainment of a minimum size may be necessary for a seedling to secure an independent existence. An increased height should be most useful to seedlings in conditions where there is a steep gradient of light (due to shade from surrounding vegetation; Grime and Jeffrey 1965, Leishman and Westoby 1994a), or for seeds germinating below litter (Molofsky and Augspurger 1992). The hypocotyl or epicotyl may elongate in response to a low red/far red ratio of light coming through surrounding vegetation (Ballaré et al. 1988, Leishman and Westoby 1994a). In relation to their habitats and phylogeny, species and ecotypes differ in sensitivity of hypocotyl extension to red/far red ratios (Morgan and Smith 1979, Corré 1983). In a study of 15 tropical tree species, hypocotyls elongate in response to red/far red ratio only in Bombacaceae, a family largely represented by pioneer species (Kitajima 1994). Similarly, ecotypes from open habitats but not from forests exhibit stem elongation response to red/far red ratios (Dudley and Schmitt 1995). Stem elongation, however, is perhaps a maladaptive response in forest understories because it does not allow escape from shade; it only makes stems weak and more likely to topple. Initial seedling morphology of each species, including the degree of stem elongation and leaf display patterns, must have evolved in relation to its regeneration niche.

Clearly, how seed reserves are allocated and how long they support the energy and nutrient demands of seedlings are important for seedling recruitment (Kitajima 2002). However, that is not the end of the regeneration phase. Eventually, seedlings must become independent of seed reserves, initiating a completely autotrophic way of life to keep growing toward reproductive maturity.

## SEEDLING GROWTH AND SURVIVAL

After initial construction of leaves and roots with seed reserves, seedlings of some species continue to grow, whereas others appear to wait with little visible growth. In general, seed size is negatively correlated with seedling relative growth rate (RGR) between species (e.g., [Figure 18.3](#) for tropical tree species; see Shipley and Peters 1990 for review). This has been found in a wide range of plant families and habitats, for example, pasture grasses and legumes (Fenner and Lee 1989); species from variety of climatic conditions in Australia (Jurado and Westoby 1992, Swanborough and Westoby 1996); and woody plants in temperate (Cornelissen et al. 1996, Reich et al. 1998a) and tropical climates (Kitajima 1994, Huante et al. 1995, Poorter and Rose 2005); Mediterranean annuals (Maranon and Grubb 1993). This negative correlation is stronger under greater light availability in which seed reserve mass represents a smaller proportion of the seedling mass. Thus, it is not a mere reflection of allometry or autocorrelation (which is indeed expected because seed mass or initial seedling mass is the denominator in RGR calculation).

Most likely, the negative interspecific correlation between seed mass and seedling RGR stems from among-species differences in allocation patterns that evolved in relation to their life-history strategies. First, small-seeded species tend to have thin, epigeal, leaf-like cotyledons (Kitajima 1996, Wright et al. 2000, Zanne et al. 2005). Photosynthetic cotyledons allows them to start using light as the main source of energy earlier than they could if they had storage-type cotyledons (Kitajima 1992b, 2002). Second, small-seeded species tend to have a higher specific leaf area (SLA, leaf area divided by leaf mass) and leaf area ratio (LAR, leaf



**FIGURE 18.3** Associations of seed mass with morphological traits and relative growth rates of seedlings for neotropical woody species in a seasonal, moist forest in Panama. Seedlings of each species were raised from seeds in controlled sun and shade conditions (23% and 1% of open sky). (a) SLA and (b) LAR were determined at the full expansion of the first true leaves, and (c) subsequent RGR was determined from harvest 10 weeks later. Large-seeded species had significantly smaller SLA, LAR, and RGR in both sun and shade (linear regressions shown;  $P < 0.002$  for SLA in sun,  $P < 0.0001$  for all others;  $n = 57\text{--}61$  and  $51\text{--}58$  for sun and shade, respectively). (Data from Kitajima, K., *The Importance of Cotyledon Functional Morphology and Patterns of Seed Reserve Utilization for the Physiological Ecology of Neotropical Tree Seedlings*. Ph.D. thesis, University of Illinois, Urbana, Illinois, 1992a.)

area divided by total plant dry mass), the two traits known to be important for explaining difference in RGR (see Chapter 3). Although seedlings of different herbaceous and woody plants differ in RGR, the relationship of RGR with SLA is very similar across growth forms (Wright and Westoby 2001). Additional correlations of early seedling morphology and seed size, such as the relationship between root architecture and seed size (Huante et al. 1992, Kohyama and Grubb 1994, Reich et al. 1998a) also contribute to the relationship between seed mass and relative growth rates.

Another general rule that has gained increasing support during the last 10 years is the negative interspecific correlation between growth rates and survival of seedlings. In general, plant species from resource-poor habitats have slower maximum growth rates than those from resource-rich habitats (Chapter 3). In high-light environments conducive to fast growth



(e.g., gaps), shade-tolerant seedlings more abundant in shaded understory exhibit lower RGR than gap specialists. What is more interesting is that shade-tolerant species also exhibit lower RGR than gap specialists when both are grown in shade. In other words, species that grow fast in one light environment also tend to grow fast in another. Such significant concordance of RGR between sun and shade is demonstrated in a number of other studies (Ellison et al. 1993, Kitajima 1994, Osunkoya et al. 1994, Kobe et al. 1995, Poorter 1999, Valladares et al. 2000, Walters and Reich 2000, Bloor and Grubb 2003, Dalling et al. 2004, Baralotos et al. 2005), with few studies showing a lack of a relationship (Popma and Bongers 1988) or the opposite pattern (Agyeman et al. 1999). However, in terms of survival, shade-tolerant tree species tend to outperform shade-intolerant tree species in both shade and gaps in Neotropical forests (Augsburger 1984a, Kobe 1999). Thus, the general functional basis for high-shade survival is not the ability to grow fast in shade, but the ability to survive through avoidance or tolerance of inevitable tissue loss to various hazards. In sum, natural enemies appear to mediate niche specialization of seedlings along light gradients.

Natural enemies are also important in mediating growth-survival trade-off and specializations to rich and poor soils. This is elegantly demonstrated by Fine et al. (2004) in the Peruvian Amazon, where fertile alluvial soil and nutrient-poor white sand support contrasting tree communities. In a factorial experiment, they demonstrate that seedlings of alluvial-soil specialists grew faster than those of white-sand specialists in both soil types when they are protected from herbivores. However, alluvial-soil specialists suffer greater herbivory and lower leaf area growth rates than white-sand specialists when grown in white sand. Other studies also found that fast-growing species in rich soil also grow fast in poor soil in environments protected from herbivores (Huante et al. 1995, Lusk et al. 1997, Schreeg et al. 2005). Species from infertile soil tend to have lower SLA and greater leaf life span than those from rich soils (Wright et al. 2002), reflecting characteristics of leaves better protected against herbivores (Wright and Cannon 2001). These results suggest that avoidance of tissue loss is an important selective pressure in resource-limited environments, in which replacement of lost tissue requires a long time (Coley et al. 1985).

Allocation to support mutualistic microbes may be equally costly but as important as allocation to defense against natural enemies. Mycorrhizal fungi are perhaps the most important group of mutualists, which not only help seedlings acquire limiting soil nutrients especially phosphorus (e.g., Allsopp and Stock 1995), but also help them defend against soil-borne pathogens (Hood et al. 2004). Since mycorrhizal fungi differ in their effectiveness, seedling performance may be significantly altered by availability of beneficial mycorrhizal fungi (Kiers et al. 2000, Bray et al. 2003). Likewise, fungi that live inside leaves (endophytes) include beneficial species that help seedlings defend against pathogenic fungi (Arnold et al. 2003). The potential benefits, as well as energy costs of supporting such microbes for seedlings (Lovelock et al. 1997), are yet to be quantified in most systems.

