ISSN 1995-4255, Contemporary Problems of Ecology, 2023, Vol. 16, No. 6, pp. 843–855. © Pleiades Publishing, Ltd., 2023.

A Guided Tour of the Soil Seed Banks

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Received May 31, 2023; revised June 16, 2023; accepted June 16, 2023

Abstract—The soil seed bank could be viewed as an optimisation of the chances of plants to meet favourable conditions in time and space. Owing to the large number of publications and the field's complexity, available reviews do not cover the entire field. My objective was to produce a synthesis. Determination of the soil seed bank needs careful planning of sampling because of variations in soil depth and clumped distributions. Sample composition is determined from plantlets coming from germinated seeds after exposure to appropriate conditions or directly from seeds after their separation from soil particles. Seed longevity varies from months to decades and depends on desiccation resistance, defences against predators and germination control, notably dormancy. Dormancy characterization and alleviation factors allow to understand species' strategies in ecosystems. In agricultural soils, weeds challenge future cultures. Research objectives are often to exhaust their seed banks before crop emergence by reducing seed production, inactivating germination, removing weeds before seed maturation, and controlling the harvest. In natural ecosystems, climax species tend to produce shorter-lived seeds compared to pioneered ones. The soil seed bank may help in restoring degraded vegetation but the similarity with the aboveground vegetation is low. Disturbances may increase or decrease the soil seed bank diversity. Restoration may often rely on natural recruitment from undisturbed areas or on artificial translocation. I emphasise the need to integrate soil seed bank knowledge into dynamic vegetation models, which generally lacks most of the soil seed bank features, while the future distribution of the plant species is one of the main questions in this climate change era.

Keywords: soil seedbank, dormancy, weed management, disturbance, restoration, dynamic vegetation model

DOI: 10.1134/S1995425523060100

1. INTRODUCTION

The composition of the soil seed banks, the emergence time of the plants, the proportions of seeds of each species germinating each year and their survival in the soils are extremely variable factors which have important consequences for understanding and predicting ecosystem sustainability and dynamics (community composition, genetic diversity), and for the management of natural (restoration, control of invasive species) and agricultural systems (weed management). The ecological significance of the soil seed bank could be viewed as an optimisation of the chances of the plants to meet favourable conditions in time and space (Long et al., 2015). Indeed, in contrast to seeds germinating in a couple of months following their dispersal, a large proportion of species in the soil seed bank relies on a *bet-hedging strategy*, i.e., the sacrifice of a massive short-term reproductive success in favour of a reduction of long-term risk of population extinction by delaying and spreading germination over many years. This phenomenon also allows the coexistence of species that leave the seed bank in different ways in response to environmental factors (Ma et al., 2021). The field of soil seed bank research is receiving considerable attention and is particularly old since the first report was by Darwin in 1859 (Baskin and Baskin, 2006; Mall and Singh, 2014; Shi et al., 2020). Owing to the large number of publications and the complexity of the field, available reviews focus on particular aspects, and it is not easy to get answers for questions on the main topics in a condensed form. It is the objective of the present work to produce such a synthesis.

2. MATERIALS AND METHODS

A SCOPUS search, on 03 February 2023 with the keyword combination (*soil seed bank*) OR (*soil seedbank*), returned 5.447 references published between 1945 and 2024. I refined my SCOPUS search by adding AND the keyword *review* and keeping only papers published between 2000 and 2023. I found 157 references with abstracts in English. I browsed titles and abstracts, and I extracted those which effectively were general reviews or reviews on other topics but included and examined some aspects of the seed bank, particularly on agricultural soils and forest soils. The reading of those selected references led me to consult a sample of cited papers. I completed with other SCOPUS searches combining (*soil seed bank*) OR (*soil seedbank*) and terms like *grazing*, *fire*, *fragmentation,* or *edge*.

