Seed Science Research (2005) **15**, 189–196 DOI: 10.1079/SSR2005209

RESEARCH OPINION

Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns

Jeffrey L. Walck[1]*, Jerry M. Baskin[2], Carol C. Baskin[2,3] and Siti N. Hidayati[1]

[1]Department of Biology, PO Box 60, Middle Tennessee State University, Murfreesboro, Tennessee 37132, USA; [2]Department of Biology, University of Kentucky, Lexington, Kentucky 40506-0225, USA; and [3]Department of Plant and Soil Science, University of Kentucky, Lexington, Kentucky 40546-0321, USA

Abstract

The most often used time-line for distinguishing a transient seed bank from a persistent seed bank is one calendar year. Thus, species whose seeds live in or on the soil for <1 year have a transient seed bank, whereas those whose seeds live for ≥ 1 year have a persistent seed bank. However, dormancy cycling of seeds buried in soil has not been given due consideration in these models. When dormancy cycling is considered, it is shown that seeds of both autumn-germinators and spring-germinators are in the dormant state when they are 1 year old. Thus, unless the seeds live until at least the second germination season (i.e. usually 16–18 months following dispersal), they are, in effect, part of a transient seed bank, having lived through only one germination season. We propose that for seeds of such species to be considered part of a short-term persistent seed bank, they should remain viable and germinable until at least the second germination season, and to be part of a long-term persistent seed bank, until at least the sixth germination season. Our definitions are applicable to seeds with physiological, physical or morphophysiological dormancy, which often require >1 year after maturity to come out of dormancy in nature. We discuss modifications of the seedling emergence method for detection of a soil seed bank, so that they correspond to our definitions of seed-bank strategies.

Keywords: autumn-germinators, dormancy cycling, persistence, spring-germinators, transient seed bank

*Correspondence
Fax: +1 615 849 5093
Email: jwalck@mtsu.edu

Introduction

A seed bank is a reserve of mature viable seeds located in fruits (or cones) on the plant (aerial seed bank), on the soil surface or buried in soil, duff or litter (Roberts, 1981). The formation of a non-aerial (soil) seed bank begins at seed dispersal and ends with germination or death of the seed. Traditionally, two broad types of soil seed banks have been designated: transient and persistent. Seeds of species with transient seed banks live for <1 year and those with persistent seed banks for ≥ 1 year (Thompson and Grime, 1979). More recent classification schemes subdivide the transient and persistent seed-bank categories into 2–3 subtypes each, delineating them by 1 year to decades (e.g. Poschlod and Jackel, 1993; Bakker *et al.*, 1996; Thompson *et al.*, 1997).

Persistence of seeds in soil in no way depends on dormancy (Thompson *et al.*, 2003). Thus, when initially entering a soil seed bank, seeds of some species may be non-dormant, or dormant (or conditionally dormant), come out of dormancy and then remain non-dormant in soil for many years (e.g. Baskin and Baskin, 1989a; Thompson *et al.*, 2003). Germination in seeds of these species could occur at any time of the year, and thus counting years to delimit types of soil seed banks seems reasonable and adequate. However, none of the current seed-bank classification systems considers timing of dispersal and germination in relation to the dynamics of dormancy change, for species that have pronounced seasonal dormancy and germination patterns, in formulating criteria to distinguish between types of seed banks (Csontos and Tamás, 2003). Roberts (1981) and Baskin and Baskin (1998) included seed dormancy cycling in their graphical models of seed banks, but this point generally has not been taken into account in seed-bank studies. Moreover, no seed-bank classification system currently incorporates species whose seeds have complex kinds of dormancy. In any case, we wish to make it clear that our proposed scheme is complementary (or supplementary) to, but does not replace, existing seed-bank classification schemes.

In the present paper, we advocate that the time-line for distinguishing (sub)types of seed banks for species with pronounced seasonal dormancy and germination patterns should be germination seasons rather than years. Such a change will put the definitions of soil seed-bank strategies into a more realistic plant life-history context and be complementary to existing seed-bank classification schemes. The purposes of this paper are the following:

(1) review the current temporal delineations of soil seed-bank classification schemes;
(2) place our definitions in an ecological and evolutionary framework;
(3) discuss our definitions in relation to classes of dormancy; and
(4) examine the implications of our definitions for detecting soil seed banks.