Maintenance of positive carbon balance is a prerequisite for long-term survival, as well as continuous growth of seedlings. However, this does not necessarily mean maximization of the rate of net carbon gain and growth. The net carbon gain rate of a seedling is a function of (a) total photosynthetic rate minus (b) total respiration rate minus (c) tissue loss rate to natural enemies, disturbance, and tissue senescence. Thus, the maintenance of positive carbon balance can be achieved by maximization of (a), minimization of (b), and minimization of (c). When multiple tree species are compared, seedlings of all species exhibit acclimation responses to shade by decreasing respiration rates at the whole-plant level, but differences in respiration rates alone do not often explain difference in shade survival among species (Kitajima 1994, Reich et al. 1998b, Kaelke et al. 2001). The negative correlation between growth rates and survival observed among species differing in seedling shade tolerance, instead, points to the importance of difference in allocation to defense and storage. Fast-growing species tend to have high SLA and LAR, which tend to make them more susceptible

to herbivory (Kitajima 1994, Cornelissen et al. 1996). Shorter leaf life span inherent to species with high SLA leads to a greater tissue loss rate in the long term, making it more difficult for them to maintain carbon balance as well (Sack and Grubb 2003). Cornelissen et al. (1996) also have shown that high tissue density is negatively correlated with RGR, and presumably positively correlated with high survival. The most direct demonstration of the importance of physical defense for seedling survival is provided by Alvarez-Clare (2005), who showed a positive correlation between tissue toughness and first-year survival among eight neotropical tree species.

Carbohydrate storage is also important for maintenance of positive carbon balance. No matter how well seedlings are defended, seedlings in canopy shade are likely to experience negative carbon balance from time to time because of variation in weather, physical disturbance, and attacks by natural enemies. For survival through such episodes of negative carbon balance, as well as to recover from it, seedlings must rely on stored carbohydrate reserves in the form of starch and sugar. In a comparison of seven neotropical tree species, Myers and Kitajima (2007) experimentally demonstrated that species that survive well in shade have greater total amount of sugar and starch in stems and roots, especially after receiving the additional stress of defoliation and heavy shading (0.08% of open sky condition). Interestingly, seedlings in stress treatments did not use carbohydrate reserves remaining in cotyledons, and cotyledon carbohydrate reserve size was uncorrelated with seedling survival. Carbohydrate reserves are also important for over-winter survival of temperate deciduous tree species (Canham et al. 1999), as well as survival of savanna tree species to fire (Hoffmann et al. 2004). Thus, carbohydrate storage is important for survival when seedlings experience negative carbon balance because of stress.

The small size of seedlings ultimately constrains strategies for the maintenance of positive carbon balance. In the studies cited in the previous paragraph, seedling survival was correlated with the total carbohydrate pool size (gram glucose equivalent), but not with tissue concentration (milligram glucose equivalent per gram dry mass) of starch and sugar. Since the total pool size is the product of concentration and biomass, there is an upper limit to the carbohydrate pool size for small seedlings. As a result, seedlings in resource-limited environments must avoid tissue loss, which would be difficult to replace (Coley et al. 1985). Thus, at the seedling stage, shade-tolerant species have leaves with low SLA and high tissue density, even though such leaves are not efficient in capture and conversion of light for photosynthetic production. However, larger plants can take a more opportunist strategy for survival in shade, by leaves with high SLA that allow high net carbon gain rates, even though faster leaf turnover poses frequent carbon demands. Thus, it is expected that a species with high SLA has a high light requirement for survival as seedlings, but once they achieve large size, they may be able to tolerate shading. For example, as seedlings, *Alseis blackiana* can grow and survive only in large gaps; however, as saplings, they can persist in shaded understories (Dalling et al. 2001). Growth, however, also brings about an increase in support biomass to leaf area, which causes a decrease in the ratio of photosynthesis to respiration at the whole plant level (Veneklaas and Poorter 1998, Delagrange et al. 2004). Thus, if they manage to survive and grow, seedlings have to deal with not only temporal changes in external environmental factors such as opening and closure of gaps, but also changes in physiological and morphological constraints associated with size.

When do plants graduate from the seedling stage? In other words, how long does the influence of seed and early seedling traits last? From a proximate perspective, seedling phase ends when the relative contribution of seed reserves becomes negligible relative to the cumulative autotrophic resource gain from their independent way of life. However, from the life-history perspective, seed and seedling traits are intimately associated with the overall life-history strategies and habitat preference of species. This point is well illustrated by the negative correlation of seed size with not only early seedling RGR, but also with sapling and

adult traits, such as RGR and maximum height. Some correlations exist because of concordance in traits at different stages; thus, a reasonable null expectation is that the relative position of species along the growth-survival trade-off line is positively correlated between seedling and sapling stages (Gilbert et al. 2005). Likewise, preferences for light environments appear to be largely concordant between small and large juvenile stages (Poorter et al. 2005), even though they are decoupled from preferred light environment as adults. Yet, ontogenetic changes may lead to diversity of overall regeneration strategies among species, significantly contributing to the maintenance of species diversity (Baralotos et al. 2005). Transition from seedlings to larger juveniles is an understudied topic particularly important for long-lived woody species.

## CONCLUSION

Regeneration from seeds is influenced by a wide range of environmental factors, plant characteristics, and stochastic events. The species composition of a plant community is a consequence of the successful regeneration of a selection of the potential species available. The long-term maintenance of each species requires the recurrent creation of suitable regeneration opportunities at appropriate intervals. At any one site, these opportunities are unlikely to remain constant with time, due to natural disturbance, human influences, and even climate change. Knowledge of regeneration requirements of key species is of great practical importance in vegetation management, either for commercial or conservation purpose. Comparative studies of the relationships between seed and seedling traits and regeneration requirements of the species are particularly useful in this context. Seed and seedling traits are the products of natural selection operating through life history trade-offs. How selective pressures on seed and seedling traits vary in contrasting environments provides insight into niche specialization, density-dependency, and colonization limitation, which are considered critical for community assembly processes at local and regional scales.

## ACKNOWLEDGMENTS

I warmly acknowledge the contribution by Michael Fenner, who was the lead author for this chapter in its earlier edition. His perspective on seed and seedling ecology had a profound influence on my research interests over the years. This revision was prepared during sabbatical in Panama under sponsorship of the Smithsonian Tropical Research Institute and financial support from NSF Grant 0093303 to KK. I would like to thank Helene Muller-Landau, Kelly Anderson, Joseph Phillips, Jim Dalling, and Amy Zanne for their constructive comments.

## REFERENCES

- Adler, F.R. and H.C. Muller-Landau, 2005. When do localized natural enemies increase species richness? *Ecology Letters* 8: 438–447.
- Aguilera, M.O. and W.K. Lauenroth, 1993. Seedling establishment in adult neighbourhoods intra-specific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. *Journal of Ecology* 81: 253–261.
- Agyeman, V.K., M.D. Swaine, and J. Thompson, 1999. Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology* 87: 815–827.
- Alcantara, J.M. and P.J. Rey, 2003. Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. *Journal of Evolutionary Biology* 16: 1168–1176.

