11 The Functional Role of Soil Seed Banks in Natural Communities

Arne Saatkamp,[1]* Peter Poschlod[2] and D. Lawrence Venable[3]

[1]*Institut Méditerranéen de Biodiversité et d'Ecologie (IMBE UMR CNRS 7263), Université d'Aix-Marseille, Marseille, France; [2]LS Biologie VIII, Universität Regensburg, Regensburg, Germany; [3]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA*

Introduction

When I was a child, playing in the meadows and woods, I (A.S.) was fascinated by all the seedlings coming out of seemingly lifeless soil where the ponds dried out, a new river bank was exposed or a mole built its hill. Beggarticks (*Bidens tripartita*) quickly covered the former pond; the river bank turned blue with forget-me-nots (*Myosotis pratensis*); and molehills were crowned with stitchwort (*Stellaria media*). It was a difficult experience when my parents had me weed out our overgrown vegetable garden where lambsquarters (*Chenopodium album*) from the seed bank grew faster than the radishes we had sown. I learned, however, to distinguish the few *Calendula* seedlings and to keep some flowers for my mother. Later, my fascination persisted as I asked myself why there were so many heather seedlings in the place where the pinewoods burned, but so few thistles? Why did many seedlings sometimes emerge in a footprint, but not just beside it? Why did the annual grass *Bromus rubens* show up every year, but on the same site *Glaucium corniculatum* only every other year? And why did

some plants make such prominent seed banks and others none at all?

Some of us would be satisfied with answers like 'the large size of *Calendula* and *Carduus* seeds limits the number that can be produced by the plant and which will get buried' or 'decades ago heathland grew where the pinewood used to be'. But others of us, inspired by Darwin's 'three table-spoonsful of mud' from which he grew 537 plants, also want to understand the evolution of soil seed banks, pursuing the deeper sense to the 'why' question in biology that Darwin (1859) gave us. The goal of this chapter is to help to answer the questions on: (i) types and definitions of soil seed banks; (ii) how soil seed reservoirs can evolve; (iii) what functional role seed banks play in the dynamics of natural communities; and (iv) what are adaptive traits to build up soil seed banks.

By the 'functional role' of soil seed banks we mean their role in population dynamics, their adaptive role, the effect seed banks have on communities and coexistence, and the role of soil seed banks in the evolution of other plant traits through interactive selection. These aspects will

* E-mail: arne.saatkamp@imbe.fr

help us to understand the build-up and existence of soil seed banks. We use 'natural communities' in a pragmatic sense to mean any spontaneous plant assemblage. The functional role of seed banks in agroecosystems is treated in detail in Chapter 10 of this volume.

Types and Definitions of Soil Seed Banks

Soil seed banks include all living seeds in a soil profile, including those on the soil surface. Here we simply speak of seeds, although in the beginning, soil seed banks are also composed of dispersal units, which are seeds or fruits surrounded by structures serving for dispersal and sometimes contain other plant parts such as bracts or stems. Over time, the dispersal structures, as well as seed coats, can decompose, leaving only germination units. For example, *Ranunculus arvensis* has a thick seed coat and spikes which both decompose after burial in soil after a few years, leaving coatless seeds (A. Saatkamp, 2009, unpublished data). Soil seed banks resemble other biological reservoirs, such as invertebrate eggs, tubercles and bulb banks, spores of non-spermatophyte plants and fungi, or seeds retained on mother plants (serotiny). Many of these resting stages share similar evolutionary constraints and physiological functioning, in such a way that hatching of invertebrate eggs and seed germination can be modelled in the same way (Trudgill *et al.*, 2005).

Soil seed banks vary much according to seed proximity, seed persistence and physiological state. Living seeds have been found in or on the soil for different durations (Duvel, 1902; Priestley, 1986; Roberts, 1986; Poschlod *et al.*, 1998), different seasons (Roberts, 1986; Poschlod and Jackel, 1993; Milberg and Andersson, 1997), at different depths (Duvel, 1902; Grundy *et al.*, 2003; Benvenuti, 2007), in different quantities (Thompson and Grime, 1979; Thompson *et al.*, 1997) and in different states of dormancy or procession to germination (Baskin and Baskin, 1998; Walck *et al.*, 2005; Finch-Savage and
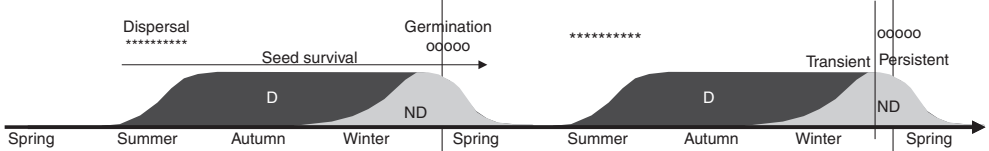
Leubner-Metzger, 2006). Seeds in the soil seed bank may occur in or on the soil, but in many situations, there is a continuity between seeds at the surface, partly buried and completely buried seeds (Thompson, 2000; Benvenuti, 2007). In practice, it is rarely possible to properly separate buried seeds from the seeds in the litter. Seeds of several plant species hardly ever enter the soil but persist at its surface or in the litter for many years, prominent examples are the large and hard fruits of *Medicago* and *Neurada*, which contain dozens of seeds and can give rise to several plants over several years.

Plants differ in the duration their seeds remain in the soil and even within a species and among seeds of the same cohort there is variability in the time they spend in the soil seed bank. Thompson and Grime (1979) proposed a system of soil seed bank types, based on the study of the seasonal dynamics and the duration of soil seed banks for the flora of Central England (Fig. 11.1). According to their data, they distinguished between transient seed banks for species that have viable seeds present for less than 1 year, and persistent seed banks for species with viable seeds that remain for more than 1 year. Persistent soil seed banks can be subdivided further into short-term persistent for seeds that are detectable for more than 1 but less than 5 years, and long-term persistent seed banks that are present for more than 5 years (Maas, 1987; Bakker, 1989; Thompson and Fenner, 1992). A classification key for the three basic types can be found in Grime (1989), which is based on the abundance and depth distribution of seeds in the soil seed bank, their seed size, their seasonality and the presence/absence of a plant in the established vegetation around the seed bank sample. More detailed classifications have been proposed but they did not gain wider usage, mostly because necessary data are rarely available (reviewed in Csontos and Tamás, 2003; e.g. Poschlod and Jackel, 1993). For temperate regions, Thompson and Grime (1979) also used seasonality to separate winter and summer seed banks for plants with autumn and spring germination (Fig 11.1). Since timing of seed dispersal and germination vary greatly among species
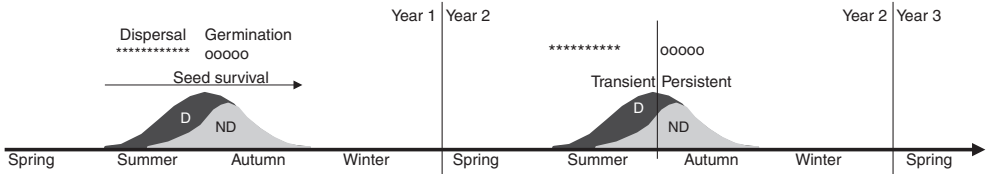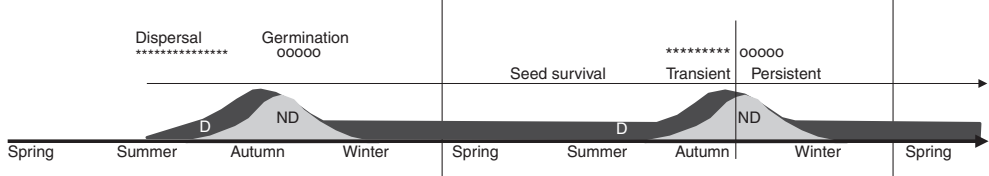
Fig. 11.1. Seed bank types according to timing of dispersal, germination and survival of seeds. (a) Transient seed bank with autumn germination; (b) transient seed bank with spring germination; (c) persistent seed bank with autumn germination. Note that the limit between transient or persistent seed banks as defined by Walck *et al.* (2005) does not coincide with a 1 year distance from the dispersal of seeds, the limit is indicated by a line (redrawn from Thompson and Grime, 1979 and Walck *et al.*, 2005). D, dormant; ND, non-dormant.

and among climates (Baskin and Baskin, 1998; Dalling *et al.*, 1998; Boedeltje *et al.*, 2004), Walck *et al.* (2005) suggested that the time between dispersal and the first germination season should be used to distinguish transient from persistent seed banks (Fig. 11.1).

Some plants produce both transient and persistent seeds, in varying ratios (Clauss and Venable, 2000; Cavieres and Arroyo, 2001; Tielbörger *et al.*, 2011) and variation in the environment leads to variable seed exit by germination from the seed bank (Meyer and Allen, 2009). Whereas simple seed bank types are useful for multi-species comparisons, we need also to consider dynamic and quantitative aspects of seed banks if we want to predict more precisely the role of seed banks. For example,

plants can build up seed banks when their seeds are buried during disturbance and stay ungerminated due to a light requirement but germinate nearly completely when they remain at the surface (see Chapters 5 and 6 of this volume). Soil seed banks are a dynamic part of plant populations with a set of factors that quantitatively influence their entry, persistence and exit, all of which vary according to plant biology, time and their environment. Such an approach will improve our ability to predict ecological outcomes in response to community disturbance and/or community invasion.

Research on soil seed banks differs in the type of data collected, sometimes consisting of (i) studying soil samples by identifying and counting seedlings, or sifting

and identifying seeds, without any precise knowledge on seed ages and the size of the original seed rain; or (ii) burial experiments, which follow, in the best case, counted numbers of seeds over time under defined conditions of depth, soil type, moisture or fertility. We propose to distinguish 'persistence' of seeds in a general sense or with undefined numbers from 'survival' of individual seeds or precisely quantified seed populations. The difference between these data types needs attention, and potentially leads to contrasting conclusions with respect to the seed size–number trade-off (see below).

Evolution of Soil Seed Banks

Soil seed banks are both the outcome of environmental or plant developmental contingencies and the result of evolutionary history. Climate, herbivory and disturbances vary and lead directly to year-to-year changes in soil seed bank density and spatial heterogeneity. Some environments particularly favour the evolution of persistent soil seed banks, such as river mud flats or ephemeral ponds, forest gaps, pastures and arable fields since they are often or intensely disturbed (Ortega *et al.*, 1997; Bekker *et al.*, 1998c) or have very variable habitat conditions (Brock, 2011). Plants with persistent soil seed banks are some of the most characteristic species of these habitats. Many other ecosystems also contain at least a few plant species with persistent soil seed banks, either with some kind of dormancy (Keeley, 1987; Baskin and Baskin, 1998), with increased germination in presence of smoke-derived substances (Brown, 1993; Flematti *et al.*, 2004), or with a gap detection mechanism (Thompson and Grime, 1983; Dalling *et al.*, 1998; Pearson *et al.*, 2003). Even if these ecosystems have low disturbance levels, they share a form of temporal and spatial unpredictability of regeneration opportunities, which may stem from disturbances including gap dynamics or climatic variability. In the following, we review theoretical works that demonstrate the adaptive

value of seed persistence, the first germination opportunity in environments with such temporal variability and also works that demonstrate how delayed germination can evolve without temporal variability. These theoretical studies will help to understand under which conditions persistent soil seed banks evolve and in which direction and relative magnitude they affect the delay of germination.

Timing of germination and fitness of individual seeds

Germination can be 'delayed' at different timescales, either from one year to later years, from one season to another season or within a given season. Also plant species differ among each other in the degree of delay at all scales. Before we discuss the evolution of persistent seed banks, let's have a look at the two shorter temporal scales. Under optimal conditions, during the appropriate germination season, early germination would seem to maximize the fitness of a seed due to longer growth and the resulting higher fecundity (Ross and Harper, 1972; Fowler, 1984; Kelly and Levin, 1997; Dyer *et al.*, 2000; Turkington *et al.*, 2005; Verdù and Traveset, 2005; De Luis *et al.*, 2008), although in some cases fitness can be reduced with early germination due to high mortality of seedlings (Marks and Prince, 1981; Jones and Sharitz, 1989; Donohue, 2005). Delay in germination can delay reproduction, which could result in a longer generation time, or, for a short-lived plant, extending reproduction into an unfavourable season. Despite the manifest advantages of early germination, many plants have delayed germination due to some form of dormancy, especially in seasonal climates (Baskin and Baskin, 1998; Jurado and Flores, 2005; Merritt *et al.*, 2007), which contributes to seed persistence in these types of ecosystems (Leck *et al.*, 1989; Thompson *et al.*, 1997). Within years, the optimal time for germination often differs from the season of seed production such that there is strong selection for delayed germination of

fresh seeds. Therefore, germination timing must be under stabilizing selection, with fitness declining for germination that is too early or too late. Likewise, the prevalence of persistent seed banks and their association with certain habitats suggests that the proportion of germinating seeds in one season compared to those that will persist to a subsequent one also has adaptive value. It is impressive on what short timescales mixtures of genotypes of *Arabidopsis thaliana*, with or without dormancy, are sorted out according to their fitness in climates contrasting in the severity of winter conditions (Donohue *et al.*, 2005; Huang *et al.*, 2010). This rapid evolution between winter and spring germination in *Arabidopsis* is astonishing, because of the recurrent differences between warm and cold germinating species when one compares many species over larger areas and which are often related to contrasting traits (Baskin and Baskin, 1998; Merritt *et al.*, 2007).

transient seed banks (Ortega *et al.*, 1997). Predictable rainfall, e.g. in monsoon climates, and frost in arctic or alpine environments have similar effects on timing of emergence from seed banks (reviewed in Baskin and Baskin, 1998).

Sometimes disturbances are predictable at longer timescales only (10–20 years), such as fires with immediately following regeneration opportunities. This leads to seed banks that persist in the interval between fires and whose germination can be stimulated by smoke or whose dormancy is released by heat, which are highly predictive of favourable regeneration opportunities (Cowling and Lamont, 1985; Thanos *et al.*, 1992; Brown, 1993; Flematti *et al.*, 2004). In other cases, habitats with periodical flooding harbour plants that only produce transient seed banks, like the very short-lived willow seeds (*Salix*), which live only for weeks (Thompson and Grime, 1979) and for which clonal reproduction may be an important alternative to seed banks.

Seed banks and the predictability of environment

Even predictable changes in the environment can lead to formation of soil seed banks, although lasting for a shorter time. Typically more predictable environmental factors include seasonal changes in temperature, moisture (Baskin and Baskin, 1998; Jurado and Flores, 2005; Merritt *et al.*, 2007), water level in some aquatic ecosystems such as flood plains of large rivers (Leck *et al.*, 1989; Kubitzki and Ziburski, 1994), and the number of competing seeds from the same mother plant or environment (Cohen, 1967; Ellner, 1986; Tielbörger and Valleriani, 2005; Valleriani and Tielbörger, 2006). When favourable environments for germination are predictable on shorter timescales, transient rather than persistent soil seed banks tend to form with germination time determined by cues for dormancy loss and germination of non-dormant seeds (Thompson and Grime, 1979). For example, many annuals in Mediterranean-type climates that germinate with autumn and winter rains have

Unpredictable environments promote evolution of persistent seed banks

We intuitively relate the evolution of delayed germination to environmental unpredictability, without invoking competition or other density-dependent effects. A prominent example of a system where the environment (rainfall) varies unpredictably is annual plants in deserts. Desert annuals reproduce or die depending on the occurrence of unpredictable rainfall events during their one and only growing season. In response to this uncertainty, they may retain a fraction of ungerminated seeds for possible future germination opportunities in potentially more favourable years. This 'bet hedging' is understood as an insurance against reproduction failure, or more generally, as a strategy that may reduce arithmetic mean fitness, but also fitness variance and hence increase long-term fitness. For bet hedging to occur in absence of density dependence, global variation in environment quality is needed.