Current temporal delineations of soil seed-bank classification schemes

The original definition of a transient versus a persistent seed bank, being separated by a 1-year time-line, was proposed by Thompson and Grime (1979) (Table 1). Use of the 1-year time-line is due to the fact that the study by Thompson and Grime (1979) was conducted over a period of 1 year in which soil samples were collected. Species were classified based on whether the occurrence of 'readily-germinable seeds' in soil samples was restricted to a well-defined peak during the year (transient) or was detected throughout the year (persistent). Csontos and Tamás (2003) remarked that 'the 1-year survival seems to be the most natural dividing value between the two types [transient and persistent], at least when seasonal dynamics of vegetation prevail'.

A major change since 1979 has been the splitting of the persistent category into short-term and long-term (Table 1). Bakker (1989) was the first person to use a three-category classification system: transient, persistent and permanent. Later, Thompson (1992) suggested use of short-term persistent and long-term persistent instead of persistent and permanent, respectively, to omit the semantic problems of using similar words (Csontos and Tamás, 2003). A 5-year period is used most often to divide short-term persistent and long-term persistent seed banks (Bakker *et al.*, 1996; Thompson *et al.*, 1997), but Bekker *et al.* (1998) recently used a 4-year period to divide the two types (Table 1). The 5-year (or 4-year?) period for separating short- and long-term persistent seed banks was selected 'admittedly arbitrar[il]y... because it is the end point of a significant number of burial experiments' (Bakker *et al.*, 1996; Thompson *et al.*, 1997).

Poschlod (1993) and Poschlod and Jackel (1993) proposed splitting the transient category into two subtypes and the persistent category into two (or three) subtypes (Table 1). The cut-off point between transient and persistent seed banks was increased to 2 years and that between the persistent category subtypes to decades. This classification was based on the seasonal dynamics of seed dispersal and of seeds in the soil, the distribution of seeds in the upper and lower soil layers, testing the persistence of buried

Table 1. Time-lines (years) among types of soil seed banks as defined by various authors

Author(s)	Seed bank types				
	Transient		Persistent		
Thompson and Grime (1979), Grime (1981, 2001)	<1		>1 or ≥1		
			Short-term	Long-term	
Bakker *et al.* (1991), Thompson (1993)	≤1		>1, but <5	≥5	
Bakker *et al.* (1996), Thompson *et al.* (1997)	<1		≥1, but <5	≥5	
McDonald *et al.* (1996)	<1		>1, but <5	≥5	
Bekker *et al.* (1998)	<1		1–4	>4	
	Type 1	Type 2	Type 3	Type 4	Type 5
Poschlod (1993)	<1	1–2	Few years	Several years to few decades	Several decades
	Type 1	Type 2	Type 3	Type 4	
Poschlod and Jackel (1993)	<1	1–2	Some years to some decades	Some decades	

https://doi.org/10.1079/SSR2005209 Published online by Cambridge University Press

seeds in soil over a short time period and a survey of seeds in the soil along successional seres or in afforestation (Poschlod, 1993; Poschlod and Jackel, 1993).

Germination season as a basis for soil seed-bank classification

Seed dispersal and germination occur at distinct times during the life cycle of many species, and these events are synchronized with seasonal changes in the environment. Environmental conditions have selected for seed germination to occur during a season that is favourable for growth, development and reproduction of the resulting plant. Dormancy is a mechanism that prevents germination at a time when seedlings are unlikely to survive. Both empirical data (reviewed in Baskin and Baskin, 1998) and models (León, 1985; Silvertown, 1988; Venable, 1989) support the notion that timing of germination is a critical aspect in the fitness of plants.

In temperate regions, the main germination period for seeds of many species is in either spring or autumn (Table 2). Seeds in a cohort that remain viable and do not germinate at the appropriate germination season may re-enter dormancy (secondary dormancy or secondary conditional dormancy) during winter (autumn-germinators) or summer (spring-germinators) (Baskin and Baskin, 1985, 1989a, 1998). As such, seeds of both types are dormant 1 year, 2 years, etc., and non-dormant 1.5 years, 2.5 years, etc., following dispersal in spring (autumn-germinators) and in autumn (spring-germinators) (Fig. 1A, B). Any of these secondarily-dormant seeds that remain viable for more than 1 year will come out of dormancy during their second summer (autumn-germinators) or second winter (spring-germinators), and thus again be capable of germinating (non-dormant) in autumn or spring, when they are considerably more than 1 year old. In other situations, seeds of some species, which apparently do not cycle, delay germination of a portion of their seed crop until the second germination season or later (e.g. Baskin and Baskin, 1975). For species whose seeds survive in the seed bank for 1 year but not until the second (or a subsequent) germination season, in effect the seed bank is transient, i.e. seeds are viable and germinable during only one season (Fig. 1C). Thus, use of 1 year as the time-line between transient and persistent soil seed banks (*sensu* Thompson and Grime, 1979; Bakker *et al.*, 1996; Thompson *et al.*, 1997) is ecologically superfluous. A 2-year time-line separating transient and persistent seed banks (*sensu* Poschlod, 1993; Poschlod and Jackel, 1993) leads to the same problems as the 1-year time-line (Fig. 1D).