- Alvarez-Clare, S., 2005. Biomechanical properties of tropical tree seedlings as a functional correlate of shade tolerance. MS thesis, University of Florida, Gainesville, USA.
- Allen, R.B. and K.H. Platt, 1990. Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, New Zealand. *Oikos* 57: 199–206.
- Allsopp, N. and W.D. Stock, 1995. Relationships between seed reserves, seedling growth and mycorrhizal responses in 14 related shrubs (Rosidae) from a low-nutrient environment. *Functional Ecology* 9: 248–254.
- Arnold, A.E., L.C. Mejia, D. Kylo, E.I. Rojas, Z. Maynard, N. Robbins, and E.A. Herre, 2003. Fungal endophytes limit pathogen damage in a tropical tree. *Proceedings of the National Academy of Sciences of the United States of America* 100: 15649–15654.
- Askew, A.P., D. Corner, D.J. Hodkinson, and K. Thompson, 1997. A new apparatus to measure the rate of fall of seeds. *Functional Ecology* 11: 121–125.
- Asquith, N.M., S.J. Wright, and M.J. Clauss, 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology* 78: 941–946.
- Augsburger, C.K., 1983a. Offspring-recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40: 189–196.
- Augsburger, C.K., 1983b. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71: 759–771.
- Augsburger, C.A., 1984a. Seedling survival of tropical tree species; interactions of dispersal distance, light gaps, and pathogens. *Ecology* 65: 1705–1712.
- Augsburger, C.K., 1984b. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72: 777–795.
- Augsburger, C.K., 1986. Morphological and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany* 73: 353–363.
- Augsburger, C.K. and S.E. Franson, 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a neotropical forest. *Journal of Tropical Ecology* 4: 239–252.
- Augsburger, C.K. and K. Kitajima, 1992. Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73: 1270–1284.
- Auld, T.D., 1986. Variation in predispersal seed predation in several Australian *Acacia* spp. *Oikos* 47: 319–326.
- Baker, H.G., 1972. Seed weight in relation to environmental condition in California. *Ecology* 53: 997–1010.
- Ballardie, R.T. and R.J. Whelan, 1986. Masting, seed dispersal and seed predation in the cycad *Macrozamia communis*. *Oecologia* 70: 100–105.
- Ballaré, C.L., R.A. Sánchez, A.L. Scopel, and C.M. Chersa, 1988. Morphological responses of *Datura ferox* L. seedlings to the presence of neighbours. *Oecologia* 76: 288–293.
- Baralotos, C., D.E. Goldberg, and D. Bonal, 2005. Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology* 86: 2461–2472.
- Barclay, A.S. and F.R. Earl, 1974. Chemical analyses of seeds. III. Oil and protein content of 1253 species. *Economic Botany* 28: 178–236.
- Barker, G.M., 1989. Slug problems in New Zealand pastoral agriculture. In: I.F. Henderson, ed. *Slugs and Snails in World Agriculture*. British Crop Protection Council, BCPC Monograph, Thornton Heath, UK, pp. 59–68.
- Baskin, J.M. and C.C. Baskin, 1980. Ecophysiology of secondary dormancy in seeds of *Ambrosia artemisiifolia*. *Ecology* 61: 475–480.
- Baskin, J.M. and C.C. Baskin, 1985. The annual dormancy cycle in buried weed seeds: a continuum. *BioScience* 35: 492–498.
- Baskin, C.C. and J.M. Baskin, 1998. *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.
- Beattie, A.J. and D.C. Culver, 1982. Inhumation: How ants and other invertebrates help seeds. *Nature* 297: 627.
- Bekker, R.M., J.P. Bakker, U. Grandin, R. Kalamees, P. Milberg, P. Poschlod, K. Thompson, and J.H. Willems, 1998. Seed size, shape and vertical distribution in the soil: Indicators of seed longevity. *Functional Ecology* 12: 834–842.

- Bell, T., R.P. Freckleton, and O.T. Lewis, 2006. Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters* 9: 569–574.
- Benkman, C.W., 1995. The impact of tree squirrels (*Tamiasciurus*) on limber pine seed dispersal adaptations. *Evolution* 49: 585–592.
- Bennet, A. and J. Krebs, 1987. Seed dispersal by ants. *Trends in Ecology & Evolution* 2: 291–292.
- Bloor, J.M.G. and P.J. Grubb, 2003. Growth and mortality in high and low light: Trends among 15 shade-tolerant tropical rain forest tree species. *Journal of Ecology* 91: 77–85.
- Bond, W. and P. Slingby, 1984. Collapse of an ant-plant mutualism: The Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology* 65: 1031–1037
- Bouwmeester, H.J., 1990. The Effect of Environmental Conditions on the Seasonal Dormancy Pattern and Germination of Weed Seeds, PhD thesis, Agricultural University of Wageningen, The Netherlands.
- Bray, S.R., K. Kitajima, and D.M. Sylvia, 2003. Mycorrhizae differentially alter growth, physiology, and competitive ability of an invasive shrub. *Ecological Applications* 13: 565–574.
- Brokaw, N.V.L., 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology* 75: 9–19.
- Brokaw, N. and R.T. Busing, 2000. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology & Evolution* 15: 183–188.
- Brown, N., 1993. The implications of climate and gap microclimate for seedling growth conditions in a Gornean lowland rain forest. *Journal of Tropical Ecology* 9: 153–168.
- Brown, N.A.C., J. van Staden, M.I. Daws, and T. Johnson, 2003. Patterns in the seed germination response to smoke in plants from the Cape Floristic Region, South Africa. *South African Journal of Botany* 69: 514–525.
- Brown, J.S. and D.L. Venable, 1986. Evolutionary ecology of seed bank annuals in temporally varying environments. *American Naturalist* 127: 31–47.
- Brown, N.D. and T.C. Whitmore, 1992. Do dipterocarp seedlings really partition tropical rainforest gaps? *Philosophical Transactions of the Royal Society of London Series B* 335: 369–378.
- Bullock, J.M., B.C. Hill, J. Silvertown, and M. Sutton, 1995. Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos* 72: 273–282.
- Burke, M.J.W. and J.P. Grime, 1996. An experimental study of plant community invasibility. *Ecology* 77: 776–790.
- Cain, M.L., B.G. Milligan, and A.E. Strand, 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87: 1217–1227.
- Cain, M.L., R. Nathan, and S.A. Levin, 2003. Long-distance dispersal. *Ecology* 84: 1943–1944.
- Canham, C.D., R.K. Kobe, E.F. Latty, and R.L. Chazdon, 1999. Interspecific and intraspecific variation in tree seedling survival: Effects of allocation to roots versus carbohydrate reserves. *Oecologia* 121: 1–11.
- Carlquist, S., 1965. *Island Life*. New York, Natural History Press.
- Chacon, P. and J.J. Armesto, 2006. Do carbon-based defences reduce foliar damage? Habitat-related effects on tree seedling performance in a temperate rainforest of Chiloe Island, Chile. *Oecologia* 146: 555–565.
- Chambers, J.C., 1995. Relationships between seed fates and seedling establishment in an alpine ecosystem. *Ecology* 76: 2124–2133.
- Chapman, C.A., L.J. Chapman, K. Vulinec, A. Zanne, and M.J. Lawes, 2003. Fragmentation and alteration of seed dispersal processes: An initial evaluation of dung beetles, seed fate, and seedling diversity. *Biotropica* 35: 382–393.
- Chesson, P.L., 1985. Coexistence of competitors in spatially and temporally varying environments: A look at the combined effects of different sorts of variability. *Theoretical Population Biology* 28: 263–287.
- Clark, D.B. and D.A. Clark, 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos* 55: 225–230.
- Clark, J.S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers, 1999. Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* 80: 1475–1494.