Even with a low frequency of total reproductive failure, populations that do not maintain a fraction of ungerminated seeds for subsequent rainfall events, would go extinct (Gutterman, 2002). Models that incorporate bet hedging and density dependence typically show the higher the variance in reproductive success, the lower the fitness-maximizing germination fraction in any given year (Cohen, 1966, 1967; Venable and Lawlor, 1980; Bulmer, 1984; Ellner, 1985a,b; Venable and Brown, 1988; Rees, 1994; Pake and Venable, 1995; Clauss and Venable, 2000; Evans and Dennehy, 2005; Venable, 2007; Tielbörger *et al.*, 2011). The basic prediction of bet hedging, has been demonstrated empirically for different sites with differing levels of risk (Clauss and Venable, 2000; Tielbörger *et al.*, 2011), and across species differing in risk levels at a given site (Venable, 2007). Bet hedging, in the form of risk spreading in temporally variable, unpredictable environments, is the best known evolutionary mechanism leading to delayed germination and the evolution of a persistent soil seed bank (Cohen, 1966; Venable, 2007; Tielbörger *et al.*, 2011).

Beyond rainfall, predation in the form of herbivory can be another factor that creates temporally unpredictable risk in reproduction and thus the conditions for bet hedging, and in this way increases the adaptive value of persistent soil seed banks. This 'escape from predators' and the influence of other disturbances of biotic origin may be an important source for the evolution of soil seed banks via bet hedging, especially in desert and grassland ecosystems, which harbour a certain number of species with persistent soil seed banks.

Evolution of persistent seed banks and density dependence: competition and predation

Bet hedging explains evolution of persistent seed banks in the absence of density-dependent effects, such as competition or density-dependent seed predation. But, in many ecosystems, competition and density-dependent seed predation play an important role and this affects the evolution of soil seed banks. For example, competition can lead to deterministic fluctuations in otherwise constant environments due to high reproductive rate and deterministic growth. In this case, competition favours evolution of persistent seed banks, because variation in density creates opportunities to escape from competition (Ellner, 1987; Venable, 1989; Lalonde and Roitberg, 2006), an effect that increases evolution of persistent seed banks in absence of global temporal variation (bet hedging) or sibling competition. Competition can promote evolution of persistent seed banks also when variance in density results from other things than competition alone. Obviously, any kind of disturbance will create such variance in density. If there is environmental variation and density dependence, then escape from competition will also promote between-year delay of germination (Venable and Brown, 1988). The difference that competition makes for the evolution of persistence is that lower probability of good years will not necessarily increase the delayed germination, rather, the variability of good/bad years and the frequency of changes will increase delayed germination. In this way, theory underlines the importance of disturbances or environmental variation for the evolution of persistent soil seed banks.

Besides temporal variability, also spatial variability in habitat conditions and competition alone can trigger the evolution of delayed germination (Venable and Lawlor, 1980; Bulmer, 1984; Ellner, 1985a,b). Interestingly, a persistent soil seed bank can also evolve because a highly dormant genotype can recolonize a previously occupied safe site more easily from the seed bank in a local patch than in a distant one (Satterthwaite, 2009). Similarly, Rees (1994) showed the adaptive advantage of a persistent soil seed bank in situations with limited patches for synchronous and age-structured plants.

Furthermore, predation is influenced by density of seeds or plants. Preferential predation of first-year seeds over those in the persistent seed bank from previous

years can result in the evolution of lower germination fractions and greater specialization of the growing phase plant to conditions found in favourable years, conditions that result in temporal clumping of reproduction (Brown and Venable, 1991). This mast-like clumping is especially favoured with negative density-dependent seed predation, i.e. if seed predators cannot consume the high number of seeds produced in favourable years, though it can evolve even with density-independent seed predation.

Competition among sib seedlings

During favourable years, a higher seed production potentially leads to more intense competition among sibling seedlings. Such a scenario favours differing germination percentages among seed produced in productive compared to unproductive years or for seeds from different watering conditions. One reason for this is the higher abundance of seeds from the same mother plant leading to increased competition among siblings. This suggests that seeds produced by highly fecund plants should have lower germination fractions compared to low fecundity plants (Silvertown, 1988; Venable, 1989; Nilsson *et al.*, 1994; Lundberg *et al.*, 1996; Hyatt and Evans, 1998; Tielbörger and Valleriani, 2005; Tielbörger and Petru, 2010; Eberhart and Tielbörger, 2012), an effect that promotes evolution of persistent seed banks independently from global temporal variation. This has been shown empirically in natural populations (Philippi, 1993; Zammit and Zedler, 1993). But also abiotic variation in the maternal environment, and, related to this, general levels of inter-specific competition may result in plastic increases in dormancy, as has been shown in several works of Tielbörger and co-workers (Tielbörger and Valleriani, 2005; Tielbörger and Petru, 2010). Nevertheless, seed production and levels of dormancy are not always negatively related among plants differing individually in fecundity in the field (Eberhart and Tielbörger, 2012).

Parent–offspring conflict, maternal effects and evolution of delayed germination

The genome of the seed embryo in most cases contains only half of the mother plant's genome. Therefore, delay in germination and its promoting factors do not affect the fitness of the mother plant and that of the offspring seed in the same way. For example, early germination of seeds may reduce the fitness of the mother plant because offspring plants may compete with the mother plant, but at the same time may increase the fitness of the offspring by shortening generation time. Spreading of germination (bet hedging) across time or space may increase the fitness of the mother plant, but the delay may reduce the fitness of an individual seed. Situations when individual seeds increase their fitness by delaying their germination result from predictable changes in favourability of the environment, most importantly, seasonal changes in water and temperature, and drought- and frost-free periods which can be predicted by temperature changes. Timing the germination to anticipate favourable periods for establishment maximizes fitness of both mother plant and offspring.

This discussion shows that in most situations, the maternal fitness is favoured more by delayed germination than offspring fitness is. That delayed germination evolved often in spite of this becomes plausible considering the dependence of zygotes on provisioning by the mother plant, and the many aspects of seed morphology and physiology that are controlled by the mother plant, such as the number and size of seeds and their protection and dispersal structures and depth of dormancy (Ellner, 1986; Silvertown, 1999). Seed dormancy mechanisms such as underdeveloped embryos, water impermeable seed coats formed by maternal tissues and germination inhibitors have also been interpreted in terms of maternal control of germination (Ellner, 1986; Silvertown, 1999). This is beyond what is habitually called 'maternal effects'. Maternal effects are usually defined as different seed and offspring features that stem from variation in the

maternal environment, such as different levels of dormancy among seeds from genetically identical mother plants grown in different temperatures or soil moisture conditions (Guttermann, 2000; Donohue, 2009; Tielbörger and Petru, 2010). The plastic maternal effects and genetically fixed maternal influences both contribute to the control of offspring seed germination and its environment-dependent fine tuning by mother plants (Zammit and Zedler, 1993; Tielbörger and Valleriani, 2005; Tielbörger and Petru, 2010).

Evolution of persistent seed banks and relation to other traits

The evolution of delayed germination and the formation of a between-year soil seed bank are not independent from other plant traits. For example, bet hedging can also act through dispersal in space or by other alternative risk-reducing traits such as stress tolerant morphology and physiology or larger seed size (Venable and Brown, 1988). Theoretical models on the interaction during selection of alternative risk-reducing traits and of persistent seed banks show that they are often, but not always negatively related (Venable and Brown, 1988; Rees, 1994; Snyder, 2006; Vitalis *et al.*, 2013). They do not evolve independently from each other and which trait will be more favoured depends on details of the environment. Contrastingly, when there is temporal autocorrelation in habitat quality the favoured association between dormancy and dispersal can also be positive (Snyder, 2006).

A long plant lifespan is another alternative risk-reducing trait which, similarly to persistent soil seed banks, allows survival through unfavourable periods for reproduction. Consequently, these strategies are negatively related in across-species comparisons (Rees, 1994, 1996; Tuljapurkar and Wiener, 2000). This further suggests that all plant traits that hedge against temporal or spatial habitat variability can have impacts on the evolution of persistent soil seed banks, and future work might explore how

and why plants with succulence, woodiness, clonality and underground storage organs rely comparatively less on persistent soil seed banks.

In conclusion, the models summarized here have elucidated some of the reasons for the evolution of persistent soil seed banks and define the conditions under which persistent soil seed banks contribute to the fitness of plant populations. They point to specific biotic and abiotic, and spatial and temporal environmental conditions whose effects often still need to be tested empirically. They also go a long way towards understanding the relations of persistent soil seed banks to other seed and plant traits. Moreover, evolutionary models provide us only with general predictions; they need to be empirically parameterized to show the magnitude of adaptive features in real plant populations. Some might show up in only very special situations, others only in controlled experiments, and again others might be too small to ever be detected in living plant populations. More precise comparative methods (Butler and King, 2004), and comparative investigations on closely related species (Evans *et al.*, 2005) or populations in different environments (Donohue *et al.*, 2005; Tielbörger and Petru, 2008; Tielbörger *et al.*, 2011) may help us to unravel the importance of these effects.

Most evolutionary models do not explain *how* persistent soil seed banks can be realized, but they explore why a fraction of ungerminated seeds remains viable and ungerminated until subsequent germination seasons contribute to fitness. It is clear that persistent seed banks can be achieved by many different mechanisms in comparable environments (impermeable seed coats, serotiny, physiological dormancy, specific germination conditions and cues), which are discussed in the subsequent sections.

Site-to-site Variation in Soil Seed Persistence

Soil seed persistence for a given species may vary from site to site, and for several species, both persistent and transient soil

seed bank types have been documented (Thompson *et al.,* 1997). Between-site variation of soil seed persistence has been attributed to variation in fungal activity, soil fertility (nitrates), oxygen supply, vegetation cover, burial depth (via different disturbance regimes or successional states), seed density and predator pressure (Wagner and Mitschunas, 2008; Koprdová *et al.*, 2010; Saatkamp *et al.*, 2011a). Moreover, since evolutionary constraints of temporal habitat variability lead to different importance of persistent seed banks, local adaptation within species is a source of site-to-site variation in soil seed persistence either directly genetically or via evolution of different levels of plasticity (Tielbörger *et al.*, 2011).

Fungi, soil fertility and moisture

Fungi, either carried by the seed itself or originating from the soil, can strongly reduce soil seed viability and modify seed germination (Wagner and Mitschunas, 2008). Both fungal sources can be additive in their detrimental effects (Kiewnick, 1964). Fungal attack on buried seed depends on soil moisture and temperature. In a series of studies it has been shown that for a given set of mesic species, seed mortality is higher in wet sites, unless fungicide is applied (Schafer and Kotanen, 2003). Also, organic matter and nitrogen content importantly influence fungal activity (Schnürer *et al.*, 1985) and together with low C:N ratio can decrease survival of seed in the soil (Pakeman *et al.*, 2012). Conversely, seedling survival is much higher in plant communities with a mycorrhiza community with affinities to the plant under consideration (reviewed by Horton and Van Der Heijden, 2008). In some plants, such as orchids or some Ericaceae, germination only occurs in the presence of symbiotic fungi in the wild (Horton and Van Der Heijden, 2008). Despite the great diversity of soil fungi and their myriad interactions with plants, studies of the role of soil fungi in soil seed bank dynamics are still scarce and more research is needed to refine this picture.

Soil fertility may also affect soil seed bank persistence. One important factor is nitrate, which promotes the germination of seeds of many species (Popay and Roberts, 1970; Hendricks and Taylorson, 1974) thereby potentially contributing to the depletion of persistent soil seed banks (Bekker *et al.*, 1998b). Stimulation of germination by nitrates may also interact with other environmental parameters such as light or fluctuating temperatures and it also depends on the dormancy state of the seed (Fenner, 1985; Benech-Arnold *et al.*, 2000).

Many plants, especially those from dry habitats, have reduced survival of seed in water-logged soils and it is argued that lack of oxygen is the proximate cause of seed mortality (Kiewnick, 1964; Wagner and Mitschunas, 2008). In contrast, some wetland species such as *Typha* specifically germinate during or after anoxic phases (Morinaga, 1926; Bonnewell *et al.*, 1983). Furthermore, some of the most long-lived seed banks are found in water-logged soils, which is sometimes related to the occurrence of physical dormancy in these habitats (Shen-Miller, 2002). Other wetland plants, such as sedges (*Carex*) show increased mortality when seeds are in a dry state for too long a time (Schütz, 2000). This suggests that wetland species have specific adaptations to survive in water-logged and anoxic conditions, and that they differ from mesic or dryland species in their pathogen defence mechanisms and in their oxygen requirements. The contrast between wetland and dryland species indicates that seeds are adapted to soil conditions of the environment they evolved in and that adaptations for long-term persistence of seeds cannot necessarily be generalized across habitats.

Vegetation cover, gap detection, depth of burial and disturbance

Dense vegetation prevents germination of some seeds. In these situations, seeds can detect vegetation cover via far-red/red light ratios at the soil surface (Kettenring *et al.*, 2006; Kruk *et al.*, 2006; Jankowska-Blaszczuk

and Daws, 2007). Others sense vegetation or gaps in it from below ground via diurnal fluctuating temperatures (Thompson *et al.*, 1977). In this way, the density and height of vegetation covering the soil seed bank has impacts on the germination of seed populations from the soil. It can be hypothesized that some gap specialists or initial successional species maintain soil seed banks under dense vegetation, whereas they are depleted more rapidly in open areas. Seed banks can also accumulate under dense vegetation where it functions as a natural seed trap.

Seeds move up and down in soil profiles due to rain (Benvenuti, 2007) or soil turbation by earthworm activity (e.g. Zaller and Saxler, 2007; reviewed by Forey *et al.*, 2011). Some plants depend on light for germination and their seeds do not germinate when buried at sufficient depth (Woolley and Stoller, 1978) and others germinate only with diurnally fluctuating temperatures (Ghersa *et al.*, 1992), so that some seeds remain ungerminated in deeper soil layers (Saatkamp *et al.*, 2011a). These germination requirements may interact with disturbance types and intensities and modify the abundance of seeds in the soil.

Postdispersal seed predation and soil seed banks

Seed predation and dispersal by animals varies over time and space in relation to their abundance and activity (Hulme, 1994, 1998a; Menalled *et al.*, 2000; Westerman *et al.*, 2003; Koprdová *et al.*, 2010). Although vertebrates are thought to play the major role (Hulme, 1998a), ground dwelling arthropods such as carabid beetles, isopods and millipedes can be very effective seed predators (Tooley and Brust, 2002; Saska, 2008; Koprdová *et al.*, 2010). They can consume large numbers of seeds in a short time. Birds, rodents and probably also fish preferentially feed on large seeds (Hulme, 1998a), whereas invertebrates often show preference for smaller seeds (Koprdová *et al.*, 2010). Hulme (1998a,b) suggested that the preference

of rodents for large seeds in northern hemisphere regions decreases the evolution of soil persistence for large-seeded plants, based on the observation that rodents dig out and eat large but not small seeds and that independently, they prefer transient over persistent seeds.

Earthworms ingest and digest seeds of a range of sizes, and earthworm species have specific upper limits to seed sizes they ingest (Shumway and Koide, 1994). After ingestion, smaller seeds are also more easily digested than larger seeds (Forey *et al.*, 2011). Since earthworm abundance and activity is not equal among soil types and specifically depends on temperature, moisture and acidity (Curry, 2004), their interaction with seeds is likely to create heterogeneity among sites in seed persistence. Not only for earthworms, postdispersal seed predation varies among sites, among feeding animal species, and between seasons, and this variation has been suggested to be of sufficient importance to drive evolution of seed persistence (Hulme, 1998a,b). It would therefore be interesting to study the persistence of soil seed banks in areas with contrasting seed predator communities, or using predator exclusion, in order to explore the effects on the evolution of persistent seed banks and to test the prediction of Brown and Venable (1991) that germination fractions should decrease in response to predation on fresh seeds.