Table 2. Examples of species that form a persistent seed bank and in which time of dispersal, germination phenology and type of dormancy cycle are known

Species	Peak dispersal[a]	Main period of germination	Length between dispersal and 2nd germination season	Dormancy state changes between germination seasons[b]	Reference(s)
Summer annuals					
Ambrosia artemisiifolia	October	April	18 months	D ↔ ND	Stoller and Wax (1973); Baskin and Baskin (1980)
Cyperus inflexus	September	April	19 months	CD[c] ↔ ND	Baskin and Baskin (1978)
Polygonum aviculare	October	April	18 months	CD[c] ↔ ND	Courtney (1968); Baskin and Baskin (1990a)
Winter annuals					
Arabidopsis thaliana	May	October	17 months	D ↔ ND	Baskin and Baskin (1972, 1983)
Lamium amplexicaule	May	September–October	16–17 months	CD[d] ↔ ND	Baskin and Baskin (1981)
Lesquerella lyrata	May	September	16 months	D ↔ ND	Baskin and Baskin (2000)
L. stonensis	May	September	16 months	D ↔ ND	Baskin and Baskin (1990b)
Nemophila aphylla	May	October	17 months	D ↔ ND	Baskin *et al.* (1993)
Phacelia ranunculoides	May	October	17 months	D ↔ ND	Baskin *et al.* (1993)
Thlaspi arvense	May	September	16 months	CD[d] ↔ ND	Baskin and Baskin (1989b)
Perennials					
Solidago altissima	November	March	16 months	CD[e] ↔ ND	Walck *et al.* (1997a, b, 1998)
S. nemoralis	November	March	16 months	CD[e] ↔ ND	Walck *et al.* (1997a, b, 1998)
S. shortii	November	March	16 months	CD[e] ↔ ND	Walck *et al.* (1997a, b, 1998)

[a] Time when ripe seeds were collected for study, or dispersal was observed.
[b] Seeds are conditionally dormant (CD), dormant (D) or non-dormant (ND).
[c] Low percentages of germination may occur throughout late spring and summer between germination seasons.
[d] Low percentages of germination may occur in early spring between germination seasons.
[e] Low percentages of germination may occur in late summer and early autumn between germination seasons.