- Cody, M.L. and J.M. Overton, 1996. Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* 84: 53–61.
- Coley, P.D., J.P. Bryant, and F.S. Chapin III, 1985. Resource availability and plant anti-herbivore defense. *Science* 230: 895–899.
- Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: P.J.D. Boer and G.R. Gradwell, eds. *Dynamics of Populations*. Pudoc, Wageningen, pp. 290–310.
- Cornelissen, J.H.C., 1999. A triangular relationship between leaf size and seed size among woody species: allometry, ontogeny, ecology and taxonomy. *Oecologia* 118: 248–255.
- Cornelissen, J.H.C., P.C. Diez, and R. Hunt, 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology* 84: 755–765.
- Corré, W.J., 1983. Growth and morphogenesis of sun and shade plants. II. The influence of light quality. *Acta Botanica Neerlandica* 32: 185–202.
- Crawley, M.J., 2000. Seed predators and plant population dynamics. In: M. Fenner, ed. *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd edition. CAB International, Wallingford, pp. 167–182.
- Crawley, M.J. and C.R. Long, 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur*. *Journal of Ecology* 83: 683–696.
- Crist, T.O. and Friese, C.F., 1993. The impact of fungi on soil seeds: implications for plants and granivores in a semiarid shrub-steppe. *Ecology* 74: 2231–2239.
- Curran, L.M. and M. Leighton, 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting dipterocarpaceae. *Ecological Monographs* 70: 101–128.
- Curran, L.M. and C.O. Webb, 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs* 70: 129–148.
- Dalling, J.W. and J.S. Denslow, 1998. Changes in soil seed bank composition along a chronosequence of lowland secondary tropical forest, Panama. *Journal of Vegetation Science* 9: 669–678.
- Dalling, J.W., K.E. Harms, and R. Aizprua, 1997a. Seed damage tolerance and seedling resprouting ability of *Prioria copaifera* in Panama. *Journal of Tropical Ecology* 13: 481–490.
- Dalling, J.W., M.D. Swaine, and N.C. Garwood, 1997b. Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *Journal of Tropical Ecology* 13: 659–680.
- Dalling, J.W., M.D. Swaine, and N.C. Garwood, 1998. Dispersal patterns and seed bank dynamics of two pioneer tree species in moist tropical forest, Panama. *Ecology* 79: 564–578.
- Dalling, J.W., K. Winter, J.D. Nason, S.P. Hubbell, D.A. Murawski, and J.L. Hamrick, 2001. The unusual life history of *Alseis blackiana*: A shade-persistent pioneer tree? *Ecology* 82: 933–945.
- Dalling, J.W., C.E. Lovelock, and S.P. Hubbell, 1999. Growth responses of seedlings of two neotropical pioneer species to simulated forest gap environments. *Journal of Tropical Ecology* 15: 827–839.
- Dalling, J.W., H.C. Muller-Landau, S.J. Wright, and S.P. Hubbell, 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology* 90: 714–727.
- Dalling, J.W., K. Winter, and S.P. Hubbell, 2004. Variation in growth responses of neotropical pioneers to simulated forest gaps. *Functional Ecology* 18: 725–736.
- Darwin, C., 1859. *The Origin of Species*. Murray, London.
- Daws, M.I., D. Burslem, L.M. Crabtree, P. Kirkman, C.E. Mullins, and J.W. Dalling, 2002a. Differences in seed germination responses may promote coexistence of four sympatric *Piper* species. *Functional Ecology* 16: 258–267.
- Daws, M.I., C.E. Mullins, D. Burslem, S.R. Paton, and J.W. Dalling, 2002b. Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil* 238: 79–90.
- Daws, M.I., N.C. Garwood, and H.W. Pritchard, 2005. Traits of recalcitrant seeds in a semi-deciduous tropical forest in Panama: some ecological implications. *Functional Ecology* 19: 874–885.
- Daws, M.I., D. Orr, D. Burslem, and C.E. Mullins, 2006. Effect of high temperature on chalazal plug removal and germination in *Apeiba tibourbou* Aubl. *Seed Science and Technology* 34: 221–225.
- Delagrangé, S., C. Messier, M.J. Lechowicz, and P. Dizengremel, 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: Importance of plant size and light availability. *Tree Physiology* 24: 775–784.

- Dessaint, F., R. Chadoeuf, and G. Barralis, 1991. Spatial pattern analysis of weed seeds in the cultivated soil seed bank. *Journal of Applied Ecology* 28: 721–730.
- Dudley, S.A. and J. Schmitt, 1995. Genetic differentiation in morphological responses to simulated foliage shade between populations of *Impatiens capensis* from open and woodland sites. *Functional Ecology* 9: 655–666.
- Edwards, G.R. and M.J. Crawley, 1999. Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia* 118: 288–296.
- Ellison, A.M., J.S. Denslow, B.A. Loiselle, and M.D. Brenes, 1993. Seed and seedling ecology of neotropical. Melastomataceae. *Ecology* 74: 1733–1749.
- Engelbrecht, B.M.J., J.W. Dalling, T.R.H. Pearson, R.L. Wolf, D.A. Galvez, T. Koehler, M.T. Tyree, and T.A. Kursar, 2006. Short dry spells in the wet season increase mortality of tropical pioneer seedlings. *Oecologia*, 148: 258–269.
- Eriksson, O., E.M. Friis, and P. Lofgren, 2000. Seed size, fruit size, and dispersal systems in angiosperms from the early cretaceous to the late tertiary. *American Naturalist* 156: 47–58.
- Ezoe, H., 1998. Optimal dispersal range and seed size in a stable environment. *Journal of Theoretical Biology* 190: 287–293.
- Fenner, M., 1978. Susceptibility to shade in seedlings of colonizing and closed turf species. *New Phytologist* 81: 739–744.
- Fenner, M., 1980. Germination tests on thirty-two East African weed species. *Weed Research* 20: 135–138.
- Fenner, M., 1983. Relationships between seed weight, ash content and seedling growth in twenty-four species of compositae. *New Phytologist* 95: 697–706.
- Fenner, M., 1991. Irregular seed crops in forest trees. *Quaternary Journal of Forestry* 85: 166–172.
- Fenner, M., 2000. *Seeds: The ecology of regeneration in plant communities*, 2nd edition. CABI, Wallingford.
- Fenner, M. and W.G. Lee, 1989. Growth of seedlings of pasture grasses and legumes deprived of single mineral nutrients. *Journal of Applied Ecology* 26: 223–232.
- Fenner, M. and K. Thompson, 2005. *Ecology of Seeds*. Cambridge University Press, Cambridge.
- Fenner, M., M.E. Hanley, and R. Lawrence, 1999. Comparison of seedling and adult palatability in annual and perennial plants. *Functional Ecology* 13: 546–551.
- Fine, P.V.A., I. Mesones, and P.D. Coley, 2004. Herbivores promote habitat specialization by trees in Amazonian forests. *Science* 305: 663–665.
- Forget, P.-M., 1990. Seed-dispersal of *Vacapoua americana* (Caesalpinaceae) by caviomorph rodents. *Journal of Tropical Ecology* 6: 459–468.
- Forget, P.M., 1997. Ten-year seedling dynamics in *Vouacapoua americana* in French Guiana: A hypothesis. *Biotropica* 29: 124–126.
- Forget, P.M. and T. Milleron, 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87: 596–599.
- Forget, P.-M., K. Kitajima and R.B. Foster, 1999. Pre- and post-dispersal seed predation in a tropical tree, *Tachigalia versicolor* (Caesalpinaceae): effects of fruiting timing and among-tree variation. *Journal of Tropical Ecology* 15: 61–81.
- Fragoso, J.M.V., K.M. Silvius, and J.A. Correa, 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology* 84: 1998–2006.
- Fredericksen, T.S. and B. Mostacedo, 2000. Regeneration of timber species following selection logging in a Bolivian tropical dry forest. *Forest Ecology and Management* 131: 47–55.
- Ganeshiah, K.N. and S.R. Uma, 1991. Seed size optimization in a wind dispersed tree *Butea monosperma* a trade-off between seedling establishment and pod dispersal efficiency. *Oikos* 60: 3–6.
- Garwood, N.C., 1983. Seed germination in a seasonal tropical forest Panama: A community study. *Ecological Monographs* 53: 159–181.
- Garwood, N.C., 1996. Functional morphology of tropical tree seedlings. In: M.D. Swaine, ed. *The Ecology of Tropical Forest Tree Seedlings*. UNESCO, Paris, pp. 59–129
- Garwood, N.C. and J.R.B. Lighton, 1990. Physiological ecology of seed respiration in some tropical species. *New Phytologist* 115: 549–558.
- Geritz, S.A., 1995. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. *American Naturalist* 146: 685–707.