Seed density

Soil seed banks show very high spatial heterogeneity as a result of dispersal contingencies, and seed densities vary considerably over small distances, leading to dense or comparatively seed-free areas (Thompson, 1986; Benoit *et al.*, 1989; Dessaint *et al.*, 1991). Densely packed seeds experience a higher incidence of fungal attack than low-density soil seed banks (Van Mourik *et al.*, 2005), and have a higher depletion rate, hence a lower survival. Since density of seeds in the soil also determines the future competitive situation after

emergence, seeds, if they sense each other, should react in two ways: either, germinate quickly to gain an advantage over slower germinating seeds, or, delay germination to another germination season in order to avoid crowding (Dyer *et al.*, 2000; Kluth and Bruelheide, 2005; Turkington *et al.*, 2005; Verdù and Traveset, 2005; Tielbörger and Prasse, 2009). It has also been suggested that delayed germination in response to high seed densities should be more readily adopted by annuals while rapid germination will be more advantageous for perennials. Working on four perennial plants in the Negev desert, Tielbörger and Prasse (2009) showed that indeed seeds sense each other below ground, leading to lower germination fractions at higher seed densities. When seedlings were not removed, their presence accelerated germination of seeds and both effects were influenced by successional position of the species in question. In this way, a late successional species, *Artemisia monosperma*, reduced germination percentages of other species and also germinated fastest, whereas germination of early successional species was suppressed. The site-to-site variation of soil seed persistence summarized here opens interesting perspectives to study the functioning of soil seed banks both in laboratory and field experiments and highlights the complex nature of soil seed-bank dynamics.

Seed Size and Number Trade-off

The soil seed bank inherits from adult plants the constraint that relates the size of a seed to the number of seeds produced per individual plant of comparable size or per canopy area (Smith and Fretwell, 1974; Jakobsson and Eriksson, 2000; Jakobsson *et al.*, 2006). As a rule of thumb, ten times smaller seeds can be produced in ten times higher number for a given canopy area (Aarssen and Jordan, 2001; Henery and Westoby, 2001; Moles and Westoby, 2002). The work of Moles and Westoby (2006) showed, in a global synthesis, that the advantage of higher numbers of small seeds is counterbalanced by

their lower survival as seedlings, and by smaller canopies and shorter reproductive lifespans. Disadvantages for small-seeded plants are detectable especially at the seedling stage and involve mortality due to drought and defoliation (Leishman *et al.*, 2000b).

How the survival of seeds in the soil is influenced by seed size is not well understood. Works using mostly seedling emergence from soil samples in temperate regions show consistently that small seeds have higher persistence in the soil in Europe and other temperate regions (Thompson and Grime, 1979; Leck *et al.*, 1989; Thompson *et al.*, 1993; Bekker *et al.*, 1998a; Moles *et al.*, 2000; Funes *et al.*, 2007). This can be explained by the fact that smaller seeds are more easily incorporated into the soil and moved to deeper soil layers (Benvenuti, 2007), which together with a higher predation pressure on large seeds prevent the evolution of persistence in large seeds (Hulme, 1998b; Thompson, 2000). In contrast, works using burial experiments with counted seed populations in arid areas showed that smaller seeds had lower survival dependent on seed size in the soil than larger seeds (Moles and Westoby, 2006; Moles *et al.*, 2003). These discrepancies among studies have been interpreted by differences in seed predators (Moles and Westoby, 2006). But also, soil factors such as moisture, organic content and seed density decrease seed survival due to enhanced fungal activity (Blaney and Kotanen, 2001; Schafer and Kotanen, 2003; Van Mourik *et al.*, 2005; Pakeman *et al.*, 2012;) and thus influence this relationship. This would probably increase mortality of small seeds more than large seeds since protection and nutrient reserves are different (Crist and Friese, 1993; Moles and Westoby, 2006). An alternative explanation is a difference in methods: seedling emergence studies do not quantify initial seed input, which is higher for small-seeded species than for large-seeded ones in many situations. Then, the sheer numbers of small seeds mean that they may be more easily detected than large seeds (Jakobsson *et al.*, 2006; Saatkamp *et al.*, 2009), leading to a higher ratio of

small-seeded species being classified as having persistent seed banks. The detection of seed size–seed persistence relations is even more complicated because the ratio of small to large seeds will decrease with time due to the higher seedling mortality of small-seeded species (Leishman *et al.*, 2000b; Moles and Westoby, 2006). From current data it seems that both seed size–persistence relations occur in nature. Probably in moist ecosystems the amount of small seeds in persistent seed banks is higher, but the precise relation to soil moisture or rainfall has yet to be quantified.

This discussion shows that the soil seed bank cannot be understood disconnected from the entire plant life history, and that the size or numbers of seeds in the soil seed bank should be interpreted in the light of the size–number trade-off. Other seed traits, such as dispersal structures, seed coat thickness or phenolic content also scale importantly with seed size (Moles and Westoby, 2006; Davis *et al.*, 2008); this is

shown for seed coat thickness in Fig 11.2. This concerns also traits that have been related to the survival rates of seeds in the soil across species (Thompson *et al.*, 1993; Bekker *et al.*, 1998a; Gardarin *et al.*, 2010).

As outlined above, seed size importantly influences the survival of seedlings and this can dramatically change the effect of the soil seed bank on community composition and change the size distributions of seeds in the seed banks versus seedlings or adult plants. Data on the relative role of soil seed-bank persistence and seedling mortality in community assembly are crucial if we want to predict their utility for restoration of plant communities (Poschlod, 1995; Bakker *et al.*, 1996; Bossuyt and Honnay, 2008). Until now, studies that analyse the effect of soil seed banks on community composition and abundance *in situ* are comparatively scarce but give an important background picture to understand the role of soil seed banks in communities (e.g. Kalamees and Zobel, 2002).
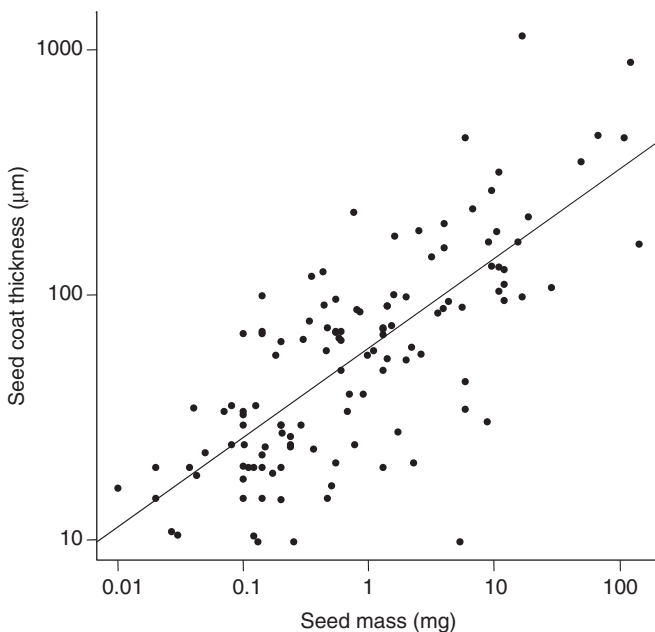

Fig. 11.2. Relation between seed coat thickness and seed weight for 123 plants of Europe and South Africa, note the logarithmic scale for both seed traits, $R^2 = 0.56$, $p < 0.001$ (A. Saatkamp, 2009, unpublished data, and data from Flynn *et al.*, 2004; Holmes and Newton, 2004; Bruun and Poschlod, 2006; Soons *et al.*, 2008; Gardarin *et al.*, 2010; Morozowska *et al.*, 2011).

Soil Seed Banks in Plant Communities

Soil seed banks and coexistence

Persistent seed banks are thought to play an important role in species coexistence through the 'storage effect' (Chesson and Warner, 1981; Facelli *et al.*, 2005; Angert *et al.*, 2009). The storage effect is a mechanism favouring coexistence of otherwise competitively excluding species due to environmental variation. Species that respond differently to environmental variation can coexist when seed banks are present to buffer them from the double disadvantage of an unfavourable environment and high competition. For example, the storage effect can promote the coexistence of dominant competitors with otherwise excluded species which differ in their reactions to disturbances, and which have a persistent soil seed bank (Fig. 11.3).

Traits that are related to different reactions of annual plants to environmental fluctuations include, among others, adaptations to cope with dry environments, which is in trade-off with their relative growth rate (Angert *et al.*, 2009). Moreover, annual plants with limited spatial dispersal and high seed mass recover more slowly from severe disturbances than do small-seeded plants from the persistent seed bank. Seeds can play further important roles in coexistence through the storage effect since differences in germination responses to environmental variation can be the temporal niches providing the mechanism of differential species responses to the environment (Facelli *et al.*, 2005).

Most plant communities show a mix of transient and persistent soil seed banks. In dense communities of annual plants with recurrent disturbances, competition colonization trade-offs are also an important mechanism to promote coexistence. In Mediterranean cereal fields and pasture communities, for instance, this probably even plays a role within the same guild of annual plants with autumn germination and winter development. Here, low seed-longevity species such as *Agrostemma githago* and *Nigella damascena* coexist with long seed-longevity species *Adonis flammea* and *Carthamus lanatus* (Saatkamp *et al.*, 2009, 2010). Figure 11.3 shows how plants with transient and persistent seed banks can coexist through a competition–colonization trade-off. In many cases of coexisting plants with different seed bank strategies, examination of the entire plant life histories will reveal that contrasting
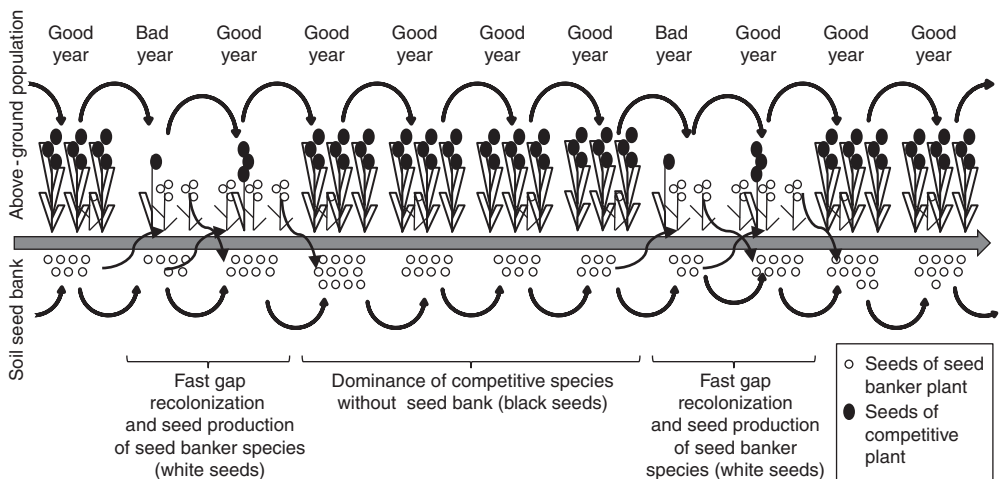

Fig. 11.3. Competition–colonization trade-off in plant communities: coexistence of a subordinate plant with a competitive plant is possible through a persistent soil seed bank of the subordinate with drought adaptation and gap detection mechanism leading to high reproduction of the subordinate in unfavourable years with less dominance of the competitive plant.

plant regeneration strategies are correlated to other (adult) plant traits, because selective interactions lead to trade-offs among risk-reducing mechanisms (Venable and Brown, 1988), and here 'storage effect' increases the possibilities of long-term coexistence (Chesson and Warner, 1981; Facelli *et al.*, 2005; Angert *et al.*, 2009).

Other communities with plants having apparently similar ecological niches and contrasting seed bank strategies include shorelines, with large bunches of sedges (*Carex*) having persistent soil seed banks (Schütz, 2000), but reed canary-grass (*Phalaris arundinacea*) or reed (*Phragmites australis*) most often having transient soil seed banks (Thompson *et al.* 1997). Similar contrasts exist among forest floor herbs with persistent-seeded *Moehringia trinervia* (Vandelook *et al.,* 2008) but transient-seeded *Oxalis acetosella* (Thompson *et al.* 1997; Thompson, 2000). These two species have similar height, seed size and dispersal type, and one might argue that *O. acetosella* is a specialist of humid acidic organic soil, a perennial, and *M. trinervia,* an annual plant on wind-blown, bare mineral soil. The latter habitat has sufficiently unpredictable conditions to evolve persistent seed banks while in the former habitat buried seed would suffer from heavy fungi attack to prevent evolution of a persistent seed bank (Brown and Venable, 1991; Schafer and Kotanen, 2003; Wagner and Mitschunas, 2008; Pakeman *et al.*, 2012). The cited examples show that soil seed banks contribute to coexistence either as a part of the storage effect or as an adaptation that increases niche partition between different microhabitats.

Disturbance, succession and soil seed banks

Whatever the reasons are for the coexistence of species with contrasting soil seed banks, disturbances will not equally affect the recovery of plant populations from transient compared to persistent soil seed banks (van der Valk and Pederson, 1989; Bakker *et al.*, 1996; von Blanckenhagen and Poschlod,

2005; Bossuyt and Honnay, 2008). Plant communities also differ in the abundance of viable seeds in soil banks, and therefore the success of restoration from them varies significantly (Venable, 1989; Bekker *et al.*, 1998c; Hopfensberger, 2007; Bossuyt and Honnay, 2008). Moreover, even plants with notoriously persistent seed banks depend crucially on time since land-use change to recover (Poschlod *et al.*, 1998; Waldhardt *et al.*, 2001; Mitlacher *et al.*, 2002). The recurrent picture from dozens of works on resemblance of soil seed bank and plant communities is that frequently disturbed ecosystems or habitats with unpredictable conditions, such as arable fields, ruderal habitats, river floodplains, deserts, arid pastures and vernal pools have a high resemblance between standing vegetation and seed banks and that relatively low disturbance systems such as heathlands, mires, humid pastures, shrublands and (especially) ancient or old grown forests have comparative lower resemblance (reviewed in Hopfensberger, 2007; Thompson and Grime, 1979; Falinska, 1999; Amiaud and Touzard, 2004; Luzuriaga *et al.*, 2005; Wellstein *et al.*, 2007). In the very open habitats of Mediterranean matorral on gypsum soils, secondary dispersal of seeds leads to rapid local recovery of soil seed banks (Olano *et al.*, 2012). These studies suggest a trade-off between seed persistence in the soil and adult lifespan, which was predicted by theoretical works (Rees, 1994), with short-living species relying on persistent soil seed banks in contrast to long-living species (Ehrlén and van Groenendal, 1998). Consequently, the recovery of communities after disturbances is habitat specific (Bossuyt and Honnay, 2008) and even more, it is site specific due to subtle variation in species composition and local adaptation of plants to form soil seed banks (Clauss and Venable, 2000; Tielbörger and Petru, 2008; Baldwin *et al.*, 2010).

This picture is completed by the temporal sequence of plants in many vegetation types after disturbances, which shows a trend of early successional species having more persistent soil seed banks than late

successional species (Grime, 1977, 1989; Thompson and Grime, 1979; Garwood, 1989; Butler and Chazdon, 1998; Grandin, 2001; Hopfensberger, 2007). The very difference of primary and secondary succession in plant communities lies in the relative importance of seed dispersal for primary succession (Walker *et al.*, 1986; Jumpponen *et al.*, 1999), and on persistent seed banks at least at the beginning for secondary succession (Jiménez and Armesto, 1992; Bekker *et al.*, 2000). But even for primary succession a higher importance of persistent seed banks in early compared to late stages has been shown (Marcante *et al.*, 2009; but see Grandin and Rydin, 1998; Bossuyt and Hermy, 2004). This can be seen as indirect evidence for the trade-off between spatial and temporal dispersal, which, to date, has strong theoretical (Venable and Lawlor, 1980; Venable and Brown, 1988) but still weak empirical (Ozinga *et al.*, 2007) support, and needs to be tested at the relevant temporal and spacial scales.