3. RESULTS

3.1. Definition

The soil seed bank (also *seedbank*) is commonly defined as *the natural bank of viable seeds in the soil or on its surface* (Shi et al., 2020). One should consider that it includes non-dispersed seeds still in the fallen fruits, whose metabolism is independent of the mother plant and whether they are dormant or not (Csontos, 2007). At the beginning of the 20th century, one considered *buried seeds*, later *buried viable seeds* and finally the *seed bank* (Shi et al., 2020). But there are differences between the *seed bank* and the *soil seed bank* because seeds can be stored elsewhere than in the soil (Csontos, 2007). In the *aerial seed bank*, seeds can be retained for months to years in fruits or cones on the mother plants, a phenomenon called *serotiny* (Baskin and Baskin, 2014), seeds of epiphytes or parasitic plants fall in cracks of the host plant's bark and can be casually caught in animal's nests in the trees or purposely hidden for instance in trunk holes. In the *aquatic seed bank*, the seeds or the fruits can float for long months before germination. Otherwise, reproductive vegetative structures (tubers, bulbs, rhizomes) may play the same role in the soil as the seeds (Ma et al., 2021; Mall and Singh, 2014).

3.2. Characterization of the Seeds in the Soil Seed Bank

A simple system is described by Bakker et al. (1996a). Since a large proportion of weed seeds germinate or die within 1 to 4 years, this pool was named the *short-term seed bank* and the rest, which survives 5 years or more, *long-term seed bank*. In another system, four types of species, according to their life cycle and survival strategy in the soil seed bank, are distinguished (Thompson and Grime, 1979). The seed bank of a particular species is *transien*t when no seed remains alive for more than one year. The other ones are said to be *persistent*. So, Type I species constitute transient seed banks, and their seeds are released in the late spring or summer and germinate in the cooler moist conditions of the autumn. Type II species are included in transient seed banks with germination delayed to the next spring. Type III species are included in persistent seed banks, but a significant proportion of their seeds behave nevertheless like those of Type I, i.e., germinating directly after dispersal, and Type IV species behave like Type III species, but very few seeds can germinate directly, and the seed banks are large compared to the seed productions. Over the course of several years, a proportion of Type III and Type IV seeds periodically germinate. The behaviour of Type I and II species could be interpreted as an adaptation to colonise vegetation gaps which occur seasonally each year. By contrast, Type IV species may take advantage of unpredictable disturbances provoking vegetation gaps, offering the capacity for vegetation regeneration in the habitats. Type III species have intermediate behaviour between Type I, Type II species and Type IV species.

Most of the flowering plants have desiccation-tolerant seeds, also qualified as *orthodox*, which have a lifespan of years up to millennia. The persistence of the seeds is broadly correlated with tolerance to desiccation and low water content (Berjak and Pammenter, 2008). Those seeds possess specific intracellular mechanisms limiting cell damage induced by water stress to cytoplasm, membranes, and DNA (Long et al., 2015). The orthodox seeds are opposed to the desiccation-sensitive ones, named *recalcitrant*. The recalcitrant seeds remain more metabolically active and hydrated at shedding and after. They do not resist water loss owing to thinner coats, and the embryo has an inherent low ability to sustain desiccation. This condition results in persistence for only days to months, rarely for one or two years for temperate species in the absence of freezing. However, the distinction between orthodox and recalcitrant seeds is not absolute (Berjak and Pammenter, 2008). In addition, the persistence of the seeds in the soil is also conditioned by investments of the plant species in chemical and physical defences of their seeds and by their dormancy. These two features are linked across ecosystem types. Non-dormant seeds often invest less in defences than dormant seeds and remain less time in the seed bank but, nevertheless, could be protected by infestation by non-pathogenic fungi preventing further infections. Also, species with physical dormancy (see below) have stronger physical protections while species with physiological dormancy (see below) contain more toxic chemicals which protect them from predation (Dalling et al., 2020; Davis et al., 2016; Zalamea et al., 2018).