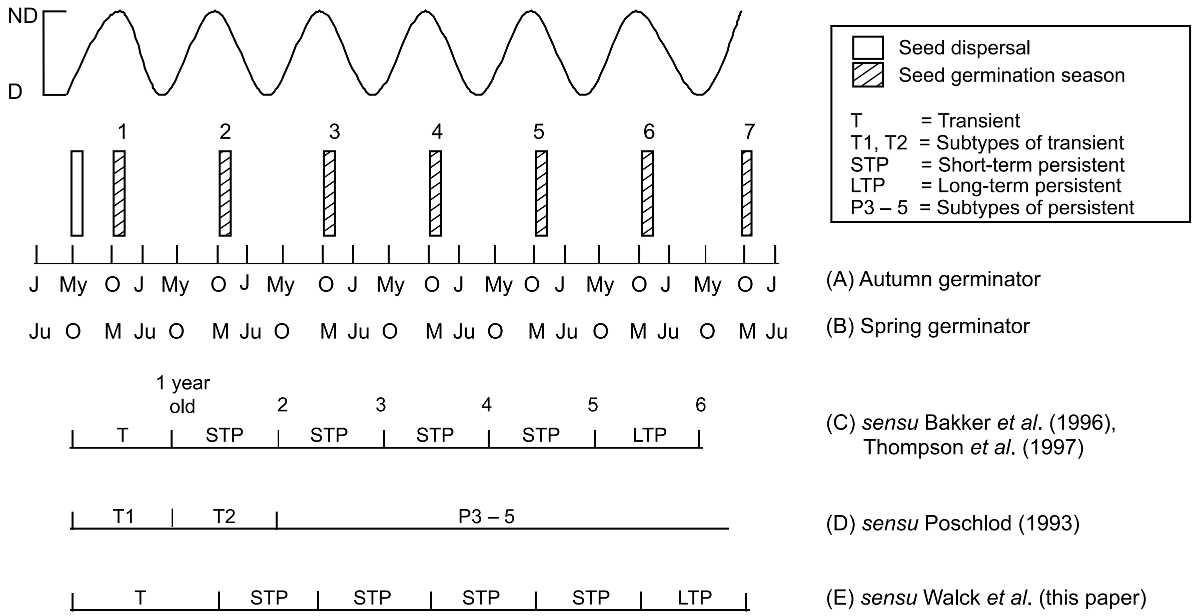

Figure 1. Dormancy cycling (D = dormant, ND = non-dormant), seed dispersal and seed germination seasons for autumn germinators (A) and spring germinators (B) in relation to the two principal models of soil seed-bank strategies based on years (C, D) and a model based on germination seasons (E). To simplify the diagram, the conditionally dormant state is not included. Note, time-lines for separating subtypes of persistent seed banks in panel D are not adequately defined for indication in the figure. Letters below the axis represent months of the year: J, January; M, March; My, May; Ju, June and O, October.

Use of the 4- (*sensu* Bekker *et al.*, 1998) or 5-year time-line (*sensu* Bakker *et al.*, 1996; Thompson *et al.*, 1997) or decades (*sensu* Poschlod, 1993; Poschlod and Jackel, 1993) for separating the subtypes of persistent seed banks runs into the same problem as that of the 1- or 2-year time-line for separating transient and persistent seed banks. Seeds would be dormant at the end of the fourth or fifth year or at the end of a particular decade and not in a germinable state (Fig. 1C, D). Moreover, the short-term persistent seed bank and shortest long-term persistent seed bank (*sensu* Bakker *et al.*, 1996; Thompson *et al.*, 1997), between *c.* 5 and 5.5 year, would have the same number of favourable seasons (five) for germination (Fig. 1C).

Overall, two problems are evident in the current models of soil seed-bank strategies as they relate to species with distinct seasonal dormancy and germination patterns. First, some seeds are dormant at the end of time-lines delineating types of seed banks. Secondly, periods that are favourable for germination (seeds non-dormant) are offset by *c.* 0.5 year with the cut-off criteria. To solve these problems, we suggest that the time-line for distinguishing transient and persistent seed banks in these species be changed from 1 year (*sensu* Thompson and Grime, 1979; Bakker *et al.*, 1996; Thompson *et al.*, 1997) or 2 years (*sensu* Poschlod, 1993) to the second germination season (Fig. 1E). A transient seed bank would then be one in which no seeds remain viable until the second germination season, i.e. 16–18 months following dispersal for most species (Table 2), and a persistent seed bank one in which seeds remain viable until at least the second germination season. Further, the minimum time-line for a long-lived persistent seed bank would be changed from 4 years (*sensu* Bekker *et al.*, 1998) or 5 years (*sensu* Bakker *et al.*, 1996; Thompson *et al.*, 1997) to the sixth germination season (Fig. 1E). Time-lines for separating the subtypes of persistent seed banks in Poschlod's classification (Poschlod, 1993; Poschlod and Jackel, 1993) are too informal to adequately suggest changes based on germination seasons.

Persistent seed banks in relation to classes of dormancy

Our discussion so far has focused on seeds that have physiological dormancy (PD), particularly those with a non-deep level of PD (see Baskin and Baskin, 2004). Moreover, current models of transient and persistent seed banks, including the ones shown in Fig. 1, are primarily for seeds with PD. However, seeds of some species with physical dormancy (PY) also have a predictable germination pattern controlled by environmental cues (Baskin *et al.*, 1998; Van Assche *et al.*, 2003; also see Baskin, 2003). Thus, a soil seed-bank definition based on germination season naturally fits the life-history pattern of some species whose seeds have PY.

This approach is reasonable since PD and PY are the two most common classes of dormancy. Considered together, they are present in freshly matured seeds of about 60% of all species and in about 86% of those whose seeds are dormant at maturity (Baskin and Baskin, 2003).

However, for seeds in which the ecology of dormancy break is more complex than it is for those with PD or PY, neither 1 year nor 16–18 months is a satisfactory time-line to separate transient and persistent seed banks. Seeds of species with morphophysiological dormancy (MPD) can also form persistent seed banks (Baskin and Baskin, 1998; Baskin *et al.*, 2003; Thompson *et al.*, 2003), and this type of dormancy occurs in fresh seeds of about 8% of all species, or in about 12% of the species whose seeds are dormant at maturity (Baskin and Baskin, 2003). While the length of dormancy break and the germination pattern in seeds of some species with MPD are similar to those with PD (e.g. Walck *et al.*, 1999), seeds of other species with MPD often require more than 1 year after they mature to come out of dormancy under natural or near-natural conditions.