Persistent soil seed banks, restoration and extinction risk

Persistent seed banks have clear relevance for the restoration of plant communities. It has been shown for several communities that persistent soil seed banks are an important tool to restore local plant communities after abandonment of human use, fire, or diverse forms of direct destruction of above-ground vegetation (van der Valk and Pederson, 1989; Bakker *et al.*, 1996; Willems and Bik, 1998; von Blanckenhagen and Poschlod, 2005; Bossuyt and Honnay, 2008). As summarized above, even within communities, plants differ in their life history strategies including their dependence on persistent soil seed banks. Only plants with persistent seed banks will recover spontaneously from soil seed banks if unfavourable conditions lasted until the second subsequent germination season. Moreover, later successional species, which only regenerate when a minimum cover of vegetation already exists, will only be able to restore by later seed arrival; thus, persistent soil seed

banks can only restore a part of the community (Kiefer and Poschlod, 1996; Bekker *et al.*, 1997; Matus *et al.*, 2003; Buisson *et al.*, 2006; Valkó *et al.*, 2011; summarized by Bossuyt and Honnay, 2008; but see Bossuyt and Hermy, 2004). Many of the most endangered species do not have persistent soil seed banks. Conversely, plant populations that can be restored from persistent seed banks are often widespread or invasive species (Bossuyt and Honnay, 2008). Only in exceptional cases is restoration from seed banks effective for rare or threatened species (Poschlod, 1996; Zehm *et al.*, 2008). This seems to be the case even when local communities remain intact but are fragmented (Stöcklin and Fischer, 1999). Persistence of seeds in the soil is an important trait related to the risk of extinction of plant species (Poschlod *et al.*, 1996) since it is indicative of a spatiotemporal strategy a given species explored in its recent evolutionary history. However, the existence of a soil seed bank does not necessarily indicate its complete independence from spatial dispersal as illustrates the work of Harrison and Ray (2002) on fragmentation of vernal pool species in California.

Seedling recruitment from seed banks and species identity

Composition and abundance of species in the soil seed bank are not directly translated into adult plant communities through germination and seedling recruitment. As previously discussed, small seeds have higher mortality during seedling establishment (Moles and Westoby, 2004); this results in lower representation of small-seeded species as seedlings than could be expected from their abundance in the soil seed bank. Additionally, the importance of recruitment from seeds compared to resprouting or lateral growth from outside the gap has been shown to depend on gap size (Milberg, 1993; Dalling and Hubbell, 2002; Kalamees and Zobel, 2002). Species that regenerate in tropical forest gaps germinate in response to red/far-red light ratios, water potential and diurnal fluctuating temperatures (Pearson *et al.*, 2003; Daws *et al.*, 2008). In large tropical forest gaps, large seeds germinate faster and in

drier conditions than small seeds, which are more specific to moist conditions of small gaps and near the edges, decreasing the drought risk (Daws *et al.*, 2008). However in other situations the distance to dispersing adult trees or seedling mortality/growth rates are more important for the identity of seedlings that establish in gaps (Dalling and Hubbell, 2002). Also, during the growth of crops, the changing light quality decreases germination of some weed species, leading to variable emergence in relation to crop age and density (Kruk *et al.*, 2006).

The timing of disturbances or gap creation is a second crucial factor that influences which species are recruited from the seed bank into gaps (Lavorel *et al.*, 1994; Pakeman *et al.*, 2005). This timing can be related to differences in seed availability, favouring persistent seeds when there is no seed rain (Pakeman *et al.*, 2005) or sorting species composition according to germination temperature requirements of involved species (Baskin and Baskin, 1998; Kruk *et al.*, 2006; Merritt *et al.*, 2007). Another factor that importantly impedes a direct relation between soil seed-bank composition and newly established plant communities is seed and seedling predation (Forget *et al.*, 2005).

Beyond the many filters, the recovery of species composition and abundance from soil seed banks depends in yet unpredictable fashions (Lavorel and Lebreton, 1992) on site history (Dupouey *et al.*, 2002), seed rain (Cubiña and Aide, 2001; Buisson *et al.*, 2006; Jakobsson *et al.*, 2006) and secondary dispersal (Luzuriaga *et al.*, 2005; Olano *et al.*, 2012). It has yet to be explored whether and how much stochasticity plays a role in recruitment from soil seed banks and whether above-ground communities are connected to soil seed banks as local communities are to regional species pools or metacommunities and their abundance and distance relationships (Zobel, 1997; Hubbell, 2001).

Seed banks, invasive species and climate change

Non-native, invasive species often have a large persistent soil seed bank (Newsome and Noble, 1986; Lonsdale *et al.*, 1988; D'Antonio and Meyerson, 2002). In some cases, they assemble a much larger seed bank in their new than in their native ranges (Noble, 1989). Even if they are still rare in the above-ground vegetation they already may have accumulated seeds in the soil (Drake, 1998). Therefore, restoration of native plant communities with a large number of persistent seeds of invasive plants may be impossible since the newly established vegetation would be dominated by the invasive, non-native species. This is especially the case in Mediterranean climate ecosystems such as those in South Africa (Holmes and Cowling, 1997a,b; Heelemann *et al.*, 2012) or Australia (Lunt, 1990) with major implications for restoration management (Richardson and Kluge, 2008; Heelemann *et al.*, 2012). Seed bank longevity data are critical for the management of invasive plants, because invasives with no or short-term persistent seed banks may be eliminated with only a few years of conscientious removal.

Climate change may affect soil seed bank persistence and composition in manifold ways (also reviewed in Chapter 9 of this volume). Warming may increase seed production and therefore, the input to the soil seed bank (Molau and Shaver, 1997; Totland, 1999; see also Akinola *et al.*, 1998a,b). In contrast, drought may also decrease seed production (Peñuelas *et al.*, 2004). In other cases, seed production may remain unchanged despite warmer temperatures and higher precipitation (Wookey *et al.*, 1995). Changes in precipitation will affect soil moisture and as a consequence seed persistence (Walck *et al.*, 2011), because soil moisture has important influences on fungal activity (Leishman *et al.*, 2000a; Blaney and Kotanen, 2001; Wagner and Mitschunas, 2008). Changes in temperature and soil moisture due to precipitation also change the dormancy state of buried seed populations, and in this way affect soil seed-bank composition (Walck *et al.*, 2011). Lastly, atmospheric CO_2 enrichment may affect seed traits and as a consequence soil seed longevity (Grünzweig and Dumbur, 2012). These works show that the directions of

changes in soil seed banks in response to climate change depend on species, traits and factors involved and cannot be generalized at the moment.

Dynamics and Mechanisms in Soil Seed Banks

Formation of persistent soil seed banks is part of a plant's strategy in habitats with variability in rainfall, drought, flooding, vegetation gaps, disturbances or frost. Additionally, soil and climate conditions, disperser and predator communities or competitors also differ among sites and influence the survival of seed in the soil. Consequently, which traits increase seed survival in soil depends on ecosystem and species. This makes it difficult to predict features of soil seed banks from plant functional traits. Moreover, across species, only a few models for soil seed-bank dynamics exist, all to our knowledge for weeds in temperate ecosystems (Forcella, 1993, 1998; Rasmussen and Holst, 2003; Meyer and Allen, 2009; Gardarin *et al.*, 2012).

One of the mechanisms that may contribute to the persistence of seeds beyond the first possible germination season is dormancy (also reviewed in Chapter 7 of this volume). Evolutionary models often refer to 'dormancy' to speak about seeds that 'did not germinate' but are still alive and able to germinate in the future. This is not perfectly congruent with the physiological definition of dormancy which means the inability to germinate in otherwise favourable conditions in which non-dormant seeds would germinate (Baskin and Baskin, 1998; Finch-Savage and Leubner-Metzger, 2006). The delay in germination treated in these evolutionary models can be realized through different mechanisms: any dormancy mechanism, such as physical or physiological dormancy (Baskin and Baskin, 1998), underdeveloped embryos (Finch-Savage and Leubner-Metzger, 2006), delayed dispersal (Cowling and Lamont, 1985; Schwilk and Ackerly, 2001), light sensitivity cycling (Thanos and Georghiou, 1988), specific temperature and moisture

requirements (Finch-Savage and Leubner-Metzger, 2006) or sensitivity to fluctuating temperatures (Thompson and Grime, 1983; Saatkamp *et al.*, 2011a; Thompson *et al.*, 1977). Seeds with underdeveloped embryos sometimes show delayed germination and are then called morphological dormant (Baskin and Baskin, 2004). Some physiologists (Carasso *et al.*, 2011) propose to consider them non-dormant, since growth in these seeds is continuous and pre-emergence drought sensitivity appears before radicles emerge (Ali *et al.*, 2007). 'Delayed germination' and some kind of seed persistence can result from seeds being dormant, or from non-dormant seeds not getting the appropriate cues for germination, which makes it very difficult to establish an exact correspondence between dormancy and persistence of seeds in the soil (Thompson *et al.*, 2003).

Another mechanism to maintain viable soil seed banks over several years is to prevent germination in unfavourable seasons through cycling dormancy. Cycling dormancy means that seeds come out of dormancy and re-enter dormancy every year depending on levels of temperature and rainfall (e.g. Baskin *et al.*, 1993; Baskin and Baskin, 1994; reviewed in Baskin and Baskin, 1998). Thus seeds will germinate, depending on the season, either over a large range of conditions (when the following season is favourable for their development) or will germinate under a restricted range or not germinate at all (when the following season is unfavourable). Plants with different dormancy cycling coexist. Figure 11.4 shows two species with cycling dormancy, a winter annual (*Lamium purpureum*, Fig. 11.4c) and a spring annual (*Polygonum aviculare*, Fig. 4b), which are dormant in winter/spring (*L. purpureum*) or summer/autumn (*P. aviculare*). Similar seasonal cycling schemes are also known for seed coat permeability in the form of sensitivity cycling of physically dormant seeds (Jayasuriya *et al.*, 2008) and for light requirements (Thanos and Georghiou, 1988). The functional role of dormancy cycling is to maximize fitness by matching the germination to seasons with optimal seedling development. Contrastingly, in some plants like Saguaro
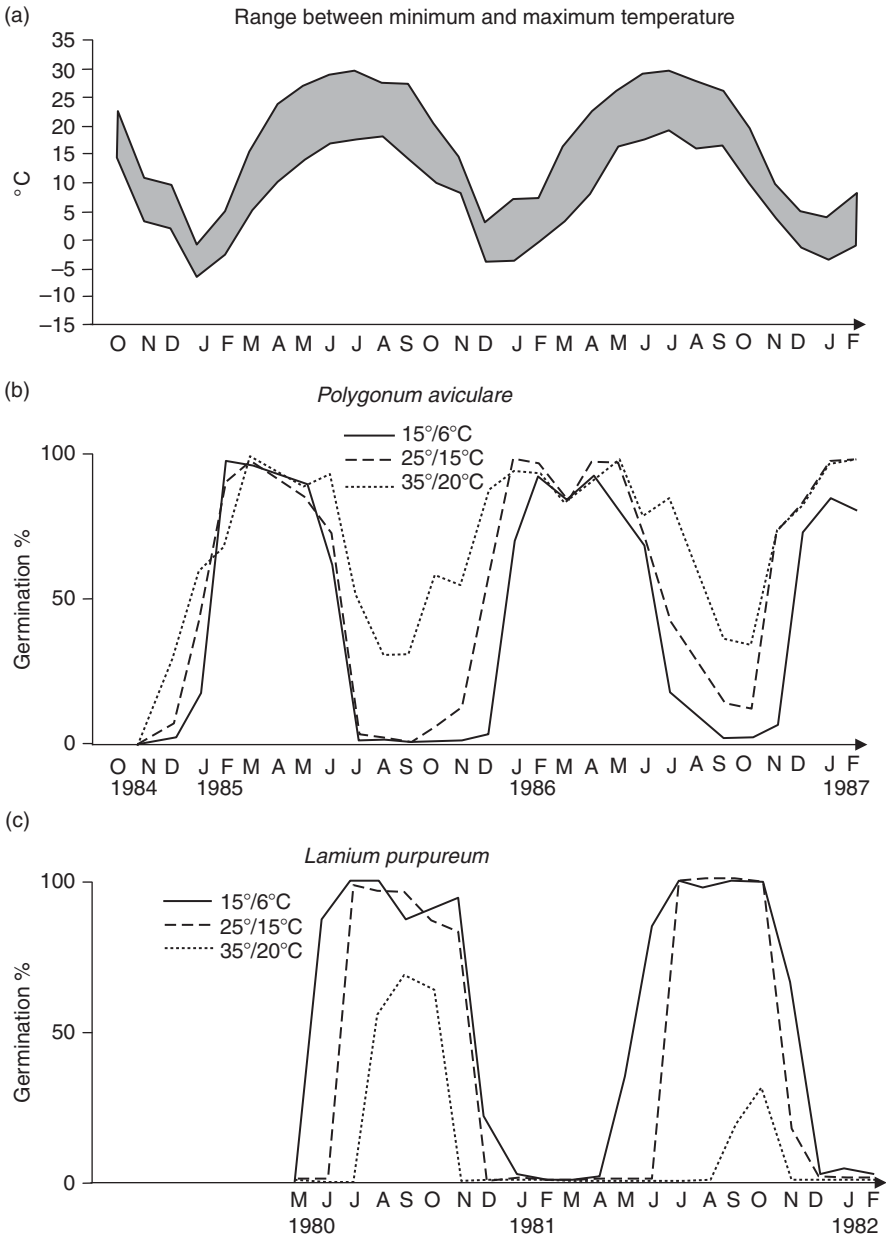
Fig. 11.4. (a) Temperature ranges in temperate regions. (b) and (c) dormancy cycles of *Polygonum aviculare* (b), a summer annual and *Lamium purpureum* (c), a winter annual; with variable germination percentages in three growth chamber conditions, seeds lots were exposed to seasonal varying temperatures (redrawn from data in Baskin and Baskin, 1984, 1990).

cactus (*Carnegia gigantean*) and Boojum (*Fouquieria columnaris*) all seeds germinate at the first opportunity or die, and they do not need dormancy cycling. Interestingly, cycling dormancy is a necessary correlate of persistent seed banks, because all species with physiological dormancy for which dormancy cycles could be studied and

which thus persisted more than one year in the experiments show dormancy cycles (Baskin and Baskin, 1998).

Mechanisms to maintain persistent soil seed banks and the traits that correlate with seed persistence may vary according to global climatic characteristics, and we will illustrate two contrasting situations in the following. Benvenuti (2007) studied how seeds with contrasting traits are buried by rain during seed-bank formation on bare soils in temperate arable land. In this case, small seeds with round shape and with smooth or alveolar surfaces are buried deeper and faster. Once buried, seed populations can be prevented from germination through a light requirement for germination (Pons, 1991; Milberg *et al.*, 2000; Saatkamp *et al.*, 2011b; Chapter 5 of this volume), detection of fluctuating temperatures (Thompson and Grime, 1983; Saatkamp *et al.*, 2011a,b), or oxygen concentrations (Benech-Arnold *et al.*, 2006). For small seeds, rapid burial also prevents predation by soil surface invertebrates and by birds, while large seeds can be dug out by rodents (Hulme, 1998a,b). Earthworms digest small seeds more easily than large ones (Forey *et al.*, 2011). In moist soils, fungi attack seeds, especially when in high density (Van Mourik *et al.*, 2005) or when organic matter content is high (Pakeman *et al.*, 2012). Seeds may differ in susceptibility to fungal attack depending on seed coat thickness (Davis *et al.*, 2008; Gardarin *et al.*, 2010) and phenolic content (Thompson, 2000; Davis *et al.*, 2008). Many seeds show cycling dormancy in response to annual temperature changes defining specific germination seasons (Baskin and Baskin, 1985, 1994, 1995, 2006; Baskin *et al.*, 1986). Cycling dormancy leads to higher depletion of soil seed reservoirs during the germination season compared to unfavourable seasons when plants die as seedlings after germination and before they could emerge at the soil surface (Saatkamp *et al.*, 2011a; Gardarin *et al.*, 2012). Desiccation sensitivity of buried seeds also changes with time after burial and can be a secondary source of mortality (Ali *et al.*, 2007). When disturbances expose non-dormant seeds from the soil bank to light and when the progress to germination depending on temperature and moisture is sufficient (Bradford, 2002; Allen *et al.*, 2007), seeds germinate and leave the soil seed bank. This picture is drawn from temperate herbaceous communities where seeds remain in the imbibed state in the soil. Here, seed persistence in the soil can be related to smaller seed size, rounder shape, light requirements for germination, seed coat thickness and high phenol content.