Germination begins with rehydratation and takes place in defined range of temperatures and oxygen concentrations, depending on the species. Some species also require conditions of light or nutrients (Hilhorst and Karssen, 2000; Pons, 2000). If the required conditions are not completed, the seeds are said to be *quiescent* and the germination, as such (radicle emergence), does not occur. If more than 80% of the seeds germinate within 30 days, when tested over a range of environmental conditions, they are qualified as *non-dormant,* and the other ones are qualified as *dormant* (Baskin and Baskin, 2006). As the orthodox seeds, the recalcitrant seeds can become dormant and acquire tolerance to slow desiccation (Farnsworth, 2000). Today, the commonly accepted view is that dormancy break and germination are not separate mechanisms, i.e., that the seeds must be exposed to sequences of environmental conditions of which the last ones allow germination (Long et al., 2015). A classification scheme for seed dormancy in five classes has been proposed (Baskin and Baskin, 2014). In *morphological dormancy*, the embryo is incompletely developed, so it must grow normally for 30 days, before germination, if it becomes possible. In *physiological dormancy*, there is a physiological inhibition of embryo growth. The dormancy break occurs in dry or wet cycling, under warm or cold regimes, under light or darkness or under the influence of chemicals like smoke, ashes, nitrates, or other natural or artificial compounds (Long et al., 2015). Over the course of the exposure, the seeds can become *conditionally dormant*, i.e., that the conditions for their germination become narrower than those initially possible for the species. The non-germinated and non-dormant seeds can also cycle back to conditional dormancy or even to dormancy under the influence of temperature. In morphological and physiological dormancy, the embryo is not able to emerge naturally from the coats because it must overcome its mechanical resistance. Water-impermeable coats induce *physical dormancy* by hindering rehydratation and lowering oxygen availability. It could be tested by weighing seed samples before and after soaking. There is no proof that microbial decay or abrasion by soil particles renders the seed coats water-permeable (Baskin and Baskin, 2000), but it may happen in the digestive tract of animals that ingest the seeds (Rolston, 1978). What is clearly established is that several types of specialised structures occur, allowing water to enter the seeds under circumstances linked to seasonal or daily variation of environmental conditions, notably variations of temperature or desiccation of the embryo (Gama-Arachchige et al., 2013; Janská et al., 2019; Rolston, 1978) or exposition to mild fire (Dell, 1980). Artificial alteration of the coats of those seeds allows them to germinate, but it also works for seeds that have morphological or physiological dormancy (Baskin and Baskin, 2006). *Morpho-physiological dormancy* is the combination of both conditions, and *combinational dormancy* occurs in seeds with impermeable coats and physiological dormancy. *Mechanical dormancy* is provoked by tough fruits (nuts) and is equivalent to physical dormancy. In *chemical dormancy*, the embryos are maintained dormant or conditionally dormant, like in physiological dormancy, but the status is induced by compounds produced by the fleshy or dry fruits. Both these conditions are particular cases of physiological dormancy because they prevent the embryo from overcoming the mechanical resistance of the coats (Baskin and Baskin, 2004). The characterization of dormancy benefits compilations in databases, collecting germination traits by species. The information remains spread out in the literature, sometimes in clusters of several thousands of species, e.g. Baskin and Baskin (2014), Nikolaeva et al., (1985, translated from Russian by Rosbakh et al., 2020). Large dynamic databases on plant traits like *TRY* (Kattge et al., 2020) specialised in germination like *SID* (2021) contain only partial information. It is only recently that the *Sylvanseeds* database, which is devoted to germination seed traits of deciduous forest species, was created by systematically searching the scientific literature with keywords and assembling the information (Fernández-Pascual, 2021).