Seeds of *Symphoricarpos orbiculatus* have non-deep complex MPD and, thus, require warm stratification followed by cold stratification to come out of dormancy (Hidayati *et al.*, 2001). Seeds of this species are dispersed in autumn and winter and do not germinate until their second spring, up to 16 months following dispersal (Fig. 2A). In seeds of species with deep simple epicotyl MPD, such as occur in those of many *Viburnum* species (Giersbach, 1937), seeds require warm temperatures that break radicle dormancy, followed by cold temperatures that break epicotyl dormancy (Fig. 2B). Since seeds are dispersed in autumn, they do not complete germination (i.e. emergence of both radicle and epicotyl from the seed) until their second spring, 15–17 months after

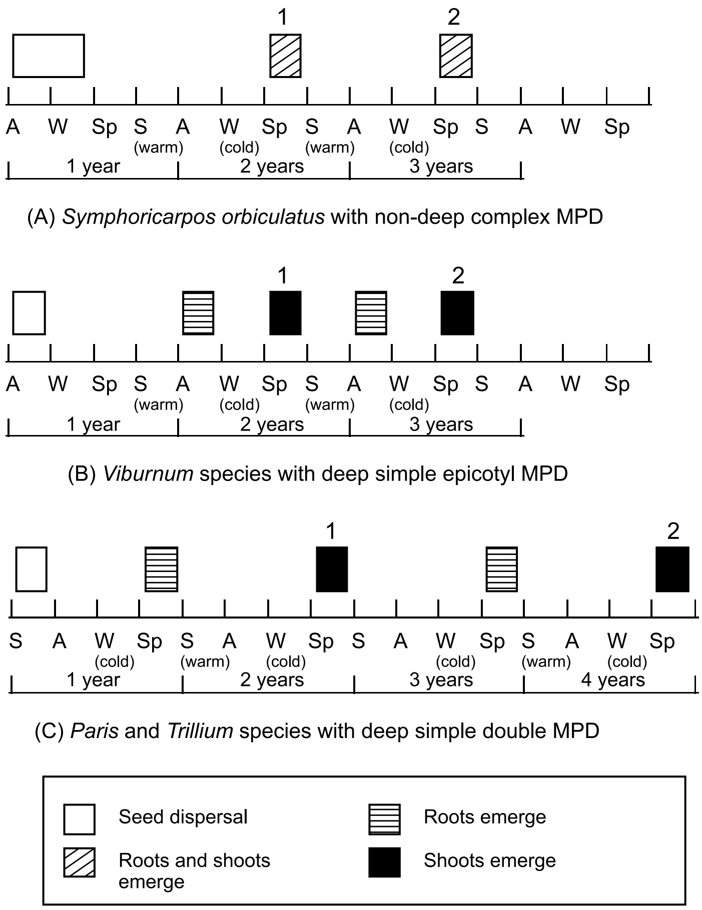

Figure 2. Seed dispersal and emergence of roots and/or shoots for seeds of (A) *Symphoricarpos orbiculatus* with non-deep complex morphophysiological dormancy (MPD); (B) *Viburnum* species with deep simple epicotyl MPD; and (C) *Paris* and *Trillium* species with deep simple double MPD. The stratification requirement is indicated in parentheses below the season in which it takes place. Successive periods for completion of germination (i.e. growth of both radicle and epicotyl) following dispersal for a cohort of seeds are shown by numbers above the appropriate time period. Letters below the axes represent the seasons of the year: S, summer; A, autumn; W, winter and Sp, spring.

https://doi.org/10.1079/SSR2005209 Published online by Cambridge University Press

dispersal. Seeds with deep simple double MPD (e.g. *Paris*, *Trillium*) require two winters and one summer to complete dormancy-break. Radicles emerge in the first spring following dispersal, but epicotyl growth does not occur until the second spring (Fig. 2C). As such, the time interval from dispersal until completion of germination is 1.5 years or longer (Barton and Schroeder, 1942; Barton, 1944; Baskin and Baskin, 1998).

Thus, in nature, seeds of some species with MPD are about 1.5–2 years old before they are non-dormant and can germinate (or complete germination), even though they do not exhibit dormancy cycling. For seeds of these species that do not germinate after their first exposure to the correct sequence of dormancy-breaking conditions, the second chance to germinate, following a second exposure to dormancy-breaking conditions, would be the third spring (both root and shoot emergence) following dispersal in *Symphoricarpos*, the second autumn (root emergence) to third spring (epicotyl emergence) for *Viburnum* and the third spring (root emergence) to fourth spring (epicotyl emergence) for *Paris* and *Trillium* (Fig. 2). Still, our criteria for separating a transient and a persistent seed bank based on survivorship until at least the second (complete) germination season, or of separating a short- and a long-term persistent seed bank based on survival until the sixth germination season, could be easily adapted to *Symphoricarpos, Viburnum, Paris, Trillium* and other species with MPD.