In contrast to moist temperate ecosystems, in arid regions, such as Australia, fungi attack is less important and predator communities are different, in such a way that larger seeds have higher survival in the soil than small seeds (Moles *et al.*, 2003; Moles and Westoby, 2006). The difference in the relation between seed size and persistence between Australian arid areas and moist temperate areas can partly be explained by different methods that have been used to measure persistence or seed survival (Saatkamp *et al.*, 2009). In arid and semiarid climates, many species have conspicuous self-burial mechanisms such as hygroscopic appendages in *Erodium* or *Aristida*. Other plants germinate in response to chemical cues, such as smoke-derived substances from vegetation fires (Brown, 1993; Flematti *et al.*, 2004), and their absence keeps large seed reservoirs in an ungerminated state. Annual plants are comparatively rare in Australia, except in seasonally wet habitats (Brock, 2011) and longevity of seeds of woody species is lower due to the alternative risk reduction mechanism of longer lifespan (Rees, 1994, 1996; Tuljapurkar and Wiener, 2000; Campbell *et al.*, 2012). Seeds with thick impermeable seed coats with physical dormancy are common in many fire-prone arid ecosystems, and thought to have evolved in dry areas (Baskin *et al.*, 2000). Arid soil seed banks also show many seeds that germinate better in darkness than in light (Baker, 1972; Baskin and Baskin, 1998), thus germinating more easily in soil than at its surface, probably because the risk of seedling death due to drought is lower when emergence starts in deeper soil layers. The contrast between seed-bank dynamics in moist temperate and dry warm regions

shows that soil seed persistence traits need to be considered in relation to a specific environment. In order to generalize this knowledge we need to study trait–environment interactions in sufficiently contrasted situations.

The understanding of soil seed banks of weeds has motivated researchers to model the dynamics of soil seed banks (Forcella, 1998; Rasmussen and Holst, 2003; Meyer and Allen, 2009; FLORSYS by Gardarin *et al.*, 2012). They brought to light that we need to model independently the processes of germination, dormancy and 'suicide germination' (Benvenuti *et al.*, 2001) compared to other processes such as mortality due to ageing, decay or predation (Gardarin *et al.*, 2012). In these models, different plant traits are used to predict mortality (before germination) and germination, the first has been related to seed coat thickness (Gardarin *et al.*, 2010), whereas the latter to base parameters of hydrothermal time models (Bradford, 2002; Allen *et al.*, 2007). These models do not include postdispersal seed predation nor do they distinguish between seed ageing and seed decay (although FLORSYS does include mortality parameters explicitly). At least for the target species, these models predict with some accuracy abundance of seed populations in soils, their movement, dormancy state, date of germination and number of seedlings emerging (Gardarin *et al.*, 2012). Limits of these models are the high number of input parameters – sometimes difficult to measure – and the difficulties of using them with other species and in other ecosystems.
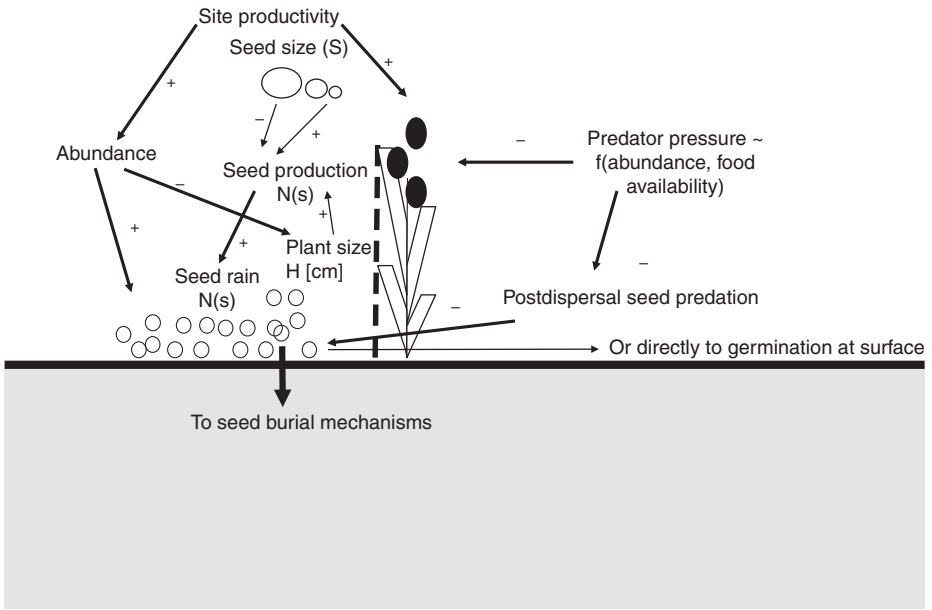
Figure 11.5 summarizes some of the processes and traits involved in soil seed-bank dynamics in temperate ecosystems. Three main processes for the exit of seeds from the soil seed bank differ in the traits that influence persistence and adaptations: (i) germination; (ii) mortality due to ageing; or (iii) mortality due to predation including microbial or fungi attack. Traits that relate to germination do not specifically reduce mortality of seeds: for example, small embryos, high levels of abscisic acid or light requirement prevent or delay germination but do not necessarily reduce predation.

Enzymes that neutralize reactive oxygen species also do not necessarily influence predation nor germination, although when oxidated they can break dormancy (Bahin *et al.*, 2011). Although Davis *et al.* (2008) concluded that ortho-dihydroxyphenols did not influence germination or ageing, but may be effective compounds for defences against microbes and fungi, Chapter 8 of this volume points out some methodological and interpretive problems associated with studies that focus on this class of phenolic compounds. It is not yet clear whether thick or impermeable seed coats influence germination as much as they influence predation, because most impermeable seed coats have specialized structures that control germination independently from coat thickness (Baskin, 2003). Moreover thick seed coats are related to larger size and hence forces of growing embryos (Mohr *et al.*, 2010). Likewise, small seed size enhances burial speed and reduces germination (for species with a light requirement) and predation (by surface-feeding animals) but for digestion by earthworms small size is disadvantageous (Forey *et al.*, 2011). These effects are independent from the higher number in which small seeds are produced, which independently results in a higher probability of seeds surviving. It is thus helpful to distinguish between effects of reproduction (seed number) and survival (individually) in our endeavour to understand how soil seed banks are influenced by adaptive traits in a series of environments.

Acknowledgements

(a) Seed input: seed production and postdispersal seed predation

Site productivity
Seed size (S)

Abundance

+

−

+

Seed production
N(s)

+

Plant size
H [cm]

Seed rain
N(s)

+

+

+

−

−

Predator pressure ~
f(abundance, food
availability)

−

Postdispersal seed predation

−

Or directly to germination at surface

To seed burial mechanisms

(b) Burial mechanisms and movement inside the soil profile

Rain

Seed size (S)

+

Disturbances

+

+

Seed rain
N(s)

Soil turbation:
wet−dry cycling forms cracks that
bury bulky seed slower and less
deep than rounded
(Burmeier *et al.*, 2010)

Burial speed
(D/t)

Actual
depth
of a seed
D [cm]

Burial by animals:
ants and small mammals bury seeds
with large seed size

Seed movement in the soil
changes depth of burial (D)

Burial depth (D) and speed (D/t) by rain
depends on seed size (S), seed surface
type (sF) and seed shape (X) (Benvenuti,
2003)

D/t ~ -S, sF, -X

and infuenced by clay content
S ~ -f(S) , clay content
(Benvenuti, 2003)

Earthworms have a specific seed
size spectrum, that they ingest and
transport, they digest small seeds
(Forey *et al.*, 2011)

Below ground viable seed
population (S_B)

To germination (G)
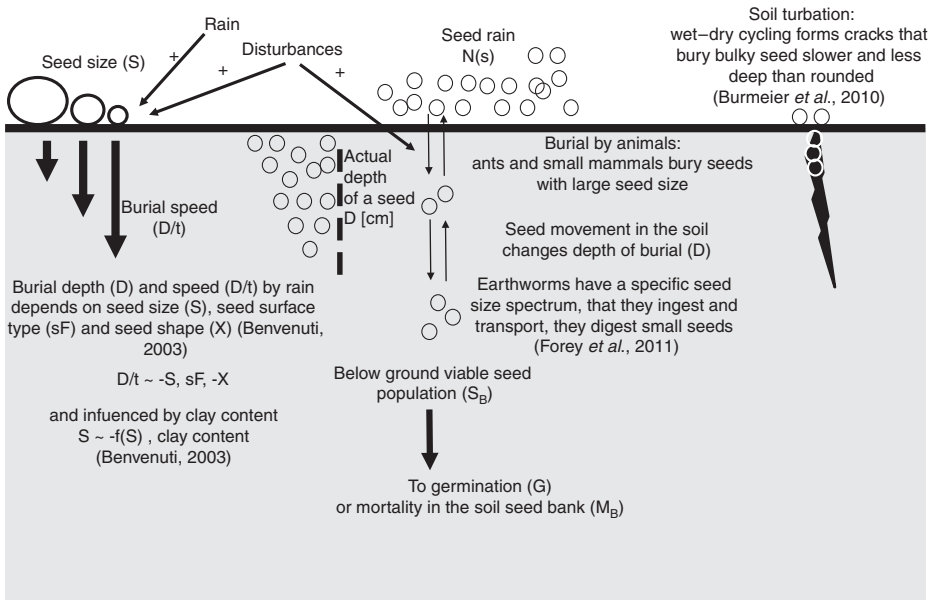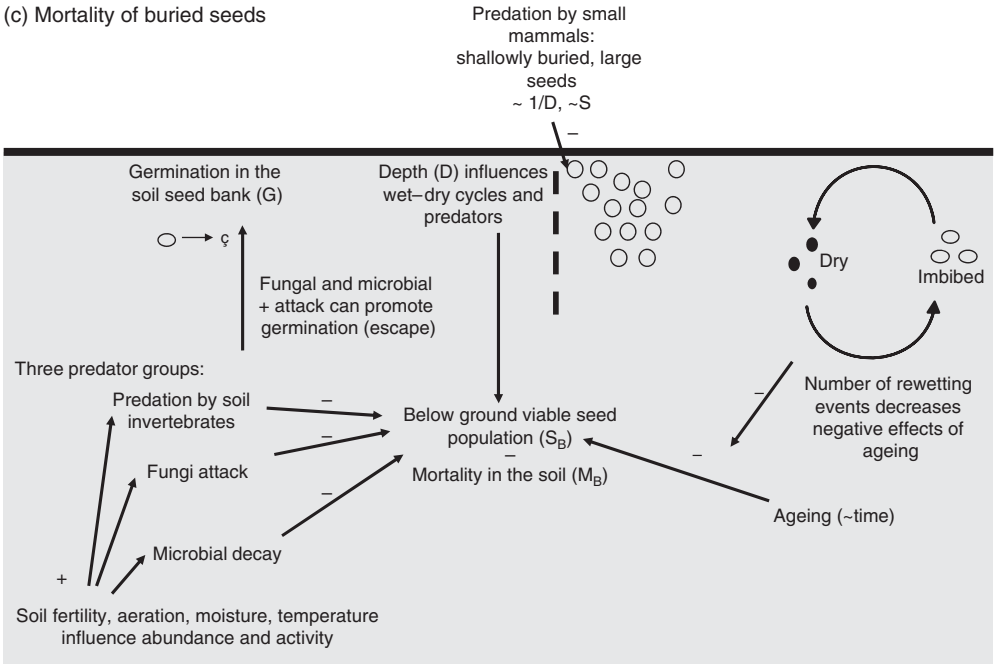or mortality in the soil seed bank (M_B)

Fig. 11.5. Soil seed-bank dynamic model, with input, dormancy cycle, movement and output in three different ways, germination, death due to ageing and death due to mortality or fungi attack and the allied sets of traits and environmental influence factors (modified from Allen *et al.*, 2007; Saatkamp *et al.*, 2011b and Gardarin *et al.*, 2012).

(c) Mortality of buried seeds

Predation by small mammals: shallowly buried, large seeds ~ 1/D, ~S

−

Germination in the soil seed bank (G)

Depth (D) influences wet–dry cycles and predators

ç

Fungal and microbial + attack can promote germination (escape)

Dry

Imbibed

Three predator groups:

Predation by soil invertebrates

−

Below ground viable seed population (S_B)

−

Mortality in the soil (M_B)

−

Fungi attack

−

−

Number of rewetting events decreases negative effects of ageing

Ageing (~time)

Microbial decay

+

Soil fertility, aeration, moisture, temperature influence abundance and activity

(d) Dormancy cycling, germination and gap detection

Dry

Imbibed

Actual depth of a seed D [cm]

ç

ç

To seedling fate and emergence

Germination cues light , light quality diurnally fluctuating temperatures (DFT), chemical compounds: nitrates,'smoke', oxygen, age of seeds

Temperature, water potential, exposure time

If optimal

Below ground viable seed population (S_B)

-

Germination in the soil seed bank (G) as a function of temperature and moisture (hydrothermal time)

Non-dormant

Dormant

Number and duration of wet–dry cycles depend on soil type, climate and burial depth:

$$\frac{dt \text{ imbibed}}{dt \text{ dry}} \sim D$$

Germination (G) is negatively related to depth (D) according to their reaction to diurnally fluctuating temperatures (DFT) or oxygen requirement (OR)
G · -f(D) ~ DFT,OR
and infuenced by clay content
G · -f(D) ~ clay content
(Saatkamp *et al.*, 2011a; Benvenuti, 2003)

If out of range
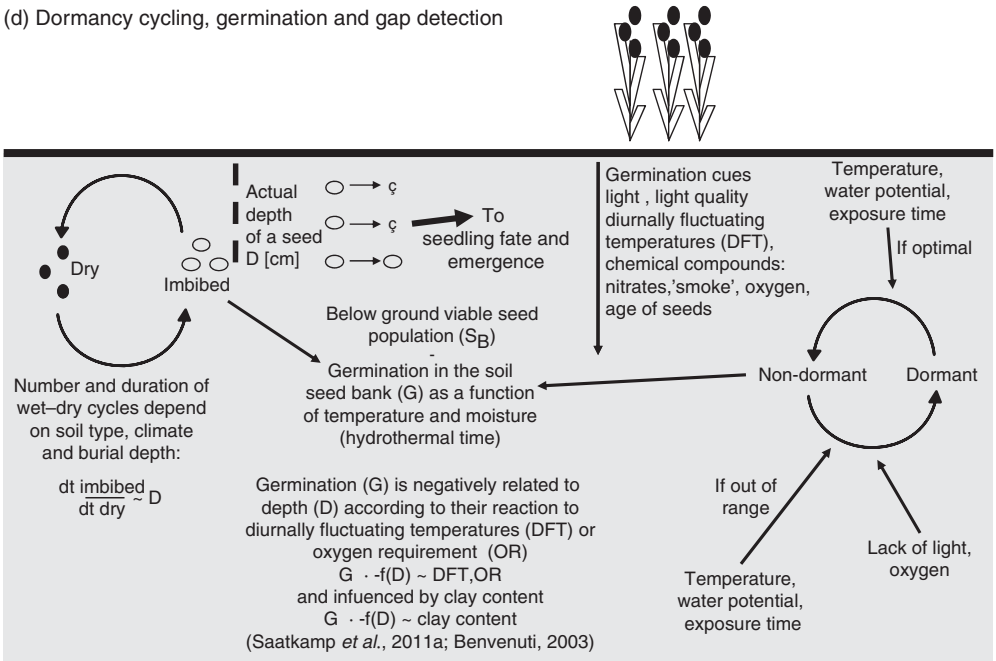
Temperature, water potential, exposure time

Lack of light, oxygen

Fig. 11.5. Continued.