From experiences consisting of burying seeds and determining their survival rate after several years, it has been established that persistence varies across species from some months to several decades or even centuries and that survivorship in the seed bank generally follows negative-exponential curves (Baskin and Baskin, 2014). Persistence laxly increases in small size seeds that are more often produced in large amounts by short-lived, pioneered species, while genetic diversity within species and plasticity may broaden the range of germination conditions and increase the probability of some seeds surviving under uncommon conditions. The hardships of the common environment (frost, water stress, predators, fire, etc.) seem favourable to persistence (Long et al., 2015).

3.3. Determination of the Soil Seed Bank Composition

First, the results could be affected by soil sampling. Indeed, the number of seeds generally decreases sharply with sampling depth, while the probability to detect a given species in a soil sample obviously increases with soil volume. In addition, the seed dispersal processes are manifold, and a large proportion of plant species, in some habitats up to 100%, have their seeds dispersed by animals whose movements are not random. For instance, the larger trees of a given species with ample fruit production could attract more dispersers than the smaller ones and constitute recruitment foci (Hambuckers et al., 2017; Trolliet et al., 2017a, 2017b). Scatterhoarding by rodents, i.e., the hiding of seeds in ground caches for later consumption but forgotten, also creates highly patchy distributions of viable seeds (Aliyu et al., 2014; Evrard et al., 2019; Moore et al., 2007). Owing to the survival of the seeds in the soil, seasonal differences may exist. Thus, careful planning of sampling is required, according to the objective of the study (Csontos, 2007; Mahé et al., 2021; Padonou et al., 2022; Rahman et al., 2001).

The other cardinal point is the methodology to estimate the viable seed pools. The methods are divided into two broad groups: extraction from the soil (enumeration method) and the emergence of seedlings (emergence method) (Mahé et al., 2021). In the enumeration method, seeds are first extracted commonly by flotation, elutriation, or sieving. In flotation, the soil sample is centrifuged in a solution with density adjusted with salts to make the most of the difference in density between the seeds and the soil particles. In elutriation, the samples are treated in a vertical tube, where they are swept by a flux of air and water, which also separates seeds from soil particles according to the difference in size and density. In sieving, the samples are washed, under running water, through one or a collection of sieves. The extraction is followed by manual separation from the soil remains, sorting, identifying, and counting the seeds under a magnifier. They must be further tested for viability using a crush test (trial of resistance to gentle pressure with forceps), a germination test on Petri dishes or the staining of cut seeds with tetrazolium chloride. In the emergence method, the soil samples are either directly scattered on gardening trays or first sieved under running water to reduce volume. The trays are then placed in substrate in greenhouses for periods ranging from 1 month to several years for monitoring of seedling emergence. To improve germination, the greenhouses can be heated, the samples can be exposed to cold temperatures or water stress and the samples can be mixed with various kinds of substrates, or treated with agents like gibberellic acid, ethephon or potassium nitrate. Possibly, non-germinated seeds that pool at the end of the monitoring period could be further analyzed with the enumeration method. The emergence and enumeration methods can provide the same proportions between species, but the emergence method provides, most of the time, lower estimates of seed numbers in the seed banks than the enumeration method, between 1.5 to 6 times less (Mahé et al., 2021). In addition, samples in the emergence method can also be contaminated by airborne seeds of some species entering the greenhouses (Pannacci et al., 2015). The lower estimates in the emergence methods are because the conditions of observation are not fully appropriate to provoke a dormancy break of all the seeds of the samples and to obtain complete germination even if the period of observation covers several years. Thus, the method to be selected should rely on the objective of the study. It has been shown that the 3 extraction methods have the same efficiency but do not allow recovery of all the present seeds, i.e., only around 68% of the seed added to their soil samples (Mesgaran et al., 2007). Even if the enumeration methods allow us to obtain results more rapidly than with the emergence method, the extraction step limits the size and the number of samples that can be processed in a study because it is time-consuming. Also, the extraction can damage some proportion of the seeds and render their identification problematic (Pannacci et al., 2015). This is the reason why a new efficient sieving system (*Seed Filter Extractor*) was conceived and tested (Pannacci et al., 2015). It is built with three commercial irrigation screen filters in which cyclical turbulent movements of water under gentle pressure are provoked to remove the soil particles. An operator can extract 40 samples per hour, and the seed recovery rate is 98.6% and independent of seed size.