Implications for methodology

The method most commonly advocated for determining whether a seed bank is transient, short-term persistent or long-term persistent deals with measuring the presence/absence of species (in the vegetation and/or as seeds in the soil) and the abundance of seeds in the upper versus lower soil depths (Thompson, 1993; Thompson *et al.*, 1997). From this single sampling occasion, seed persistence is then inferred (Bekker *et al.*, 1998). Other methods, such as seed burial or seedling emergence, can directly measure the longevity of seeds in soil. While both types of methods, i.e. single point-in-time inference versus monitoring over time, hopefully yield similar results, the dynamic aspects of dispersal, dormancy and germination are missed in the single point-in-time inference. We have modified the seedling emergence method so that our definitions of seed-bank strategies correspond closely to the detection of a soil seed bank.

Our method for determining seed longevity in soil requires information on timing of seed dispersal (i.e. seeds enter the seed bank) and of seed germination (i.e. seeds exit the seed bank). The easiest way to detect whether a species forms a persistent seed bank is to collect soil samples after the first germination season for a seed cohort, but before dispersal of the next cohort. Moreover, collection of soil samples during a time when seeds are dormant eliminates confounding effects of germination flushes following collection and exposure of soil. Samples should be kept at natural, or at near-natural, temperature regimes and monitored for seedling emergence until at least the second germination season for the species. Soil samples collected after dispersal, but before the first germination season, may contain a transient seed bank only (species currently growing at the study site), or a mixed transient/persistent seed bank (species currently growing at the study site, plus those present only as seeds in/on the soil). In this case, a species currently growing at the site for which no seeds remain viable until the second germination season has a transient seed bank only, whereas if some seeds of this species remain viable until the second or a later germination season, it has a persistent seed bank. However, for a species that is present at the site only as seeds in the soil, any seeds that survive until the first or a later germination season after soil samples are collected probably has a persistent seed bank.

Our protocol differs from those generally recommended for the seedling emergence method for studying soil seed banks in two respects. First, the soil samples (kept under natural or near-natural conditions) should be monitored for seedling emergence until at least the end of the second germination season. If soil samples are collected during seed dispersal, then they need to be monitored for a minimum of 16–19 months for seeds with PD or PY (Table 2) and longer for seeds with some types of MPD (Fig. 2). This length of time could be shortened by several months by collecting samples after the current year's seed crop is dispersed and as close to the beginning of the first germination season as possible. Protocols published on the seedling emergence method recommend keeping samples for 6 months (Warr *et al.*, 1993), 3 months (reduced samples) to 1 year (unreduced samples) (Thompson *et al.*, 1997) and 2 years (Roberts, 1981). We understand that space and time, as well as other difficulties such as risk of contamination with seeds from outside, development of a moss layer that suppresses seed germination and/or seedling emergence and seed and/or pre-emergent seedling predation by snails and insect larvae, may be limitations in conducting seedling emergence studies over long periods. However, we feel that there is no 'quick and dirty' method for directly determining the persistence of seeds for a species, particularly for those currently growing at a study site.

Secondly, the time for collection of the soil samples needs to be placed into perspective with regard to the dispersal and germination seasons. Further, researchers need to report the number of seedlings emerging from soil samples during each germination season. Seedlings emerging during the first germination season after collection of soil samples would be part of the transient seed bank or of a mixed transient/persistent seed bank, but those emerging during the second germination season would be part of a persistent seed bank only. Warr *et al.* (1993) and Thompson *et al.* (1997) recommended collecting soil samples in early spring, since (1) natural (cold) stratification has already taken place in the field, and (2) most germination occurs between May and July. However, this method considers only spring germinators, and more attention needs to be given to autumn germinators.

The methods and information provided in many seed-bank studies are such that it is not possible to determine the type of seed bank present in a soil sample (Thompson *et al.*, 1997; Baskin and Baskin, 1998). Walck *et al.* (1998) found that the majority of studies reporting seeds of *Solidago* species in soil samples contained a transient, as well as perhaps a persistent, seed bank. Most of the studies employed the seedling emergence method, and the primary problems were that: (1) the germination period following sampling was not long enough to separate seedlings resulting from seeds dispersed one (recently) and/or greater than one dispersal season(s) ago; and (2) although the germination period was long enough, seedlings from a transient seed bank could not be distinguished from those of a persistent seed bank, since timing of emergence over the entire test period was pooled in the results (Walck *et al.*, 1998). Although the sort of information our scheme requires for the identification of soil seed-bank strategies might not be available for many species at the present time, it is hoped that future seed-bank studies will recognize the importance of placing seed-bank methods into a life-cycle framework.