(e) Seedling fate and emergence in the soil: effects of burial depth (D) and seed mass (S)

Postemergence seedling mortality (M_{ES}) is related to seed size (S), drought (dr) and herbivore pressure (he)

$$M_{ES} \sim -S \cdot dr + he$$

(Moles and Westoby, 2006; Leishman *et al.*, 2000a)

Seedling mortality

M_{ES}

Seedlings in the soil seed bank (Se)

Actual depth of a seed D [cm]

M_{PE}

DE_{max}

Seed mass (S)

Dry

Imbibed

Number and duration of wet–dry cycles depend on soil type, weather and burial depth:

$$\frac{dt\ imbibed}{dt\ dry} \sim D$$

Pre-emergence mortality (MPE): seedlings die if $DE_{max} < D$ and if dry before emergence (Gardarin *et al.*, 2012)

Maximum depth of emergence (DE_{max}) depends on seed mass (S):

$$DE_{max} = 27 \cdot S^{0.0334}$$

for sand: Bond *et al.*, 1999

Delay of emergence (dE) depends on actual burial depth (D):

$$dE = 1.43 \cdot D$$

for silt-loam, after data in Benvenuti *et al.*, 2001, and depends on temperature and moisture

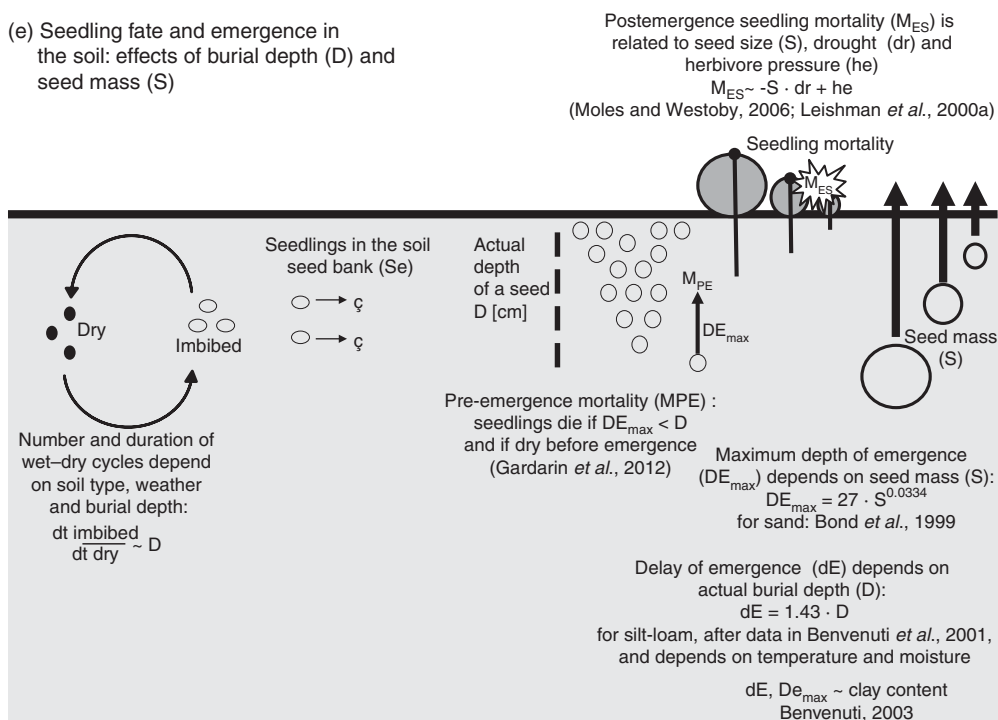$$dE, De_{max} \sim clay\ content$$

Benvenuti, 2003

Fig. 11.5. Continued.

References

Aarssen, L.W. and Jordan, C.Y. (2001) Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Ecoscience* 8, 471–477.

Akinola, M.O., Thompson, K. and Buckland, S.M. (1998a) Soil seed bank of an upland calcareous grassland after 6 years of climate and management manipulations. *Journal of Applied Ecology* 35, 544–552.

Akinola, M.O., Thompson, K. and Hillier, S.H. (1998b) Development of soil seed banks beneath synthesized meadow communities after seven years of climate manipulations. *Seed Science Research* 8, 493–500.

Ali, N., Probert, R., Hay, F., Davies, H. and Stuppy, W. (2007) Post-dispersal embryo growth and acquisition of desiccation tolerance in *Anemone nemorosa* L. seeds. *Seed Science Research* 17, 155–163.

Allen, P.S., Benech-Arnold, R.L., Batlla, D. and Bradford, K.J. (2007) Modeling of seed dormancy. In: Bradford, K.J. and Nonogaki, H. (eds) *Annual Plant Reviews Volume 27: Seed Development, Dormancy and Germination*. Wiley-Blackwell, Oxford, pp. 72–112.

Amiaud, B. and Touzard, B. (2004) The relationships between soil seed bank, aboveground vegetation and disturbances in old embanked marshlands of Western France. *Flora* 199, 25–35.

Angert, A.L., Huxman, T.E., Chesson, P. and Venable, D.L. (2009) Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences* 106, 11641–11645.

Bahin, E., Bailly, C., Sotta, B., Kranner, I., Corbineau, F. and Leymarie, J. (2011) Crosstalk between reactive oxygen species and hormonal signalling pathways regulates grain dormancy in barley. *Plant Cell and Environment* 34, 980–993.

Baker, H.G. (1972) Seed weight in relation to environmental conditions in California. *Ecology* 53, 997–1010.

Bakker, J.P. (1989) *Nature Management by Grazing and Cutting: on the Ecological Significance of Grazing and Cutting Regimes Applied to Restore Former Species-Rich Grassland Communities in the Netherlands*. Kluwer Academic Publishers, Denmark.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. and Thompson, K. (1996) Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* 45, 461–490.

Baldwin, A.H., Kettenring, K.M. and Whigham, D.F. (2010) Seed banks of *Phragmites australis*-dominated brackish wetlands: Relationships to seed viability, inundation, and land cover. *Aquatic Botany* 93, 163–169.

Baskin, C.C. (2003) Breaking physical dormancy in seeds – focussing on the lens. *New Phytologist* 158, 229–232.

Baskin, C.C. and Baskin, J.M. (1994) Germination requirements of *Oenothera biennis* seeds during burial under natural seasonal temperature cycles. *Canadian Journal of Botany* 72, 779–782.

Baskin, C.C. and Baskin, J.M. (1998) *Seeds: ecology, biogeography and evolution of dormancy and germination*. Academic Press, San Diego.

Baskin, C.C. and Baskin, J.M. (2006) The natural history of soil seed banks of arable land. *Weed Science* 54, 549–557.

Baskin, C.C., Chesson, P.L. and Baskin, J.M. (1993) Annual seed dormancy cycles in two desert winter annuals. *Journal of Ecology* 81, 551–556.

Baskin, J.M. and Baskin, C.C. (1984) Role of temperature in regulating timing of germination in soil seed reserves of *Lamium purpureum* L. *Weed Science* 24, 341–349.

Baskin, J.M. and Baskin, C.C. (1985) The annual dormancy cycle in buried weed seeds: a continuum. *BioScience* 35, 492–498.

Baskin, J.M. and Baskin, C.C. (1990) The role of light and alternating temperatures on germination of *Polygonum aviculare* seeds exhumed on various dates. *Weed Research* 30, 397–402.

Baskin, J.M. and Baskin, C.C. (1995) Variation in the annual dormancy cycle in buried seeds of the weedy winter annual *Viola arvensis. Weed Science* 35, 353–362.

Baskin, J.M. and Baskin, C.C. (2004) A classification system for seed dormancy. *Seed Science Research* 14, 1–16.

Baskin, J.M., Baskin, C.C. and Parr, J.C. (1986) Field emergence of *Lamium amplexicaule* L. and *L. purpureum* L. in relation to the annual seed dormancy cycle. *Weed Science* 26, 185–190.

Baskin, J.M., Baskin, C.C. and Xiaojie, L. (2000) Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology* 15, 139–152.

Bekker, R.M., Verweij, G.L., Smith, R.E.N., Reine, R., Bakker, J.P. and Schneider, S. (1997) Soil seed banks in European grasslands: does land use affect regeneration perspectives? *Journal of Applied Ecology* 34, 1293–1310.

Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. and Willems, J.H. (1998a) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology* 12, 834–842.

Bekker, R.M., Knevel, I.C., Tallowin, J.B.R., Troost, E.M.L. and Bakker, J.P. (1998b) Soil nutrient input effects on seed longevity: a burial experiment with fen meadow species. *Functional Ecology* 12, 673.

Bekker, R.M., Schaminée, J.H.J., Bakker, J.P. and Thompson, K. (1998c) Seed bank characteristics of Dutch plant communities. *Acta Botanica Neerlandica* 47, 15–26.

Bekker, R.M., Verweij, G.L., Bakker, J.P. and Fresco, L.F.M. (2000) Soil seed bank dynamics in hayfield succession. *Journal of Ecology* 88, 594–607.

Benech-Arnold, R.L., Sánchez, R.A., Forcella, F., Kruk, B.C. and Ghersa, C.M. (2000) Environmental control of dormancy in weed seed banks in soil. *Field Crops Research* 67, 105–122.

Benech-Arnold, R.L., Gualano, N., Leymarie, J., Côme, D. and Corbineau, F. (2006) Hypoxia interferes with ABA metabolism and increases ABA sensitivity in embryos of dormant barley grains. *Journal of Experimental Botany* 57, 1423–1430.

Benoit, D., Kenkel, N.C. and Cavers, P.B. (1989) Factors influencing the precision of soil seed bank estimates. *Canadian Journal of Botany* 67, 2833–2840.

Benvenuti, S. (2003) Soil texture involvement in germination and emergence of buried weed seeds. *Agronomy Journal* 95, 191–198.

Benvenuti, S. (2007) Natural weed seed burial: effect of soil texture, rain and seed characteristics. *Seed Science Research* 17, 211–219.

Benvenuti, S., Macchia, M. and Miele, S. (2001) Quantitative analysis of emergence of seedlings from buried weed seeds with increasing soil depth. *Weed Science* 49, 528–535.

Blaney, C.S. and Kotanen, P.M. (2001) Effects of fungal pathogens on seeds of native and exotic plants: a test using congeneric pairs. *Journal of Applied Ecology* 38, 1104–1113.

Boedeltje, G., Bakker, J.P., Ten Brinke, A., van Groenendael, J.M. and Soesbergen, M. (2004) Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. *Journal of Ecology* 92, 786–796.

Bond, W.J., Honig, M. and Maze, K.E. (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. *Oecologia* 120, 132–136.

Bonnewell, V., Koukkari, W.L. and Pratt, D.C. (1983) Light, oxygen, and temperature requirements for *Typha latifolia* seed germination. *Canadian Journal of Botany* 61, 1330–1336.

Bossuyt, B. and Hermy, M. (2004) Seed bank assembly follows vegetation succession in dune slacks. *Journal of Vegetation Science* 15, 449–456.

Bossuyt, B. and Honnay, O. (2008) Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science* 19, 875–884.

Bradford, K.J. (2002) Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Science* 50, 248–260.

Brock, M.A. (2011) Persistence of seed banks in Australian temporary wetlands. *Freshwater Biology* 56, 1312–1327.

Brown, J.S. and Venable, D.L. (1991) Life history evolution of seed-bank annuals in response to seed predation. *Evolutionary Ecology* 5, 12–29.

Brown, N.A.C. (1993) Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytologist* 123, 575–583.

Bruun, H.H. and Poschlod, P. (2006) Why are small seeds dispersed through animal guts: large numbers or seed size per se? *Oikos* 113, 402–411.

Buisson, E., Dutoit, T., Torre, F., Römermann, C. and Poschlod, P. (2006) The implications of seed rain and seed bank patterns for plant succession at the edges of abandoned fields in Mediterranean landscapes. *Agriculture Ecosystems & Environment* 115, 6–14.

Bulmer, M.G. (1984) Delayed germination of seeds: Cohen's model revisited. *Theoretical Population Biology* 26, 367–377.

Burmeier, S., Eckstein, R.L., Otte, A. and Donath, T.W. (2010) Desiccation cracks act as natural seed traps in flood-meadow systems. *Plant and Soil* 333, 351–364.

Butler, B.J. and Chazdon, R.L. (1998) Species richness, spatial variation, and abundance of the soil seed bank of a secondary tropical rain forest. *Biotropica* 30, 214–222.

Butler, M.A. and King, A.A. (2004) Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *American Naturalist* 164, 683–695.

Campbell, M.L., Clarke, P.J. and Keith, D.A. (2012) Seed traits and seed bank longevity of wet sclerophyll forest shrubs. *Australian Journal of Botany* 60, 96–103.

Carasso, V., Hay, F.R., Probert, R.J. and Mucciarelli, M. (2011) Temperature control of seed germination in *Fritillaria tubiformis* subsp. *moggridgei* (Liliaceae) a rare endemic of the South-west Alps. *Seed Science Research* 21, 33–38.

Cavieres, L.A. and Arroyo, M.T.K. (2001) Persistent soil seed banks in *Phacelia secunda* (Hydrophyllaceae): experimental detection of variation along an altitudinal gradient in the Andes of Central Chile. *Journal of Ecology* 89, 31–39.

Chesson, P.L. and Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117, 923–943.

Clauss, M.J. and Venable, D.L. (2000) Seed germination in desert annuals: an empirical test of adaptive bet hedging. *American Naturalist* 155, 168–186.

Cohen, D. (1966) Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12, 119–129.

Cohen, D. (1967) Optimizing reproduction in a randomly varying environment, when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *Journal of Theoretical Biology* 16, 1–14.

Cowling, R.M. and Lamont, B.B. (1985) Variation in serotiny of three *Banksia* species along a climatic gradient. *Australian Journal of Ecology* 10, 345–350.

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.

Csontos, P. and Tamás, J. (2003) Comparisons of soil seed bank classification systems. *Seed Science Research* 13, 101–111.

Cubiña, A. and Aide, T.M. (2001) The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica* 33, 260–267.

Curry, J.P. (2004) Factors affecting the abundance of earthworms in soils. In: Edwards, A.C. (ed.) *Earthworm Ecology*. CRC Press, Boca Raton, pp. 91–113.

Dalling, J.W. and Hubbell, S.P. (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology* 90, 557–568.

Dalling, J.W., Swaine, M.D. and Garwood, N.C. (1998) Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* 79, 564–578.

D'Antonio, C. and Meyerson, L.A. (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology* 10, 703–713.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life*, 1st edn. Murray.

Davis, A.S., Schutte, B.J., Iannuzzi, J. and Renner, K.A. (2008) Chemical and physical defense of weed seeds in relation to soil seedbank persistence. *Weed Science* 56, 676–684.

Daws, M.I., Crabtree, L.M., Dalling, J.W., Mullins, C.E. and Burslem, D.F.R.P. (2008) Germination responses to water potential in neotropical pioneers suggest large-seeded species take more risks. *Annals of Botany* 102, 945–951.

De Luis, M., Verdù, M. and Raventós, J. (2008) Early to rise makes a plant healthy, wealthy, and wise. *Ecology* 89, 3061–3071.

Dessaint, F., Chadoeuf, R. and Barralis, G. (1991) Spatial pattern analysis of weed seeds in the cultivated soil seed bank. *Journal of Applied Ecology* 28, 721.

Donohue, K. (2005) Seeds and seasons: interpreting germination timing in the field. *Seed Science Research* 15, 175–187.

Donohue, K. (2009) Completing the cycle: maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, 1059–1074.

Donohue, K., Dorn, L., Griffith, C., Kim, E., Aguilera, A., Polisetty, C.R. and Schmitt, J. (2005) Environmental and genetic influences on the germination of *Arabidopsis thaliana* in the field. *Evolution* 59, 740–757.

Drake, D. (1998) Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *Journal of Vegetation Science* 9, 103–112.

Dupouey, J.L., Dambrine, E., Laffite, J.D. and Moares, C. (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83, 2978–2984.

Duvel, J.W.T. (1902) Seeds buried in soil. *Science* 17, 872–873.

Dyer, A.R., Fenech, A. and Rice, K.J. (2000) Accelerated seedling emergence in interspecific competitive neighbourhoods. *Ecology Letters* 3, 523–529.