3.4. Seed Banks in Agricultural Soils

The agricultural soils have the potential to contain an incredibly large number of seeds, up to almost 10^6/sq. m, with longevity that could reach several decades (Baskin and Baskin, 2006). A large proportion of them are dormant or conditionally dormant (Mall and Singh, 2014), but the viability often drops after 3 to 4 years (Schwartz-Lazaro and Copes, 2019). In this context, the soil seed bank is called the *weed seed bank*. It is the result of past management but puts future harvests at risk. Understanding its dynamics, particularly the emergence rates, can help in weed management without altering crop yields. The objective of the management of the weed seed bank is often to exhaust a particular weed species before crop emergence (Long et al., 2015; Mahé et al., 2021; Mall and Singh, 2014; Schwartz-Lazaro and Copes, 2019). From, this point of view, evaluation of the seed bank using an emergence method would be more appropriate than using an extraction method (Baskin and Baskin, 2006), since the enumeration of weed seeds focuses directly on the variable of interest. Evidence shows that the seed bank of the outer areas of arable lands harbour more weeds than the inside. In the absence of agriculture disturbance or control of seed return, the weed seed density could drop to around 5% of the initial value in a couple of years, but alternatively, one year without control could be sufficient to reach almost the initial level in the absence of management (Rahman et al., 2001; Schwartz-Lazaro and Copes, 2019). In general, less than 10% of the weed seed bank develops annually into viable seedlings, and 95% of seeds entering the weed seed bank comes from annuals (Mall and Singh, 2014).

The main actions that are undertaken to reduce the incidence of the weed seed banks are to reduce seed production by inactivating germination, to remove weeds before seed maturation and to control the harvest of weed seed, i.e., to mechanically sort the weed seeds from the crops at harvest (Schwartz-Lazaro and Copes, 2019). The two last methods have been progressively abandoned with the increased availability of herbicides. Infestation of fields with herbicide-resistant weeds, but also the need for agricultural methods more based on ecological principles revive interest in these methods (Korres et al., 2019). Increasing seed germination and weed emergence are other possible management strategies. On the one hand, false seedbed, followed by hand labour and shallow tillage, may largely reduce weed presence in the next year's crop by depleting the weed seedbank (Jernigan et al., 2017) but requires the field to lie fallow for one year and is therefore unprofitable. This kind of method is not new since it was the way of proceeding in the Middles Ages, in combination with range pasturing (Mazoyer and Roudart, 1997). Varying soil preparation also does not seem effective, whatever the method compared to no-disturbance (Rahman et al., 2001). On the contrary, tarping, i.e., covering the soil with opaque plastic sheets for a couple of weeks or during the winter preceding the crop is sufficient to favour germination, kill emergent weeds and provide 95 to 100% surfaces free of weeds at tarp removal (Kubalek et al., 2022). Alternatively, the introduction of crop rotations of cleaning plants like turnip, beetroot or potato at the dawn of the 18th century in Europe was particularly successful at maintaining yield and weed infestation at tolerable levels because those crops allow weed germination but thwart their further development (Mazoyer and Roudart, 1997). Crop rotation, which empirically developed from the discovery of agriculture principles and progress over the course of the centuries, seems to be one of the appropriate ways of managing weed seed banks (Schwartz-Lazaro and Copes, 2019). Weed seeds could also be killed before the crop in various ways, such as thermal treatment with flame or steam, cryogenic treatment with solid CO_2, liquid nitrogen or salt solutions on snow cover inducing freezing point depression. In this regard, there are also treatments with bio-based products or bioherbicides, like corn gluten meal, acetic acid, fatty acid, secondary metabolites, or microorganisms (Cordeau et al., 2016; Korres et al., 2019). Those preparations may directly target and kill the seeds, but they may also enhance soil microbial activity which can precipitate seed decay or reduce germination rates. It is also important to note that in conservation agriculture, which is characterized by no-till or reduced till and permanent organic soil cover (living or dead), the efficiency of the treatments with bio-based products has been improved because the weed seeds remain in the upper soil layer (Cordeau et al., 2016). Fire of post-harvest crop residue could also be used to kill the weed seeds grown with the crop (Spaunhorst et al., 2019). A combination of methodologies, like *solarisation*, i.e., passive solar heating of the soil under a clear plastic tarp, in combination with organic amendments, may be also a promising methodology. It can almost completely inactivate seeds after a couple of days thanks to the emission of volatile fatty acids (Achmon et al., 2017).