References

Bakker, J.P. (1989) *Nature management by grazing and cutting*. Dordrecht, Kluwer, Academic Publishers.

Bakker, J.P., **Bos, A.F.**, **Hoogveld, J. and Muller, H.J.** (1991) The role of the seed bank in restoration management of semi-natural grasslands. pp. 449–455 *in* Ravera, O. (Ed.) *Terrestrial and aquatic ecosystems: perturbation and recovery*. New York, Ellis Horwood.

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.

Barton, L.V. (1944) Some seeds showing special dormancy. *Contributions from Boyce Thompson Institute* **13**, 259–271.

Barton, L.V. and Schroeder, E.M. (1942) Dormancy in seeds of *Convallaria majalis* L. and *Smilacina racemosa* (L.) Desf. *Contributions from Boyce Thompson Institute* **12**, 277–300.

Baskin, C.C. (2003) Breaking physical dormancy in seeds - focusing on the lens. *New Phytologist* **158**, 229–232 (commentary on paper by Van Assche *et al.*, 2003).

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

Baskin, C.C. and Baskin, J.M. (2000) Seed germination ecology of *Lesquerella lyrata* Rollins (Brassicaceae), a federally threatened winter annual. *Natural Areas Journal* **20**, 159–165.

Baskin, C.C., **Baskin, J.M. and Chester, E.W.** (1993) Seed germination ecology of two mesic woodland winter annuals, *Nemophila aphylla* and *Phacelia ranunculacea* (Hydrophyllaceae). *Bulletin of the Torrey Botanical Club* **120**, 29–37.

Baskin, C.C., **Baskin, J.M. and Chester, E.W.** (2003) Ecological life cycle of *Trepocarpus aethusae* (Nutt.) ex DC. and comparisons with two other winter annual Apiaceae native to Eastern United States. *Castanea* **68**, 43–55.

Baskin, J.M. and Baskin, C.C. (1972) Ecological life cycle and physiological ecology of seed germination of *Arabidopsis thaliana*. *Canadian Journal of Botany* **50**, 353–360.

Baskin, J.M. and Baskin, C.C. (1975) Seed dormancy in *Isanthus brachiatus* (Labiatae). *American Journal of Botany* **62**, 623–627.

Baskin, J.M. and Baskin, C.C. (1978) Seasonal changes in the germination response of *Cyperus inflexus* seeds to temperature and their ecological significance. *Botanical Gazette* **139**, 231–235.

Baskin, J.M. and Baskin, C.C. (1980) Ecophysiology of secondary dormancy in seeds of *Ambrosia artemisiifolia*. *Ecology* **61**, 475–480.

Baskin, J.M. and Baskin, C.C. (1981) Seasonal changes in the germination responses of buried *Lamium amplexicaule* seeds. *Weed Research* **21**, 299–306.

Baskin, J.M. and Baskin, C.C. (1983) Seasonal changes in the germination responses of buried seeds of *Arabidopsis thaliana* and ecological interpretation. *Botanical Gazette* **144**, 540–543.

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. (1989a) Physiology of dormancy and germination in relation to seed bank ecology. pp. 53–66 *in* Leck, M.A.; Parker, V.T.; Simpson, R.L. (Eds) *Ecology of soil seed banks*. San Diego, Academic Press.

Baskin, J.M. and Baskin, C.C. (1989b) Role of temperature in regulating timing of germination in soil seed reserves of *Thlaspi arvense* L. *Weed Research* **29**, 317–326.

Baskin, J.M. and Baskin, C.C. (1990a) 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. (1990b) Seed germination biology of the narrowly endemic species *Lesquerella stonensis* (Brassicaceae). *Plant Species Biology* **5**, 205–213.

Baskin, J.M. and Baskin, C.C. (2003) New approaches to the study of the evolution of physical and physiological dormancy, the two most common classes of seed