Eberhart, A. and Tielbörger, K. (2012) Maternal fecundity does not affect offspring germination – an empirical test of the sibling competition hypothesis. *Journal of Arid Environments* 76, 23–29.

Ehrlén, J. and van Groenendal, J.M. (1998) The trade-off between dispersability and longevity – an important aspect of plant species diversity. *Applied Vegetation Science* 1, 29–36.

Ellner, S. (1985a) ESS germination strategies in randomly varying environments. I. Logistic-type models. *Theoretical Population Biology* 28, 50–79.

Ellner, S. (1985b) ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. *Theoretical Population Biology* 28, 80–116.

Ellner, S. (1986) Germination dimorphisms and parent offspring conflict in seed-germination. *Journal of Theoretical Biology* 123, 173–185.

Ellner, S. (1987) Competition and dormancy: a reanalysis and review. *American Naturalist* 130, 798–803.

Evans, M.E.K. and Dennehy, J.J. (2005) Germ banking: bet-hedging and variable release from egg and seed dormancy. *The Quarterly Review of Biology* 80, 431–451.

Evans, M.E.K., Hearn, D.J., Hahn, W.J., Spangle, J.M. and Venable, D.L. (2005) Climate and life-history evolution in evening primroses (*Oenothera*, Onagraceae): a phylogenetic comparative analysis. *Evolution* 59, 1914–1927.

Facelli, J.M., Chesson, P.L. and Barnes, N. (2005) Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. *Ecology* 86, 2998–3006.

Falinska, K. (1999) Seed bank dynamics in abandoned meadows during a 20-year period in the Bialowieza National Park. *Journal of Ecology* 87, 461–475.

Fenner, M. (1985) *Seed Ecology*. Chapman and Hall, London and New York.

Finch-Savage, W.E. and Leubner-Metzger, G. (2006) Seed dormancy and the control of germination. *New Phytologist* 171, 501–523.

Flematti, G.R., Ghisalberti, E.L., Dixon, K.W. and Trengove, R.D. (2004) A compound from smoke that promotes seed germination. *Science* 305, 977.

Flynn, S., Turner, R.M. and Dickie, J.B. (2004) Seed Information Database (release 6.0, October 2004) http://www.rbgkew.org.uk/data/sid. Kew Botanical Gardens.

Forcella, F. (1993) Seedling emergence model for Velvetleaf (*Abutilon theophrasti*). *Agronomy Journal* 85, 929–933.

Forcella, F. (1998) Real-time assessment of seed dormancy and seedling growth for weed management. *Seed Science Research* 8, 201–210.

Forey, E., Barot, S., Decaëns, T., Langlois, E., Laossi, K.R., Margerie, P., Scheu, S. and Eisenhauer, N. (2011) Importance of earthworm-seed interactions for the composition and structure of plant communities: A review. *Acta Oecologica* 37, 594–603.

Forget, P.M., Lambert, J.E., Hulme, P.E. and Vander Wall, S.B. (2005) *Seed Fate: Predation, Dispersal and Seedling Establishment*. CAB International, Wallingford, UK.

Fowler, N.L. (1984) The role of germination date, spatial arrangement, and neighbourhood effects in competitive interactions in *Linum. The Journal of Ecology* 307–318.

Funes, G., Basconcelo, S., Díaz, S. and Cabido, M. (2007) Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. *Seed Science Research* 9, 341–345.

Gardarin, A., Dürr, C., Mannino, M.R., Busset, H. and Colbach, N. (2010) Seed mortality in the soil is related to seed coat thickness. *Seed Science Research* 20, 243–256.

Gardarin, A., Dürr, C. and Colbach, N. (2012) Modeling the dynamics and emergence of a multispecies weed seed bank with species traits. *Ecological Modelling* 240, 123–138.

Garwood, N.C. (1989) Tropical soil seed bank: a review. In: Leck, M.A., Parker, V.T. and Simpson, R.L. (eds) *Ecology of Soil Seed Banks*. London Academic Press, London, pp. 149–209.

Ghersa, C.M., Arnold, R.L.B. and Martinez-Ghersa, M.A. (1992) The role of fluctuating temperatures in germination and establishment of *Sorghum halepense* – regulation of germination at increasing depths. *Functional Ecology* 6, 460–468.

Grandin, U. (2001) Short-term and long-term variation in seed bank/vegetation relations along an environmental and successional gradient. *Ecography* 24, 731–741.

Grandin, U. and Rydin, H. (1998) Attributes of the seed bank after a century of primary succession on islands in Lake Hjälmaren, Sweden. *Journal of Ecology* 86, 293–303.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111, 1169–1194.

Grime, J.P. (1989) Seed banks in ecological perspective. In: Leck, M.A., Parker, V.T. and Simpson, R.L. (eds) *Ecology of Soil Seed Banks*. London Academic Press, London, pp. xv-xxii.

Grundy, A.C., Mead, A. and Burston, S. (2003) Modelling the emergence response of weed seeds to burial depth: interactions with seed density, weight and shape. *Journal of Applied Ecology* 40, 757–770.

Grünzweig, J.M. and Dumbur, R. (2012) Seed traits, seed-reserve utilization and offspring performance across pre-industrial to future CO_2 concentrations in a Mediterranean community. *Oikos* 121, 579–588.

Guttermann, Y. (2000) Maternal effects on seeds during development. In: Fenner, M. (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, UK, pp. 59–84.

Gutterman, Y. (2002) *Survival Strategies of Annual Desert Plants*. Springer, New York.

Harrison, S. and Ray, C. (2002) Plant population viability and metapopulation-level processes. In: Beissinger, S. and McCullough, D.R. (eds) *Population Viability Analysis*. University of Chicago Press, Chicago, pp. 109–122.

Heelemann, S., Krug, C.B., Esler, K.J., Reisch, C. and Poschlod, P. (2012) Pioneers and perches - promising restoration methods for degraded Renosterveld habitats? *Restoration Ecology* 20, 18–23.

Hendricks, S.B. and Taylorson, R.B. (1974) Promotion of seed germination by nitrate, nitrite, hydroxylamine, and ammonium salts. *Plant Physiology* 54, 304–309.

Henery, M.L. and Westoby, M. (2001) Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* 92, 479–490.

Holmes, P.M. and Cowling, R.M. (1997a) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrubland. *Plant Ecology* 133, 107–122.

Holmes, P.M. and Cowling, R.M. (1997b) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *Journal of Applied Ecology* 4, 317–332.

Holmes, P.M. and Newton, R.J. (2004) Patterns of seed persistence in South African fynbos. *Plant Ecology* 172, 143–158.

Hopfensberger, K. (2007) A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos* 116, 1438–1448.

Horton, T.R. and Van Der Heijden, M.G.A. (2008) The role of symbioses in seedling establishment and survival. *Seedling Ecology & Evolution* 189–213.

Huang, X., Schmitt, J., Dorn, L., Griffith, C., Effgen, S., Takao, S., Koorneef, M. and Donohue, K. (2010) The earliest stages of adaptation in an experimental plant population: strong selection on QTLS for seed dormancy. *Molecular Ecology* 19, 1335–1351.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.

Hulme, P.E. (1994) Post-dispersal seed predation in grassland: its magnitude and sources of variation. *Journal of Ecology* 82, 645–652.

Hulme, P.E. (1998a) Post-dispersal seed predation and seed bank persistence. *Seed Science Research* 8, 513–519.

Hulme, P.E. (1998b) Post-dispersal seed predation: consequences for plant demography and evolution. *Perspectives in Plant Ecology, Evolution and Systematics* 1, 32–46.

Hyatt, L.A. and Evans, A.S. (1998) Is decreased germination fraction associated with risk of sibling competition? *Oikos* 29–35.

Jakobsson, A. and Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88, 494–502.

Jakobsson, A., Eriksson, O. and Bruun, H.H. (2006) Local seed rain and seed bank in a species-rich grassland: effects of plant abundance and seed size. *Canadian Journal of Botany* 84, 1870–1881.

Jankowska-Blaszczuk, M. and Daws, M.I. (2007) Impact of red: far red ratios on germination of temperate forest herbs in relation to shade tolerance, seed mass and persistence in the soil. *Functional Ecology* 21, 1055–1062.

Jayasuriya, K.M.G.G., Baskin, J.M. and Baskin, C.C. (2008) Cycling of sensitivity to physical dormancy-break in seeds of *Ipomoea lacunosa* (Convolvulaceae) and ecological significance. *Annals of Botany* 101, 341–352.

Jiménez, H.E. and Armesto, J.J. (1992) Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. *Journal of Vegetation Science* 3, 579–586.

Jones, R.H. and Sharitz, R.R. (1989) Potential advantages and disadvantages of germinating early for trees in floodplain forests. *Oecologia* 81, 443–449.

Jumpponen, A., Vöre, H., Mattson, K.G., Ohtonen, R. and Trappe, J.M. (1999) Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain. *Journal of Ecology* 87, 98–105.

Jurado, E. and Flores, J. (2005) Is seed dormancy under environmental control or bound to plant traits? *Journal of Vegetation Science* 16, 559–564.

Kalamees, R. and Zobel, M. (2002) The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology* 83, 1017–1025.

Keeley, J.E. (1987) Role of fire in seed-germination of woody taxa in California chaparral. *Ecology* 68, 434–443.

Kelly, M.G. and Levin, D.A. (1997) Fitness consequences and heritability aspects of emergence date in *Phlox drummondii*. *Journal of Ecology* 755–766.

Kettenring, K.M., Gardner, G.M. and Galatowitsch, S.M. (2006) Effect of light on seed germination of eight wetland *Carex* species. *Annals of Botany* 98, 869–874.

Kiefer, S. and Poschlod, P. (1996) Restoration of fallow or afforested calcareous grasslands by clear-cutting. In: *Species Survival in Fragmented Landscapes*. Kluwer, Dordrecht, pp. 209–218.

Kiewnick, L. (1964) Untersuchungen über den Einfluss der Samen-und Bodenmikroflora auf die Lebensdauer der Spelzfrüchte des Flughafers (*Avena fatua* L.). *Weed Research* 4, 31–43.

Kluth, C. and Bruelheide, H. (2005) Effects of range position, inter-annual variation and density on demographic transition rates of *Hornungia petraea* populations. *Oecologia* 145, 382–393.

Koprdová, S., Saska, P., Honek, A. and Martinková, Z. (2010) Seed consumption by millipedes. *Pedobiologia* 54, 31–36.

Kruk, B., Insausti, P., Razul, A. and Benech-Arnold, R.L. (2006) Light and thermal environments as modified by a wheat crop: effects on weed seed germination. *Journal of Applied Ecology* 43, 227–236.

Kubitzki, K. and Ziburski, A. (1994) Seed dispersal in flood plain forests of Amazonia. *Biotropica* 30–43.

Lalonde, R.G. and Roitberg, B.D. (2006) Chaotic dynamics can select for long-term dormancy. *American Naturalist* 168, 127–131.

Lavorel, S. and Lebreton, J.D. (1992) Evidence for lottery recruitment in Mediterranean old fields. *Journal of Vegetation Science* 3, 91–100.

Lavorel, S., Lepart, J., Debussche, M., Lebreton, J.D. and Beffy, J.L. (1994) Small scale disturbances and the maintenance of species diversity in Mediterranean old fields. *Oikos* 70, 455–473.

Leck, M.A., Parker, T.V. and Simpson, R.L. (1989) *Ecology of Soil Seed Banks*. London Academic Press, London.

Leishman, M.R., Masters, G.J., Clarke, I.P. and Brown, V.K. (2000a) Seed bank dynamics: the role of fungal pathogens and climate change. *Functional Ecology* 14, 293–299.

Leishman, M.R., Wright, I.J., Moles, A.T. and Westoby, M. (2000b) The evolutionary ecology of seed size. In: Fenner, M. (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*. CABI, Wallingford.

Lonsdale, W.M., Harley, K.L.S. and Gillett, J.D. (1988) Seed bank dynamics in *Mimosa pigra*, an invasive tropical shrub. *Journal of Applied Ecology* 25, 963–976.

Lundberg, S., Nilsson, P. and Fagerström, T. (1996) Seed dormancy and frequency dependent selection due to sib competition: the effect of age specific gene expression. *Journal of Theoretical Biology* 183, 9–17.

Lunt, I.D. (1990) The soil seed bank of a long-grazed *Themeda triandra* grassland in Victoria (Australia). *Proceedings of the Royal Society of Victoria* 102, 53–58.

Luzuriaga, A.L., Escudero, A., Olano, J.M. and Loidi, J. (2005) Regenerative role of seed banks following an intense soil disturbance. *Acta Oecologica* 27, 57–66.

Maas, D. (1987) Keimungsansprüche von Streuwiesenpflanzen und deren Auswirkung auf das Samenpotential. PhD thesis, Technical University of Munich.

Marcante, S., Schwienbacher, E. and Erschbamer, B. (2009) Genesis of a soil seed bank on a primary succession in the Central Alps (Ötztal, Austria). *Flora* 204, 434–444.

Marks, M. and Prince, S. (1981) Influence of germination date on survival and fecundity in wild lettuce *Lactuca serriola*. *Oikos* 326–330.

Matus, G., Verhagen, R., Bekker, R.M. and Grootjans, A.P. (2003) Restoration of the Cirsio dissecti-Molinietum in The Netherlands: Can we rely on soil seed banks? *Applied Vegetation Science* 6, 73–84.

Menalled, F.D., Marino, P.C., Renner, K.A. and Landis, D.A. (2000) Post-dispersal weed seed predation in Michigan crop fields as a function of agricultural landscape structure. *Agriculture, Ecosystems & Environment* 77, 193–202.

Merritt, D.J., Turner, S.R., Clarke, S. and Dixon, K.W. (2007) Seed dormancy and germination stimulation syndromes for Australian temperate species. *Australian Journal of Botany* 55, 336–344.

Meyer, S.E. and Allen, P.S. (2009) Predicting seed dormancy loss and germination timing for *Bromus tectorum* in a semi-arid environment using hydrothermal time models. *Seed Science Research* 19, 225–239.

Milberg, P. (1993) Seed bank and seedlings emerging after soil disturbance in a wet semi-natural grassland in Sweden. *Annales Botanici Fennici* 30, 9–03.

Milberg, P. and Andersson, L. (1997) Seasonal variation in dormancy and light sensitivity in buried seeds of eight annual weed species. *Canadian Journal of Botany* 75, 1998–2004.

Milberg, P., Andersson, L. and Thompson, K. (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Science Research* 10, 99–104.

Mitlacher, K., Poschlod, P., Rosén, E. and Bakker, J.P. (2002) Restoration of wooded meadows-a comparative analysis along a chronosequence on Öland (Sweden). *Applied Vegetation Science* 5, 63–73.

Mohr, H., Schopfer, P., Lawlor, G. and Lawlor, D.W. (2010) *Plant Physiology*. Springer.

Molau, U. and Shaver, G.R. (1997) Controls on seed production and seed germinability in *Eriophorum vaginatum. Global Change Biology* 3, 80–88.

Moles, A.T. and Westoby, M. (2002) Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos* 99, 241–248.

Moles, A.T. and Westoby, M. (2004) Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92, 372–383.

Moles, A.T. and Westoby, M. (2006) Seed size and plant strategy across the whole life cycle. *Oikos* 113, 91–105.

Moles, A.T., Hodson, D.W. and Webb, C.J. (2000) Seed size and persistence in the soil in the New Zealand flora. *Oikos* 89, 679–685.

Moles, A.T., Warton, D.I. and Westoby, M. (2003) Seed size and survival in the soil in arid Australia. *Austral Ecology* 28, 575–585.

Morinaga, T. (1926) The favorable effect of reduced oxygen supply upon the germination of certain seeds. *American Journal of Botany* 159–166.

Morozowska, M., Czarna, A., Kujawa, M. and Jagodzinski, A.M. (2011) Seed morphology and endosperm structure of selected species of Primulaceae, Myrsinaceae, and Theophrastaceae and their systematic importance. *Plant Systematics and Evolution* 291, 159–172.