3.5. Seed Banks in Natural and Semi-Natural Ecosystems

Contrary to weed seed banks in agricultural soils, the soil seed bank in natural and semi-natural ecosystems is positively viewed because it may offer regeneration potential from which may grow back desired communities along successional trajectories (Bakker et al., 1996b). However, the similarity between the standing vegetation and the soil seed bank is general low. The seed bank is less rich than the standing vegetation, e.g. (Daïnou et al., 2011; Medeiros-Sarmento et al., 2021; Ninot et al., 2008; Sanou et al., 2019; Savadogo et al., 2016; Zida et al., 2020). Similarity with the original standing vegetation and the soil seed bank may decrease with the intensity of the disturbance in the ecosystems, e.g. (Honnay et al., 2002; Roovers et al., 2006). It generally decreases with ecosystem stability. This is because species of stable habitats often produce shorter-lived seeds compared to more pioneered species, which would rather produce dormant seeds, for instance under high grazing intensity or along successional gradients (Mall and Singh, 2014). As an example, according to data compiled in Baskin and Baskin (2014), 53% of the sampled trees of matorrales (bush to forest vegetation type under Mediterranean climates) have non-dormant seeds. Shrubs, which are more pioneered than trees in these vegetations have 10% non-dormant seeds among which a significant proportion remains in hard fruits on the mother plants for several years or until a fire occurs, while herbs, also more pioneered than trees, have only 3% of species with non-dormant seeds. Non-pioneered evergreen rainforest trees have more than 59% of non-dormant seeds and 57% of the sampled herbaceous species of the underwood have non-dormant seeds while pioneered tree species reach only 41%. However, the seed bank may sometimes contain living dormant seeds of the ecosystems to be restored. Indeed, specific conditions in each biome may require dormancy for the survival of all the species, not only for those having a transient presence. Thus, in the temperate nemoral forest biome, winter lasts 3 to 6 months, with temperatures below 10°C which are unfavourable for germination and plantlet growth. In those ecosystems, only 14% of the trees have non-dormant seeds and 83% have physiological dormancy – possibly combined with physical or morphological dormancy – often broken by cold stratification. Non-weedy herbaceous species of non-forested habitats exhibit the same scheme with only 5% non-dormant and 86% with physiological or morpho-physiological dormancy. Also, in tropical biomes, the proportion of species with dormant seeds increases with aridity, from rainforests to hot deserts (Baskin and Baskin, 2014).