- Gilbert, B., S.J. Wright, H. Muller-Landau, K. Kitajima, and A. Hernandez, 2005. Life history trade-offs in tropical trees and lianas. *Ecology* 87: 1271–1288.
- Gillman, L.N., J. Ogden, S.D. Wright, K.L. Stewart, and D.P. Walsh, 2004. The influence of macro-litterfall and forest structure on litterfall damage to seedlings. *Austral Ecology* 29: 305–312.
- Godnan, D., 1983. *Pest Slugs and Snails*. Springer-Verlag, Berlin.
- Gonzalez, E., 1993. Effect of seed size on germination and seedling vigor of *Virola koschny* Warb. *Forest Ecology Management* 57: 275–281.
- Gorski, T., K. Gorska, and J. Nowicki, 1977. Germination of seeds of various species under leaf canopy. *Flora* 166: 249–259.
- Goulding, M., 1980. *The Fishes and the Forest*. University of California Press, Berkeley, CA.
- Gray, A.N. and T.A. Spies, 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *Journal of Ecology* 84: 635–645.
- Green, P.T. and P.A. Juniper, 2004. Seed-seedling allometry in tropical rain forest trees: Seed mass-related patterns of resource allocation and the ‘reserve effect’. *Journal of Ecology* 92: 397–408.
- Greene, D.F., C.D. Canham, K.D. Coates, and P.T. Lepage, 2004. An evaluation of alternative dispersal functions for trees. *Journal of Ecology* 92: 758–766.
- Greig, N., 1993. Predispersal seed predation on five *Piper* species in tropical rainforest. *Oecologia* 93: 412–420.
- Grime, J.P. and D.W. Jeffrey, 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology* 53: 621–642.
- Gross, K., 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology*: 369–387.
- Gross, C.L., M.A. Whalen, and M.H. Andrew, 1991. Seed selection and removal by ants in a tropical savanna woodland in northern Australia. *Journal of Tropical Ecology* 7: 99–112.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107–145.
- Grubb, P.J., D.J. Metcalfe, and D. Coomes, 2005. Comment on “A brief history of seed size.” *Science* 310: 783A.
- Hammond, D.S. and V.K. Brown, 1998. Disturbance, phenology and life-history characteristics: Factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: D.M. Newberry, H.H.T. Prins, and N.D. Brown, eds. *Dynamics of Tropical Communities*. Blackwell Scientific, Oxford, pp. 51–78.
- Hanley, M.E. and M. Fenner, 1997. Seedling growth of four fire-following Mediterranean plant species deprived of single mineral nutrients. *Functional Ecology* 11: 398–405.
- Hanley, M.E. and M. Fenner, 1998. Pre-germination temperature and the survivorship and onward growth of Mediterranean fire-following plant species. *Acta Oecologica* 19: 181–187.
- Hanley, M.E., M. Fenner, and P.J. Edwards, 1995. The effect of seedling age on the likelihood of herbivory by the slug *Deroceras reticulatum*. *Functional Ecology* 9: 754–759.
- Hanley, M.E., M. Fenner, and P.J. Edwards, 1996. Mollusc grazing and seedling survivorship of four common grassland plant species: the role of gap size, species and season. *Acta Oecologica* 17: 331–341.
- Hardesty, B.D., C.W. Dick, A. Kremer, S. Hubbell, and E. Bermingham, 2005. Spatial genetic structure of *Simarouba amara* Aubl. (Simaroubaceae), a dioecious, animal-dispersed Neotropical tree, on Barro Colorado Island, Panama. *Heredity* 95: 290–297.
- Harms, K.E., S.J. Wright, O. Calderon, A. Hernandez, and E.A. Herre, 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404: 493–495.
- Harper, J.L., 1977. *Population Biology of Plants*. Academic Press, London.
- Hewitt, N., 1998. Seed size and shade-tolerance—a comparative analysis of north American temperate trees. *Oecologia* 114: 432–440.
- Hilhorst, H.W.M. and Karssen, C.M., 2000. Effect of chemical environment on seed germination. In: M. Fenner, ed. *Seeds. The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, UK, pp. 293–310.
- Hladik, A. and S. Miquel, 1990. Seedling types and plant establishment in an African rain forest. In: K.S. Bawa and M. Hadley, eds. *Reproductive Ecology of Tropical Forest Plants*, Parthenon, Carnforth, UK, pp. 261–282.



- Hnatiuk, S.H., 1978. Plant dispersal by the Aldabran giant tortoise *Geochelone gigantea* (Scheigger). *Oecologia* 36: 345–350.
- Hodkinson, D.J., A.P. Askew, K. Thompson, J.G. Hodgson, J.P. Bakker, and R.M. Bekker, 1998. Ecological correlates of seed size in the British flora. *Functional Ecology* 12: 762–766.
- Hoffmann, W.A., B. Orthen, and A.C. Franco, 2004. Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. *Oecologia* 140: 252–260.
- Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain, seed germination, microclimate, and soil. *Biotropica* 31: 229–242.
- Hood, L.A., M.D. Swaine, and P.A. Mason, 2004. The influence of spatial patterns of damping-off disease and arbuscular mycorrhizal colonization on tree seedling establishment in Ghanaian tropical forest soil. *Journal of Ecology* 92: 816–823.
- Hopkins, M.S. and A.W. Graham, 1987. The viability of seeds of rainforest species after experimental soil burials under wet lowland forest in northeastern Australia. *Australian Journal of Ecology* 12: 97–108.
- Horn, M.H., 1997. Evidence for dispersal of fig seeds by the fruit-eating characid fish *Brycon guatemalensis regan* in a Costa Rican tropical rain forest. *Oecologia* 109: 259–264.
- Horvitz, C.C. and D.W. Schemske, 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. *Ecology* 75: 1949–1958.
- Howe, H.F., 1989. Scatter and clump-dispersal and seedling demography: Hypothesis and implications. *Oecologia* 79: 417–426.
- Huante, P., E. Rincon, and M. Gavito, 1992. Root system analysis of seedlings of seven tree species from a tropical dry forest in Mexico. *Trees: Structure and Function* 6: 77–82.
- Huante, P., E. Rincón, and I. Acosta, 1995. Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico. *Functional Ecology* 9: 849–858.
- Hubbell, S.P., R.B. Foster, S.T. O'Brien, K.E. Harms, R. Condit, B. Wechsler, S.J. Wright, and S.L. de Lao, 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554–557.
- Hughes, L. and M. Westoby, 1992. Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. *Ecology* 73: 1285–1299.
- Hulme, P.E., 1994. Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. *Journal of Ecology* 82: 873–880.
- Hyatt, L.A., M.S. Rosenberg, T.G. Howard, G. Bole, W. Fang, J. Anastasia, K. Brown, R. Grella, K. Hinman, J.P. Kurdziel, and J. Gurevitch, 2003. The distance dependence prediction of the Janzen-Connell hypothesis: A meta-analysis. *Oikos* 103: 590–602.
- Ibarra-Manriquez, G., M.M. Ramos, and K. Oyama, 2001. Seedling functional types in a lowland rain forest in Mexico. *American Journal of Botany* 88: 1801–1812.
- Jansen, P.A., F. Bongers, and L. Hemerik, 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs* 74: 569–589.
- Janzen, D.H., 1969. Seed-eaters vs seed size, number, toxicity and dispersal. *Evolution* 23: 1–27.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104: 501–528.
- Janzen, D.H., 1974. Tropical Blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica*, 6: 69–103.
- Janzen, D.H., 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *American Naturalist* 123: 338–353.
- Jensen, T.S., 1985. Seed-seed predator interactions of European beech, *Fagus sylvatica*, and forest rodent, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos* 44: 149–156.
- Joel, D.M., J.C. Steffens, and D.E. Matthews, 1995. Germination of weedy root parasites. In: J. Kigel and G. Galili, eds. *Seed Development and Germination*. Marcel Dekker, New York, pp. 567–597.
- Johnson, W.C. and C.S. Adkisson, 1985. Dispersal of beech nuts by blue jays in fragmented landscapes. *American Midland Naturalists* 113: 319–324.
- Jones, F.A., J. Chen, G.J. Weng, and S.P. Hubbell, 2005. A genetic evaluation of seed dispersal in the neotropical tree *Jacaranda copaia* (Bignoniaceae). *American Naturalist* 166: 543–555.
- Jurado, E. and M. Westoby, 1992. Seedling growth in relation to seed size among species of arid Australia. *Journal of Ecology* 80: 407–416.