Newsome, A.E. and Noble, I.R. (1986) Ecological and physiological characters of invading species. In: Groves, R.H. and Burdon, J.J. (eds) *Ecology of Biological Invasions: an Australian Perspective*. Cambridge University Press, New York, pp. 1–20.

Nilsson, P., Fagerström, T., Tuomi, J. and Åström, M. (1994) Does seed dormancy benefit the mother plant by reducing sib competition? *Evolutionary Ecology* 8, 422–430.

Noble, I.R. (1989) Attributes of invaders and the invading process: terrestrial and vascular plants. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, B., Rejmanek, M. and Williamson, M. (eds) *Biological Invasions: a Global Perspective*. Wiley & Sons, New York, pp. 301.

Olano, J.M., Caballero, I. and Escudero, A. (2012) Soil seed bank recovery occurs more rapidly than expected in semi-arid Mediterranean gypsum vegetation. *Annals of Botany* 109, 299–307.

Ortega, M., Levassor, C. and Peco, B. (1997) Seasonal dynamics of Mediterranean pasture seed banks along environmental gradients. *Journal of Biogeography* 24, 177–195.

Ozinga, W.A., Hennekens, S.M., Schaminée, J.H.J., Smits, N.A.C., Bekker, R.M., Romermann, C., Klimes, L., Bakker, J.P. and van Groenendael, J.M. (2007) Local above-ground persistence of vascular plants: Life-history trade-offs and environmental constraints. *Journal of Vegetation Science* 18, 489–497.

Pake, C.E. and Venable, D.L. (1995) Is coexistence of Sonoran desert annuals mediated by temporal variability in reproductive success? *Ecology* 76, 246–261.

Pakeman, R.J., Small, J.L. and Wilson, J.B. (2005) The role of the seed bank, seed rain and the timing of disturbance in gap regeneration. *Journal of Vegetation Science* 16, 121–130.

Pakeman, R.J., Small, J.L. and Torvell, L. (2012) Edaphic factors influence the longevity of seeds in the soil. *Plant Ecology* 213, 57–65.

Pearson, T.R.H., Burslem, D.F.R.P., Mullins, C.E. and Dalling, J.W. (2003) Functional significance of photoblastic germination in neotropical pioneer trees: a seed's eye view. *Functional Ecology* 17, 394–402.

Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M. and Terradas, J. (2004) Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist* 161, 837–846.

Philippi, T. (1993) Bet-hedging germination of desert annuals: beyond the first year. *American Naturalist* 474–487.

Pons, T.L. (1991) Induction of dark dormancy in seeds – its importance for the seed bank in the soil. *Functional Ecology* 5, 669–675.

Popay, A.I. and Roberts, E.H. (1970) Factors involved in the dormancy and germination of *Capsella bursa-pastoris* (L.) Medik. and *Senecio vulgaris* L. *Journal of Ecology* 58, 103–122.

Poschlod, P. (1995) Diaspore rain and diaspore bank in raised bogs and its implication for the restoration of peat mined sites. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J. and Robertson, R.A. (eds) *Restoration of Temperate Wetlands*. Wiley, Chichester, pp. 471.

Poschlod, P. (1996) Population biology and dynamics of a rare short-lived pond mud plant, *Carex bohemica* Schreber. *Verhandlungen der Gesellschaft für Ökologie* 25, 321–337.

Poschlod, P. and Jackel, A.K. (1993) Untersuchungen zur Dynamik von generativen Diasporenbanken von Samenpflanzen in Kalkmagerrasen. I. Jahreszeitliche Dynamik des Diasporenregens und der Diasporenbank auf zwei Kalkmagerrasenstandorten der Schwäbischen Alb. *Flora* 188, 49–71.

Poschlod, P., Fischer, S. and Kiefer, S. (1996) A coenotical approach of plant population viability analysis on successional and afforested calcareous grassland sites. In: Settele, J., Margules, C., Poschlod, P. and Henle, K. (eds) *Species Survival in Fragmented Landscapes.* Kluwer, Dordrecht, pp. 219–228.

Poschlod, P., Kiefer, S., Tränkle, U., Fischer, S.F. and Bonn, S. (1998) Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Applied Vegetation Science* 1, 75–90.

Priestley, D.A. (1986) *Seed aging – implications for seed storage and persistence in the soil.* Comstock Publishing, New York.

Rasmussen, I.A. and Holst, N. (2003) Computer model for simulating the long-term dynamics of annual weeds: from seedlings to seeds. *Aspects of Applied Biology* 277–284.

Rees, M. (1994) Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist* 43–64.

Rees, M. (1996) Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society of London, Series B* 351, 1299–1308.

Richardson, D.M. and Kluge, R.L. (2008) Seedbanks of invasive Australian Acacia species in South Africa: Role in invasiveness and options for management. *Perspectives in Plant Ecology, Evolution and Systematics* 10, 161–177.

Roberts, H.A. (1986) Seed persistence in soil and seasonal emergence in plant species from different habitats. *Journal of Applied Ecology* 23, 639–656.

Ross, M.A. and Harper, J.L. (1972) Occupation of biological space during seedling establishment. *The Journal of Ecology* 77–88.

Saatkamp, A., Affre, L., Dutoit, T. and Poschlod, P. (2009) The seed bank longevity index revisited: limited reliability evident from a burial experiment and database analyses. *Annals of Botany* 104, 715–724.

Saatkamp, A., Römermann, C. and Dutoit, T. (2010) Plant functional traits show non-linear response to grazing. *Folia Geobotanica* 45, 239–252.

Saatkamp, A., Affre, L., Baumberger, T., Dumas, P.J., Gasmi, A., Gachet, S. and Arène, F. (2011a) Soil depth detection by seeds and diurnally fluctuating temperatures: different dynamics in 10 annual plants. *Plant and Soil* 349, 331–340.

Saatkamp, A., Affre, L., Dutoit, T. and Poschlod, P. (2011b) Germination traits explain soil seed persistence across species: the case of Mediterranean annual plants in cereal fields. *Annals of Botany* 107, 415.

Saska, P. (2008) Granivory in terrestrial isopods. *Ecological Entomology* 33, 742–747.

Satterthwaite, W.H. (2009) Competition for space can drive the evolution of dormancy in a temporally invariant environment. *Plant Ecology* 208, 167–185.

Schafer, M. and Kotanen, P.M. (2003) The influence of soil moisture on losses of buried seeds to fungi. *Acta Oecologica* 24, 255–263.

Schnürer, J., Clarholm, M. and Rosswall, T. (1985) Microbial biomass and activity in an agricultural soil with different organic matter contents. *Soil Biology and Biochemistry* 17, 611–618.

Schütz, W. (2000) Ecology of seed dormancy and germination in sedges (*Carex*). *Perspectives in Plant Ecology, Evolution and Systematics* 3, 67–89.

Schwilk, D.W. and Ackerly, D.D. (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94, 326–336.

Shen-Miller, J. (2002) Sacred lotus, the long-living fruits of China Antique. *Seed Science Research* 12, 131–144.

Shumway, D.L. and Koide, R.T. (1994) Preferences of *Lumbricus terrestris* L. *Applied Soil Ecology* 1, 11–15.

Silvertown, J. (1988) The demographic and evolutionary consequences of seed dormancy. In: Davy, A.J., Hutchings, M.J. and Watkinson, A.R. (eds) *Plant population ecology*. Blackwell, London.

Silvertown, J. (1999) Seed ecology, dormancy and germination: a modern synthesis from Baskin and Baskin. *American Journal of Botany* 86, 903–905.

Smith, C.C. and Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist* 499–506.

Snyder, R.E. (2006) Multiple risk reduction mechanisms: can dormancy substitute for dispersal? *Ecology Letters* 9, 1106–1114.

Soons, M.B., van der Vlugt, C., van Lith, B., Heil, G.W. and Klaassen, M. (2008) Small seed size increases the potential for dispersal of wetland plants by ducks. *Journal of Ecology* 96, 619–627.

Stöcklin, J. and Fischer, M. (1999) Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950-1985. *Oecologia* 120, 539–543.

Thanos, C.A. and Georghiou, K. (1988) On the mechanism of skotodormancy induction in grand rapids lettuce (*Lactuca sativa* L) Seeds. *Journal of Plant Physiology* 133, 580–584.

Thanos, C.A., Georghiou, K., Kadis, C. and Pantazi, C. (1992) Cistaceae – a plant family with hard seeds. *Israel Journal of Botany* 41, 251–263.

Thompson, K. (1986) Small-scale heterogeneity in the seed bank of an acidic grassland. *Journal of Ecology* 74, 733–738.

Thompson, K. (2000) The functional ecology of seed banks. In: Fenner, M. (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, UK, pp. 215–235.

Thompson, K. and Fenner, M. (1992) The functional ecology of seed banks. In: Fenner, M. (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, UK, pp. 231–258.

Thompson, K. and Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67, 893–921.

Thompson, K. and Grime, J.P. (1983) A comparative study of germination responses to diurnally fluctuating temperatures. *Journal of Applied Ecology* 20, 141–156.

Thompson, K., Grime, J.P. and Mason, G. (1977) Seed germination in response to diurnal fluctuations of temperature. *Nature* 267, 147–149.

Thompson, K., Band, S.R. and Hodgson, J.G. (1993) Seed size and shape predict persistence in soil. *Functional Ecology* 7, 236–241.

Thompson, K., Bakker, J.P. and Bekker, R.M. (1997) *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge.

Thompson, K., Ceriani, R.M., Bakker, J.P. and Bekker, R.M. (2003) Are seed dormancy and persistence in soil related? *Seed Science Research* 13, 97–100.

Tielbörger, K. and Petru, M. (2008) Germination behaviour of annual plants under changing climatic conditions: separating local and regional environmental effects. *Oecologia* 155, 717–728.

Tielbörger, K. and Petru, M. (2010) An experimental test for effects of the maternal environment on delayed germination. *Journal of Ecology* 98, 1216–1223.

Tielbörger, K. and Prasse, R. (2009) Do seeds sense each other? Testing for density-dependent germination in desert perennial plants. *Oikos* 118, 792–800.

Tielbörger, K. and Valleriani, A. (2005) Can seeds predict their future? Germination strategies of density-regulated desert annuals. *Oikos* 111, 235–244.

Tielbörger, K., Petru, M. and Lampei, C. (2011) Bet-hedging germination in annual plants: a sound empirical test of the theoretical foundations. *Oikos* 121, 1860–1868.

Tooley, J. and Brust, G.E. (2002) Weed seed predation by carabid beetles. In: *The Agroecology of Carabid Beetles.* pp. 215–229.

Totland, Ø. (1999) Effects of temperature on performance and phenotypic selection on plant traits in alpine *Ranunculus acris. Oecologia* 120, 242–251.

Trudgill, D.L., Honek, A., Li, D. and Straalen, N.M. (2005) Thermal time-concepts and utility. *Annals of Applied Biology* 146, 1–14.

Tuljapurkar, S. and Wiener, P. (2000) Escape in time: stay young or age gracefully? *Ecological Modelling* 133, 143–159.

Turkington, R., Goldberg, D.E., Olsvig-Whittaker, L. and Dyer, A.R. (2005) Effects of density on timing of emergence and its consequences for survival and growth in two communities of annual plants. *Journal of Arid Environments* 61, 377–396.

Valkó, O., Török, P., Tóthmérész, B. and Matus, G. (2011) Restoration potential in seed banks of acidic fen and dry-mesophilous meadows: can restoration be based on local seed banks? *Restoration Ecology* 19, 9–15.

Valleriani, A. and Tielbörger, K. (2006) Effect of age on germination of dormant seeds. *Theoretical Population Biology* 70, 1–9.

van der Valk, A.G. and Pederson, R.L. (1989) Seed banks and the management and restoration of natural vegetation. In: Leck, M.A., Parker, V.T. and Simpson, R.L. (eds) *Ecology of Soil Seed Banks*. London Academic Press, London, pp. 329–346.

Van Mourik, T.A., Stomph, T.J. and Murdoch, A.J. (2005) Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks. *Journal of Applied Ecology* 42, 299–305.

Vandelook, F., Van de Moer, D. and Van Assche, J.A. (2008) Environmental signals for seed germination reflect habitat adaptations in four temperate Caryophyllaceae. *Functional Ecology* 22, 470–478.

Venable, D.L. (1989) Modelling the evolutionary ecology of soil seed banks. In: Leck, M.A., Parker, V.T. and Simpson, R.L. (eds) *Ecology of Soil Seed Banks.* London Academic Press, London, pp. 67–87.

Venable, D.L. (2007) Bet hedging in a guild of desert annuals. *Ecology* 88, 1086–1090.

Venable, D.L. and Brown, J.S. (1988) The selective interaction of dispersal, dormancy and seed size as adaptations for reducing risks in variable environments. *American Naturalist* 131, 360–384.

Venable, D.L. and Lawlor, L. (1980) Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* 46, 272–282.

Verdù, M. and Traveset, A. (2005) Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology* 86, 1385–1394.

Vitalis, R., Rousset, F., Kobayashi, Y., Olivieri, I. and Gandon, S. (2013) The joint evolution of dispersal and dormancy in a metapopulation with local extinctions and kin competition. *Evolution* 67, 1676–1691.

von Blanckenhagen, B. and Poschlod, P. (2005) Restoration of calcareous grasslands: the role of the soil seed bank and seed dispersal for recolonisation processes. *Biotechnology, Agronomy, Society and Environment* 9, 143–149.

Wagner, M. and Mitschunas, N. (2008) Fungal effects on seed bank persistence and potential applications in weed biocontrol a review. *Basic and Applied Ecology* 9, 191–203.

Walck, J.L., Baskin, J.M., Baskin, C.C. and Hidayati, S.N. (2005) Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. *Seed Science Research* 15, 189–196.

Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K. and Poschlod, P. (2011) Climate change and plant regeneration from seed. *Global Change Biology* 17, 2145–2161.

Waldhardt, R., Fuhr-Bossdorf, K. and Otte, A. (2001) The significance of the seed bank as a potential for the reestablishment of arable-land vegetation in a marginal cultivated landscape. *Web Ecology* 2, 83–87.

Walker, L.R., Zasada, J.C. and Chapin III, F.S. (1986) The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* 67, 1243–1253.

Wellstein, C., Otte, A. and Waldhardt, R. (2007) Seed bank diversity in mesic grasslands in relation to vegetation type, management and site conditions. *Journal of Vegetation Science* 18, 153–162.

Westerman, P.R., Hofman, A., Vet, L. and van der Werf, W. (2003) Relative importance of vertebrates and invertebrates in epigeaic weed seed predation in organic cereal fields. *Agriculture, Ecosystems & Environment* 95, 417–425.

Willems, J.H. and Bik, L.P.M. (1998) Restoration of high species density in calcareous grassland: the role of seed rain and soil seed bank. *Applied Vegetation Science* 1, 91–100.

Wookey, P.A., Robinson, C.H., Parsons, A.N., Welker, J.M., Press, M.C., Callaghan, T.V. and Lee, J.A. (1995) Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high Arctic polar semi-desert, Svalbard. *Oecologia* 102, 478–489.

Woolley, J.T. and Stoller, E.W. (1978) Light penetration and light-induced seed germination in soil. *Plant Physiology* 61, 597–600.

Zaller, J.G. and Saxler, N. (2007) Selective vertical seed transport by earthworms: Implications for the diversity of grassland ecosystems. *European Journal of Soil Biology* 43, Supplement 1, S86-S91.

Zammit, C.A. and Zedler, P.H. (1993) Size structure and seed production in even-aged populations of *Ceanothus greggii* in mixed chaparral. *Journal of Ecology* 81, 499–511.

Zehm, A., von Brackel, W. and Mitlacher, K. (2008) Hochgradig bedrohte Strandrasenarten - Artenhilfsprogramm am bayerischen Bodenseeufer unter besonderer Berücksichtung der Diasporenbank. *Naturschutz und Landschaftspflege* 40, 73–80.

Zobel, M. (1997) The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends in Ecology & Evolution* 12, 266–269.