The understanding and prediction of the phenomena affecting the seed bank characteristics under the consequences of anthropic disturbances, e.g., habitat loss, fragmentation, grazing, fire or invasive species, are factors that are important to consider because they affect the processes of seed dispersal and therefore the seed banks (Bakker et al., 1996b; Csontos, 2007; Mall and Singh, 2014; Wang et al., 2013). Under limited disturbance, like the slash-and-burn agriculture regime with a return time of several decades, the natural processes of seed dispersal, particularly zoochory in tropical ecosystems, progressively bring back the missing seeds of the non-pioneered trees while the presence of desiccation-tolerant orthodox seeds in the seed bank decline with time and standing vegetation richness (Medeiros-Sarmento et al., 2021). Fragmentation and habitat loss are two main signs of ecosystem degradation. They occur abruptly as a consequence of timber harvesting and land conversion or gradually under uncontrolled wood extraction, often combined with unsustainable slash-and-burn agriculture, i.e., with a return time of a couple of years, provoking soil degradation. Fragmentation and habitat loss are accompanied by loss of connectivity, poaching and commercial hunting, provoking large-bodied species (>2 kg) rarefaction (Malhi et al., 2014). Therefore, seed dispersal processes are impaired, which challenges the composition of the soil seed bank and the regeneration of the climax trees by recruitment, e.g.

(Boissier et al., 2020; Markl et al., 2012; Trolliet et al., 2017a). The frequency of seeds of pioneered species and species typical of disturbed habitats in the soil seed bank has been shown to increase as fragment size decreases (Sousa et al., 2017). Also, the frequency of seeds of generalist species—not typical of forest habitats—could be higher near the edge compared to the interior of the forest, but the frequency of seeds of specialist species may not be affected by distance to the edge (Gasperini et al., 2022; Gasperini et al., 2021). Yet, while the effect of habitat loss *per se* on seed dispersal is obvious and negative in temperate and tropical ecosystems, the effect of fragmentation *per se* seems rather weak (Cazetta and Fahrig, 2022). This is probably because fragmentation *per se* (disconnected from habitat loss) increases animal diversity and abundance (Cazetta and Fahrig, 2022; Fahrig et al., 2019) and improves connectivity (Cazetta and Fahrig, 2022), which finally increase interactions between animals and seeds. Since habitat loss and fragmentation are partially linked, it most likely explains why the seed removal rate – an indicator of seed predation and dispersion – in forests can peak at intermediate values of forest cover in the landscape (Hambuckers et al., 2020). In a meta-analysis, it has been found that grazing reduces the abundance of seeds in the soil seed bank but not the species richness and the similarity with the aboveground vegetation (Shi et al., 2022a). Light grazing increases species richness while high grazing decreases it. In habitats naturally prone to fire, fire and smoke may alleviate dormancy, favour the germination of the seed bank, the occurrence of native species, and modulate the regeneration according to fire intensity, season and climate conditions (Ellsworth and Boone Kauffman, 2013; Odion and Davis, 2000; Williams, 2000; Williams et al., 2005; Wright et al., 2019; Wright and Fensham, 2016). The seeds are protected from too elevated temperatures by natural burial, but excessive depth may challenge the seedling's emergence (Tangney et al., 2020). In those habitats, the number of seeds in the seed bank could increase with fire frequency for all the life forms, but nevertheless, higher fire frequency favours the presence of the smaller plant reaching faster reproductive maturity (Santana et al., 2014). Thus, plant species which are killed by fire, and which need heat exposure to germinate may be at risk of extinction if fire frequency is too high because they are not able to reconstitute their seed bank quickly enough (Odion and Tyler, 2002). Fire could exhaust the seed banks by killing the seeds and intense fire in vegetation not prone to fire may threaten diversity by provoking local extinctions (Shi et al., 2022b; Tesfaye et al., 2004). Thus, the slash-and-burn agriculture regime and repeated fires drastically impoverish the local soil seed bank of equatorial and tropical forests in terms of species diversity and notably of rare species (Bezerra et al., 2022; Cury et al., 2020; Flores and Holmgren, 2021). Invasive species with seeds resistant to heat may increase fuel availability and fire intensity which may kill the seeds of the native species, even in habitats naturally prone to fire, and boost the stranglehold of the invasive species (Gómez-González and Cavieres, 2009; Pauchard et al., 2008; Wagner and Fraterrigo, 2015). What happens to the invasive species favoured by fire is more general: invasive species constitute their own seed banks and modify the conditions, favouring them and possibly also alien species, i.e., not indigenous but not invasive species, and challenging the germination of the indigenous species (Gioria and Pyšek, 2015).