- Kaelke, C.M., E.L. Kruger, and P.B. Reich, 2001. Trade-offs in seedling survival, growth, and physiology among hardwood species of contrasting successional status along a light-availability gradient. *Canadian Journal of Forest Research* 31: 1602–1616.
- Keeley, J.E., 1991. Seed germination and life history syndromes in the California Chaparral. *Botanical Review* 57: 81–116.
- Keeley, J.E. and C.J. Fotheringham, 1998. Mechanism of smoke-induced seed germination in a post-fire chaparral annual. *Journal of Ecology* 86: 27–36.
- Kelly, D. and V.L. Sork, 2002. Mast seeding in perennial plants: Why, how, where? *Annual Review of Ecology and Systematics* 33: 427–447.
- Kennedy, P.G., N.J. Hausmann, E.H. Wenk, and T.E. Dawson, 2004. The importance of seed reserves for seedling performance: An integrated approach using morphological, physiological, and stable isotope techniques. *Oecologia* 141: 547–554.
- Kiers, E.T., C.E. Lovelock, E.L. Krueger, and E.A. Herre, 2000. Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: implications for tropical forest diversity. *Ecology Letters* 3: 106–113.
- Kikuzawa, K. and H. Koyama, 1999. Scaling of soil water absorption by seeds: An experiment using seed analogues. *Seed Science Research* 9: 171–178.
- Kitajima, K., 1992a. The Importance of Cotyledon Functional Morphology and Patterns of Seed Reserve Utilization for the Physiological Ecology of Neotropical Tree Seedlings. Ph.D. thesis, University of Illinois, Urbana, Illinois.
- Kitajima, K., 1992b. Relationship between photosynthesis and thickness of cotyledons for tropical tree species. *Functional Ecology* 6: 582–589.
- Kitajima, K., 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98: 419–428.
- Kitajima, K., 1996. Cotyledon functional morphology, seed reserve utilization, and regeneration niches of tropical tree seedlings. In: M.D. Swaine, ed. *The Ecology of Tropical Forest Tree Seedlings*. UNESCO, Paris, pp. 193–208.
- Kitajima, K., 2002. Do shade-tolerant tropical tree seedlings depend longer on seed reserves? *Functional Ecology* 16: 433–444.
- Kitajima, K. and C.K. Augspurger, 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. *Ecology* 70: 1102–1114.
- Kitajima, K. and D. Tilman, 1996. Seed banks and seedling establishment on an experimental productivity gradient. *Oikos*, 76:381–391.
- Kivilaan, A. and R.S. Bandurski, 1981. The one hundred-year period for Dr. Beal's seed viability experiment. *American Journal of Botany* 68: 1290–1292.
- Kobe, R.K., 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80: 187–201.
- Kobe, R.K., S.W. Pacala, J.A.J. Silander, and C.D. Canham, 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* 5: 517–532.
- Kohyama, T. and P.J. Grubb, 1994. Below- and above-ground allometries of shade-tolerant seedlings in a Japanese warm-temperate rain forest. *Functional Ecology* 8: 229–236.
- Kolb, P.F. and R. Robberecht, 1996. *Pinus ponderosa* seedling establishment and the influence of competition with the bunchgrass *Agropyron spicatum*. *International Journal of Plant Science* 157: 509–515.
- Kubitzki, K. and A. Ziburski, 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica*, 26: 30–43.
- Kwit, C., D.J. Levey, and C.H. Greenberg, 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. *Oikos* 107: 303–308.
- Leck, M.A., V.T. Parker, and R.L. Simpson, 1989. *Ecology of soil seed banks*. Academic Press, San Diego, CA.
- Lee, W.G., M. Fenner, and R.P. Duncan, 1993. Pattern of natural regeneration of narrow leaved snow tussock *Chionochloa rigida* ssp. *rigida* in Central Otago, New Zealand. *New Zealand Journal of Botany* 31: 117–125.
- Leishman, M.R., 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93: 294–302.

- Leishman, M.R. and M. Westoby, 1994a. The role of large seed size in shaded conditions: Experimental evidence. *Functional Ecology* 8: 205–214.
- Leishman, M.R. and M. Westoby, 1994b. The role of seed size in seedling establishment in dry soil conditions: experimental evidence from semi-arid species. *Journal of Ecology* 82: 249–258.
- Leishman, M.R. and M. Westoby, 1998. Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Functional Ecology* 12: 480–485.
- Leishman, M.R., M. Westoby, and E. Jurado, 1995. Correlates of seed size variation—a comparison among 5 temperate floras. *Journal of Ecology* 83: 517–529.
- Levey, D.J. and M.M. Byrne, 1993. Complex ant plant interactions—rain-forest ants as secondary dispersers and postdispersal seed predators. *Ecology* 74: 1802–1812.
- Levin, S.A., H.C. Muller-Landau, R. Nathan, and J. Chave, 2003. The ecology and evolution of seed dispersal: A theoretical perspective. *Annual Review of Ecology Evolution and Systematics* 34: 575–604.
- Ligon, D.J., 1978. Reproductive interdependence of pinyon jays and pinyon pines. *Ecological Monographs* 48: 111–126.
- Lopez, O.R., 2001. Seed flotation and postflooding germination in tropical terra firme and seasonally flooded forest species. *Functional Ecology* 15: 763–771.
- Lott, R.H., G.N. Harrington, A.K. Irvine, and S. McIntyre, 1995. Density-dependent seed predation and plant dispersion of the tropical palm *Normanbya normanbyi*. *Biotropica* 27: 87–95.
- Louda, S.M., 1982. Limitations of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. *Journal of Ecology* 70: 43–53.
- Louda, S.M. and M.A. Potvin, 1995. Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* 76: 229–245.
- Lovelock, C.E., D. Kyllö, M. Popp, H. Isopp, A. Virgo, and K. Winter, 1997. Symbiotic vesicular-arbuscular mycorrhizae influence maximum rates of photosynthesis in tropical tree seedlings grown under elevated CO<sub>2</sub>. *Australian Journal of Plant Physiology* 24: 185–194.
- Lusk, C.H., O. Contreras, and J. Figueroa, 1997. Growth, biomass allocation and plant nitrogen concentration in Chilean temperate rainforest tree seedlings: effects of nutrient availability. *Oecologia* 109: 49–58.
- Lusk, C.H. and C.K. Kelly, 2003. Interspecific variation in seed size and safe sites in a temperate rain forest. *New Phytologist* 158: 535–541.
- Mack, R.N. and D.A. Pyke, 1984. The demography of *Bromus tectorum*: The role of microclimate, grazing and disease. *Journal of Ecology* 72: 731–748.
- Makana, J.R. and S.C. Thomas, 2004. Dispersal limits natural recruitment of African mahoganies. *Oikos* 106: 67–72.
- Makana, J.R. and S.C. Thomas, 2005. Effects of light gaps and litter removal on the seedling performance of six African timber species. *Biotropica* 37: 227–237.
- Maranon, T. and P.J. Grubb, 1993. Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. *Functional Ecology* 7: 591–599.
- Maron, J.L. and S.N. Gardner, 2000. Consumer pressure, seed versus safe-site limitation, and plant population dynamics. *Oecologia* 124: 260–269.
- Maruta, E., 1976. Seedling establishment of *Polygonum cuspidatum* on Mt. Fuji. *Japanese Journal of Ecology* 26: 101–105.
- Mazer, S.J., 1989. Ecological, taxonomic, and life history correlates of seed mass among Indiana dune angiosperms. *Ecological Monographs* 59: 153–175.
- McConnaughay, K.D.M. and F.A. Bazzaz, 1987. The relationships between gap size and performance of several colonizing annuals. *Ecology* 68: 411–416.
- McEuen, A.B. and L.M. Curran, 2004. Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. *Ecology* 85: 507–518.
- McRill, M. and G.R. Sagar, 1973. Earthworms and seeds. *Nature* 243: 482.
- Metcalfe, D.J. and P.J. Grubb, 1995. Seed mass and light requirements for regeneration of Southeast Asian rain forest. *Canadian Journal of Botany* 73: 817–826.
- Milberg, P., M.A. Perez-Fernandez, and B.B. Lamont, 1998. Seedling growth response to added nutrients depends on seed size in three woody genera. *Journal of Ecology* 86: 624–632.