dormancy on earth. pp. 371–380 *in* Nicolás, G.; Bradford, K.J.; Côme, D.; Pritchard, H.W. (Eds) *The biology of seeds: Recent research advances*. Wallingford, CABI Publishing.
Baskin, J.M. and Baskin, C.C. (2004) A classification system for seed dormancy. *Seed Science Research* **14**, 1–16.
Baskin, J.M., Nan, X. and Baskin, C.C. (1998) A comparative study of seed dormancy and germination in an annual and a perennial species of *Senna* (Fabaceae). *Seed Science Research* **8**, 501–512.
Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. and Willems, J.H. (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology* **12**, 834–842.
Courtney, A.D. (1968) Seed dormancy and field emergence in *Polygonum aviculare*. *Journal of Applied Ecology* **5**, 675–684.
Csontos, P. and Tamás, J. (2003) Comparisons of soil seed bank classification systems. *Seed Science Research* **13**, 101–111.
Giersbach, J. (1937) Germination and seedling production of species of *Viburnum*. *Contributions from Boyce Thompson Institute* **9**, 79–90.
Grime, J.P. (1981) The role of seed dormancy in vegetation dynamics. *Annals of Applied Biology* **98**, 555–558.
Grime, J.P. (2001) *Plant strategies, vegetative processes, and ecosystem properties* (2nd edition). Chichester, John Wiley & Sons.
Hidayati, S.N., Baskin, J.M. and Baskin, C.C. (2001) Dormancy-breaking and germination requirements for seeds of *Symphoricarpos orbiculatus* (Caprifoliaceae). *American Journal of Botany* **88**, 1444–1451.
León, J.A. (1985) Germination strategies. pp. 129–142 *in* Greenwood, P.J.; Harvey, P.H.; Slatkin, M. (Eds) *Evolution: Essays in honour of John Maynard Smith*. Cambridge, Cambridge University Press.
McDonald, A.W., Bakker, J.P. and Vegelin, K. (1996) Seed bank classification and its importance for the restoration of species-rich flood-meadows. *Journal of Vegetation Science* **7**, 157–164.
Poschlod, P. (1993) Die Dauerhaftigkeit von generativen Diasporenbanken in Böden am Beispiel von Kalkmagerasenpflanzen und deren Bedeutung für den botanischen Arten- und Biotopschutz. *Verhandlungen der Gesellschaft für Ökologie* **22**, 229–240.
Poschlod, P. and Jackel, A.-K. (1993) The dynamics of the generative diaspore bank of calcareous grassland plants. I. Seasonal dynamics of diaspore rain and diaspore bank in two calcareous grassland sites of the Suebian Alb. *Flora* **188**, 49–71.
Roberts, H.A. (1981) Seed banks in soils. *Advances in Applied Biology* **6**, 1–55.
Silvertown, J. (1988) The demographic and evolutionary consequences of seed dormancy. pp. 205–219 *in* Davy, A.J.; Hutchings, M.J.; Watkinson, A.R. (Eds) *Plant population ecology*. Oxford, Blackwell Scientific Publications.
Stoller, E.W. and Wax, L.M. (1973) Periodicity of germination and emergence of some annual weeds. *Weed Science* **21**, 574–580.
Thompson, K. (1992) The functional ecology of seed banks. pp. 231–258 *in* Fenner, M. (Ed.) *The ecology of regeneration in plant communities* (1st edition). Wallingford, CAB International.
Thompson, K. (1993) Persistence in soil. pp. 199–202 *in* Hendry, G.A.F.; Grime, J.P. (Eds) *Methods in comparative plant ecology: A laboratory manual*. London, Chapman & Hall.
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., Bakker, J.P. and Bekker, R.M. (1997) *The soil seed banks of North West Europe: Methodology, density and longevity*. Cambridge, Cambridge University Press.
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.
Van Assche, J.A., Debucquoy, K.L.A. and Rommens, W.A.F. (2003) Seasonal cycles in the germination capacity of buried seeds of some Leguminosae (Fabaceae). *New Phytologist* **158**, 315–323.
Venable, D.L. (1989) Modeling the evolutionary ecology of seed banks. pp. 67–87 *in* Leck, M.A.; Parker, V.T.; Simpson, R.L. (Eds) *Ecology of soil seed banks*. San Diego, Academic Press.
Walck, J.L., Baskin, J.M. and Baskin, C.C. (1997a) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 1. Germination phenology and effect of cold stratification on germination. *Seed Science Research* **7**, 47–58.
Walck, J.L., Baskin, J.M. and Baskin, C.C. (1997b) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 2. Germination responses of buried seeds in relation to seasonal temperature cycles. *Seed Science Research* **7**, 209–220.
Walck, J.L., Baskin, J.M. and Baskin, C.C. (1998) A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 6. Seed bank. *Seed Science Research* **8**, 65–74.
Walck, J.L., Baskin, C.C. and Baskin, J.M. (1999) Seeds of *Thalictrum mirabile* (Ranunculaceae) require cold stratification for loss of nondeep simple morphophysiological dormancy. *Canadian Journal of Botany* **77**, 1769–1776.
Warr, S.J., Thompson, K. and Kent, M. (1993) Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progress in Physical Geography* **17**, 329–347.

Received 1 October 2004
accepted after revision 22 April 2005

https://doi.org/10.1079/SSR2005209 Published online by Cambridge University Press