Despite restoration of favourable conditions in degraded ecosystems, key species are often absent from the soil seed bank, and feedback mechanisms, like high seed production by the species favoured by the disturbance, may maintain the ecosystem in its former degraded state (Honnay et al., 2002; Ma et al., 2021; Roovers et al., 2006). Restoring degraded abandoned lands often relies on seed rain coming from adjacent plots and configurations at the landscape scale, i.e., patch distances and connectivity, which is a major driver of success (Caughlin et al., 2016). Sometimes, the soil seed bank may have a high potential for regeneration, e.g. (Ma et al., 2021), but generally, according to circumstances, additional efforts, such as artificial translocation of seeds or plantlets, weed suppression, soil improvement and most of all management of human threats, are necessary (Buisson et al., 2021; Di Sacco et al., 2021; Morris, 2022).

3.6. Perspectives

The available knowledge on seed banks should be combined more intensively in the field of application of mathematical modelling. On the one hand, models of seed dispersal by wind have already been developed and largely validated (Kruse et al., 2018; Näther and Waelder, 2003; Nuttle and Haefner, 2005; van Putten et al., 2012). Various methods have also been tested and validated to model animal movements in their habitat in relation to the distribution of the resources, see (Gavrilitchenko et al., 2022; Raghunathan et al., 2020). While it appears relatively easy to compute the spatial deposition of the ingested seeds by individuals of animal species using information on the gastrointestinal transit time, e.g. (Gazagne et al., 2020; Raghunathan et al., 2020; Russo et al., 2006), modelling the spatial seed recruitment of a given plant species may be more challenging. Indeed, travel information and gut transit time distribution of each disperser of the focal plant species must be found to parametrise the models. Such models are individual-based, i.e., they simulate the deposition of individual seeds over the home-range of the involved animal species. On the other hand, a large community has developed dynamic vegetation models (DVMs) that are driven by climate, soil properties and plant traits. These mechanistic models simulate the growth of plants in terms of productivity and biomass, most often on grid cells without explicitly computing the growth of individual plants even if they simulate mortality. They are also able to keep intermediate information produced all over the simulation, like soil water content, gross photosynthesis, or dark respiration rate. Those models still continue to be tested and their features developed, e.g. (Chen et al., 2017; Dury et al., 2011, 2018; Fronzek et al., 2018; Hambuckers et al., 2022; Martín Belda et al., 2022; Snell, 2014). The DVMs are used for example to test the response of vegetation or species to past and future climate, to evaluate CO_2 fixation by terrestrial ecosystems or to compute the evolution of land use and culture production (Fontaine et al., 2014; Fronzek et al., 2018; Jacquemin et al., 2021). However, DVMs only partially integrate the processes of seed dispersal and seed banks, with some exceptions (Kruse et al., 2018; Snell, 2014). This is certainly one of their main limitations and they often work as seed dispersal and seed presence would not be limiting species regeneration and migration (François and Hambuckers, 2020). Now, seed dispersal is probably one of the main processes which conditions plant species turnover under changing climates, and there is an urgent need to try to integrate the two types of models, the seed deposition models and the DVMs. Both are admittedly, for most part, working on very different spatial scales, pixel scale for the DVMs and individual for the seed deposition models. The DVMs would improve the practicality of their predictions while the seed bank science would benefit from the dynamic property of the DVM computations. The edited book of Baskin and Baskin (2022) has brought together 21 contributions of seed science experts covering different types of ecosystems. They highlight previously observed responses on species and on their seeds and point out the priorities, thus indicating to the modellers the most interesting cases to be studied with their tools.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The author declares that he has no conflicts of interest.

Statement of the welfare of animals. The article does not contain any studies involving animals in experiments performed by the author.

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