- Miles, J., 1972. Early mortality and survival of self-sown seedlings in Glenfeshie, Inverness-shire. *Journal of Ecology* 61: 93–98.
- Moegenburg, S.M., 1996. Sabal palmetto seed size: Causes of variation, choices of predators, and consequences for seedlings. *Oecologia* 106: 539–543.
- Moles, A.T. and M. Westoby, 2003. Latitude, seed predation and seed mass. *Journal of Biogeography* 30: 105–128.
- Moles, A.T. and M. Westoby, 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92: 372–383.
- Moles, A.T. and M. Westoby, 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113: 91–105.
- Moles, A.T., D.D. Ackerly, C.O. Webb, J.C. Tweddle, J.B. Dickie, and M. Westoby, 2005. A brief history of seed size. *Science* 307: 576–580.
- Molofsky, J. and C.K. Augspurger, 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73: 68–77.
- Molofsky, J. and B.L. Fisher, 1993. Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. *Ecology* 74: 261–264.
- Morgan, D.C. and H. Smith, 1979. A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145: 253–258.
- Muller-Landau, H.C. and B.D. Hardesty, 2005. Seed dispersal of woody plants in tropical forests: concepts, examples, and future directions. In: D. Burslem, M. Pinar, and S. Hartley, eds. *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity*. Cambridge University Press, Cambridge, pp. 267–309.
- Myers, J. and K. Kitajima, 2007. Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. *Journal of Ecology* 95: 383–395.
- Nathan, R. and R. Casagrandi, 2004. A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen–Connell and beyond. *Journal of Ecology* 92: 733–746.
- Nathan, R. and H.C. Muller-Landau, 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15: 278–285.
- Ng, F.S.P., 1978. Strategies of establishment in Malayan forest trees. In: T.B. Tomlinson and H.M. Zimmerman, eds. *Tropical Trees as Living Systems*. Cambridge University Press, Oxford, pp. 129–162.
- Norton, D.A. and D. Kelly, 1988. Mast seedling over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology* 2: 399–408.
- O’Dowd, D.J. and P.S. Lake, 1991. Red crabs in rain forest, Christmas Island: Removal and fate of fruits and seeds. *Journal of Tropical Ecology* 7: 113–122.
- Okubo, A. and S.A. Levin, 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70: 329–338.
- Oladokun, M.A.O., 1989. Nut weight and nutrient contents of *Cola acuminata* and *C. nitida* (Sterculiaceae). *Economic Botany* 43: 17–22.
- Osunkoya, O.O., J.E. Ash, M.S. Hopkins, and A.W. Graham, 1994. Influence of seed size and seedling ecological attributes on shade-tolerance of rain forest tree species in Northern Queensland. *Journal of Ecology* 82: 149–163.
- Packer, A. and K. Clay, 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404: 278–281.
- Pammenter, N.W. and P. Berjak, 2000. Some thoughts on the evolution and ecology of recalcitrant seeds. *Plant Species Biology* 15: 153–156.
- Pate, J.S., E. Rasins, J. Rullo, and J. Kuo, 1985. Seed nutrient reserves of Proteaceae with special reference to protein bodies and their inclusions. *Annals of Botany* 57: 747–770.
- Paz, H. and M. Martinez-Ramos, 2003. Seed mass and seedling performance within eight species of *Psychotria* (Rubiaceae). *Ecology* 84: 439–450.
- Pearson, T.R.H., D. Burslem, C.E. Mullins, and J.W. Dalling, 2002. Germination ecology of neotropical pioneers: Interacting effects of environmental conditions and seed size. *Ecology* 83: 2798–2807.

- Pearson, T.R.H., D. Burslem, R.E. Goeriz, and J.W. Dalling, 2003. Interactions of gap size and herbivory on establishment, growth and survival of three species of neotropical pioneer trees. *Journal of Ecology* 91: 785–796.
- Penning de Vries, F.W.T. and H.H. Van Laar, 1977. Substrate utilization in germinating seeds. In: J.J. Landsberg and C.V. Cutting, eds. *Environmental Effects on Crop Physiology*. Academic Press, London, pp. 217–228.
- Pearce, T.G., N. Roggero, and R. Tipping, 1994. Earthworms and seeds. *Journal of Biological Education* 28: 195–202.
- Pons, T.L., 1989. Breaking of seed dormancy by nitrate as a gap detection mechanism. *Annals of Botany* 63: 139–143.
- Poorter, L., 1999. Growth responses of 15 rain-forest tree species to a light gradient: The relative importance of morphological and physiological traits. *Functional Ecology* 13: 396–410.
- Poorter, L. and S. Rose, 2005. Light-dependent changes in the relationship between seed mass and seedling traits: a meta-analysis for rain forest tree species. *Oecologia* 142: 378–387.
- Poorter, L., F. Bongers, F.J. Sterck, and H. Woll, 2005. Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *Journal of Ecology* 93: 256–267.
- Popma, J. and F. Bongers, 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* 75: 625–632.
- Pritchard, H.W., M.I. Daws, B.J. Fletcher, C.S. Gamene, H.P. Msanga, and W. Omondi, 2004. Ecological correlates of seed desiccation tolerance in tropical African dryland trees. *American Journal of Botany* 91: 863–870.
- Reader, R.J., 1993. Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology* 81: 169–175.
- Reich, P.B., M.G. Tjoelker, M.B. Walters, D.W. Vanderklein, and C. Bushena, 1998a. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology* 12: 327–338.
- Reich, P.B., M.B. Walters, M.G. Tjoelker, D. Vanderklein, and C. Buschena, 1998b. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology* 12: 395–405.
- Roberts, H.A. and P.M. Feast, 1972. Fate of seed of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research* 4: 296–307.
- Roberts, H.A. and P.M. Feast, 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. *Journal of Applied Ecology* 10: 133–143.
- Rodriguez, M.D., A. Orozco-Segovia, M.E. Sanchez-Coronado, and C. Vazquez-Yanes, 2000. Seed germination of six mature neotropical rain forest species in response to dehydration. *Tree Physiology* 20: 693–699.
- Russi, L., P.S. Cocks, and E.H. Roberts, 1992. The fate of legume seeds eaten by sheep from a mediterranean grassland. *Journal of Applied Ecology* 29: 772–778.
- Russo, S.E. and C.K. Augspurger, 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters* 7: 1058–1067.
- Sack, L. and P.J. Grubb, 2003. Crossovers in seedling relative growth rates between low and high irradiance: analyses and ecological potential (reply to Kitajima and Bolker 2003). *Functional Ecology* 17: 281–287.
- Salisbury, E.J., 1942. *The Reproductive Capacity in Plants: Studies in Quantitative Biology*. Bell, London.
- Sanchez-Hidalgo, M.E., M. Martinez-Ramos, and J. Espinosa-Garcia, 1999. Chemical differentiation between leaves of seedlings and spatially close adult trees from the tropical rain-forest species *Nectandra ambigens* (Lauraceae): An alternative test of the Janzen-Connell model. *Functional Ecology* 13: 725–732.
- Saverimuttu, T. and M. Westoby, 1996. Seedling longevity under deep shade in relation to seed size. *Journal of Ecology* 84: 681–689.
- Scariot, A., 2000. Seedling mortality by litterfall in Amazonian forest fragments. *Biotropica* 32: 662–669.
- Schreeg, L.A., R.K. Kobe, and M.B. Walters, 2005. Tree seedling growth, survival and morphology in response to landscape-level variation in soil resource availability in northern Michigan. *Canadian Journal of Forest Research* 35: 263–273.

- Seiwa, K., A. Watanabe, K. Irie, H. Kanno, T. Saitoh, and S. Akasaka, 2002. Impact of site-induced mouse caching and transport behaviour on regeneration in *Castanea crenata*. *Journal of Vegetation Science* 13: 517–526.
- Sevilla, G.H., O.N. Fernandez, D.P. Minon, and L. Montes, 1996. Emergence and seedling survival of *Lotus tenuis* in *Festuca arundinacea* pastures. *Journal of Range Management* 49: 509–511.
- Shibata, M., H. Tanaka, S. Iida, S. Abe, T. Masaki, K. Niiyama, and T. Nakashizuka, 2002. Synchronized annual seed production by 16 principal tree species in a temperate deciduous forest, Japan. *Ecology* 83: 1727–1742.
- Shipley, B. and R.H. Peters, 1990. The allometry of seed weight and seedling relative growth rate. *Functional Ecology* 4: 523–529.
- Silva, H.R.D., M.C.D. Britto-Pereira, and U. Caramaschi, 1989. Frugivory and seed dispersal by *Hyla truncata*; a neotropical tree frog. *Copeia* 3: 781–783.
- Silvera, K., J.B. Skillman, and J.W. Dalling, 2003. Seed germination, seedling growth and habitat partitioning in two morphotypes of the tropical pioneer tree *Trema micrantha* in a seasonal forest in Panama. *Journal of Tropical Ecology* 19: 27–34.
- Silvertown, J.W., 1980a. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* 14: 235–250.
- Silvertown, J.W., 1980b. Leaf-canopy-induced seed dormancy in a grassland flora. *New Phytologist* 85: 109–118.
- Slocum, M.G. and C.C. Horvitz, 2000. Seed arrival under different genera of trees in a neotropical pasture. *Plant Ecology* 149: 51–62.
- Smyth, N., 1978. The natural history of the Central American agouti (*Dasypracta punctata*). *Smithsonian Contribution to Zoology* 257: 20.
- Stanton, M., 1984. Seed variation in wild radish: Effect of seed size on components of seedling and adult fitness. *Ecology* 65: 1105–1112.
- Stiles, E.W., 2000. Animals as seed dispersers. In: M. Fenner, ed. *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd edition. CAB International, Wallingford, Oxford, pp. 111–124.
- Stock, W.D., J.S. Pate, and J. Delfs, 1990. Influence of seed size and quality on seedling development under low nutrient conditions in five Australian and South African members of the Proteaceae. *Journal of Ecology* 78: 1005–1020.
- Svenning, J.C. and S.J. Wright, 2005. Seed limitation in a Panamanian forest. *Journal of Ecology*, 93: 853–862.
- Swanborough, P. and M. Westoby, 1996. Seedling relative growth rate and its components in relation to seed size: Phylogenetically independent contrasts. *Functional Ecology* 10: 176–184.
- Tapper, P.G., 1996. Irregular fruiting in *Fraxinus excelsior*. *Journal of Vegetation Science* 3: 41–46.
- Templeton, A.R. and D.R. Levin, 1979. Evolutionary consequences of seed pools. *American Naturalist* 114: 232–249.
- Terborgh, J. and S.J. Wright, 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. *Ecology* 75: 1829–1833.
- Thompson, K., 1986. Small-scale heterogeneity in the seed bank of an acidic grassland. *Journal of Ecology* 74: 733–738.
- Thompson, K. and J.P. Grime, 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67: 893–921.
- Thompson, K., J.P. Grime, and A.G. Mason, 1977. Seed germination in response to diurnal fluctuations of temperature. *Nature* 267: 147–149.
- Thompson, K., S.R. Band, and J.G. Hodgson, 1993. Seed size and shape predict persistence in soil. *Functional Ecology* 7: 236–241.
- Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2–16.
- Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81–92.
- Toole, E.H., 1946. Final results of the Duval buried seed experiment. *Journal of Agricultural Research*. 72: 201–210.
- Tyler, C.M. and C.M. Dantonio. 1995. The effects of neighbors on the growth and survival of shrub seedlings following fire. *Oecologia* 102: 255–264.

- Valladares, F., S.J. Wright, E. Lasso, K. Kitajima, and R.W. Pearcy, 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* 81: 1925–1936.
- van Rheenen, H., R.G.A. Boot, M.J.A. Werger, and M.U. Ulloa, 2004. Regeneration of timber trees in a logged tropical forest in North Bolivia. *Forest Ecology and Management* 200: 39–48.
- Vaughan, J.G., 1970. *The Structure and Utilization of Oil Seeds*. Chapman and Hall, London.
- Vaughton, G. and M. Ramsey, 1998. Sources and consequences of seed mass variation in *Banksia marginata* (Proteaceae). *Journal of Ecology* 86: 563–573.
- Vegis, A., 1964. Dormancy in higher plants. *Annual Review of Plant Physiology* 15: 185–224.
- Veneklaas, E.J. and L. Poorter, 1998. Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. In: H. Lambers, H. Poorter, and M.M.I. Van Vuuren, eds. *Inherent variation in plant growth. Physiological mechanisms and ecological consequences*. Backhuys Publishers, Leiden, pp. 337–361.
- Vormisto, J., J.C. Svenning, P. Hall, and H. Balslev, 2004. Diversity and dominance in palm (Arecaceae) communities in terra firme forests in the western Amazon basin. *Journal of Ecology* 92: 577–588.
- Walters, M.B. and P.B. Reich, 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology* 81: 1887–1901.
- Wang, B.C. and T.B. Smith, 2002. Closing the seed dispersal loop. *Trends in Ecology & Evolution* 17: 379–385.
- Washitani, I., 1985. Field fate of *Amaranthus patulus* seeds subjected to leaf-canopy inhibition of germination. *Oecologia* 66: 338–342.
- Washitani, I. and M. Masuda, 1990. A comparative study of the germination characteristics of seeds from a moist tall grassland community. *Functional Ecology* 4: 543–557.
- Webb, C.O. and D.R. Peart, 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80: 2006–2017.
- Wenny, D.G., 2001. Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3: 51–74.
- Wenny, D.G. and D.J. Levey, 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America* 95: 6204–6207.
- Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213–227.
- Westoby, M., K. French, L. Hughes, B. Rice, and L. Rogerson, 1991. Why do more plant species use ants for dispersal on infertile compared with fertile soils? *Australian Journal of Ecology* 16: 445–455.
- Westoby, M., E. Jurado, and M. Leishman. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology & Evolution* 7: 368–372.
- Williamson, G.B. and K. Ickes. 2002. Mast fruiting and ENSO cycles—does the cue betray a cause? *Oikos* 97: 459–461.
- Willson, M.F., 1993. Dispersal mode, seed shadows and colonization patterns. *Vegetatio* 107/108: 261–281.
- Wolff, J.O., 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy* 77: 850–856.
- Wright, I.J. and K. Cannon, 2001. Relationships between leaf lifespan and structural defences in a low-nutrient, sclerophyll flora. *Functional Ecology* 15: 351–359.
- Wright, S.J. and H.C. Duber. 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33: 583–595.
- Wright, I.J. and M. Westoby, 1999. Differences in seedling growth behaviour among species: Trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* 87: 85–97.
- Wright, I.J. and M. Westoby, 2001. Understanding seedling growth relationships through specific leaf area and leaf nitrogen concentration: Generalisations across growth forms and growth irradiance. *Oecologia* 127: 21–29.
- Wright, S.J., C. Carrasco, O. Calderon, and S. Paton. 1999. The El Niño Southern Oscillation variable fruit production, and famine in a tropical forest. *Ecology* 80: 1632–1647.

- Wright, I.J., H.T. Clifford, R. Kidson, M.L. Reed, B.L. Rice, and M. Westoby, 2000. A survey of seed and seedling characters in 1744 Australian dicotyledon species: cross-species trait correlations and correlated trait-shifts within evolutionary lineages. *Biological Journal of the Linnean Society* 69: 521–547.
- Wright, I.J., M. Westoby, and P.B. Reich, 2002. Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology* 90: 534–543.
- Wright, S.J., H.C. Muller-Landau, O. Calderon, and A. Hernandez. 2005. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology* 86: 848–860.
- Wulff, R.D., 1986. Seed Size variation in *Desmodium paniculatum*. II. Effects on seedling growth and physiological performance. *Journal of Ecology* 74: 99–114.
- Zahawi, R.A. and C.K. Augspurger, 1999. Early plant succession in abandoned pastures in Ecuador. *Biotropica* 31: 540–552.
- Zanne, A.E., C.A. Chapman, and K. Kitajima, 2005. Evolutionary and ecological correlates of early seedling morphology in East African trees and shrubs. *American Journal of Botany* 92: 972–978.
- Zettler, J.A., T.P. Spira, and C.R. Allen, 2001. Ant-seed mutualisms: can red imported fire ants sour the relationship? *Biological Conservation* 101: 249–253.



