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RESEARCH OPINION

Comparisons of soil seed bank classification systems

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Abstract

Since 1969, ten soil seed bank classification systems have been published. Among these systems, the number of recognized seed bank categories varies from three to twelve. Seed longevity is the main factor used for distinguishing categories, but dormancy and germination types are also important. Systems considering relatively few seed bank categories have been the most commonly proposed in contemporary plant ecology. In contrast, systems involving high numbers of categories have received limited interest because the detailed ecological knowledge of individual species required for their successful categorization is usually missing. A comprehensive table on the main features of seed bank classification systems is provided.

Keywords: dormancy, persistent seed bank, seed bank classification, transient seed bank

Introduction

Knowledge of soil seed banks, i.e. the seeds reaching the soil surface after seed dispersal and then buried, is quite old. It is likely that the first farmers recognized the phenomena of seed germination, dormancy in unfavourable conditions, and the appearance of non-sown plants (weeds). Today, we think that it was Charles Darwin who made the first scientific observations of seed banks, noting the number of seedlings that germinated from a cup of mud taken from a pond. However, he also made other observations about seed banks during his everyday walks in Down, as well as during travels to faraway lands, and discussed these experiences in *On the origin of species*. For example he wrote: ' … on a piece of ground three feet long and two wide, dug and cleared, and where there could be no choking from other plants, I marked all the seedlings of our native weeds as they came up, and out of the 357 no less than 295 were destroyed, chiefly by slugs and insects', and another, probably the most curious, ' … when irregularly shaped stones are embedded in the roots of trees, small parcels of earth are very frequently enclosed in their interstices and behind them, … out of one small portion of earth thus completely enclosed by wood in an oak about 50 years old, three dicotyledonous plants germinated: I am certain of the accuracy of this observation' (Darwin, 1859).

By the end of the 1960s, our knowledge of seed banks had reached a 'critical data mass' permitting synthesis. Probably the first attempt to create a system for classifying soil seed banks was published by Schafer and Chilcote in 1969, but since then a number of other researchers have also proposed various classification systems. Below, we will consider these in order of appearance, followed by a critical evaluation of concepts in a separate section. A table with the main characteristics of each system is also provided (Table 1).

A comparative understanding of different seed bank classification systems can facilitate choosing an appropriate system for specific research objectives. Beyond this intrinsic advantage, classification systems may also promote several important aspects of seed ecology. Accumulating evidence shows that seed dispersal may be at least as important as the seed bank in restoration ecology (Beatty, 1991; Bakker *et al.*, 1996; Halassy, 2001). However, in the debate on dispersal versus recruitment from seed banks, the fact that seeds migrating by seed rain also spend some time in the seed bank, mostly as transient members, is often missed. A classification system that considers types of dispersal, longevity and dormancy would certainly be a useful tool in restoration ecology. Finding a strong correlation between seed bank types and any 'easy to measure' seed or plant attribute, or

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†The authors dedicate this paper to Professor Tamás Pócs (Eger, Hungary) upon the occasion of his 70th birthday.

Table 1. Comprehensive table of seed bank classification systems[a]

Reference	Total no. of types	Number of types based on:		Further details	Relevant vegetation type	Remark
		longevity	dormancy or germination properties			
Schafer and Chilcote (1969)	4	–	3	Includes non-viable seeds	Agricultural land	–
Thompson and Grime (1979)	4	2; T and P	2 within group T	Portion of a year's seed crop that enters the seed bank (within group P)	Temperate climate vegetation	Hierarchical system; the main division is based on longevity
Grime (1981)	8	2; T and P	5 within group T; 2 within group P	Ratio of yearly input and total amount of seed bank (within group P)	Temperate climate vegetation	Hierarchical system; the main division is based on longevity
Nakagoshi (1985)	12; $(3 \times 3 + 3)$	2; T and P	–	Ratio of yearly input and total amount of seed bank (within group P); the 3 main types are multiplied by 3 life-form categories	Restricted to case studies in Japanese forests	3 additional categories for species with 'usually no seed production'
Grubb (1988)	3	–	3; 'disturbance broken', 'risk spreading', 'weather dependent'	–	Applicable everywhere	Dormancy and germination activity are discussed from the viewpoint of the effect of environment
Garwood (1989)	5	3; T, SP and LP	2 within group T	'Pseudo-persistent'; seemingly P due to continuous seeding	Rain forests and related vegetation types under equatorial climate	SP is called 'delayed-transient' by Garwood
Thompson (1993)	3	3; T, SP and LP	–	–	Developed for temperate vegetation but applicable everywhere	Supported by a dichotomous key for common data types (Thompson *et al*., 1997)
Poschlod and Jackel (1993)	7	4; T_1 (<1 year), T_2 (1–2 years) and P_1, P_2	The first 3 longevity types have 2 subtypes (with and without innate dormancy)	–	Temperate climate vegetation	A modified version of this system was reported by Poschlod (1993)

Abbreviations: T, transient; P, persistent; SP, short-term persistent; LP, long-term persistent.
[a] Bakker's (1989) system is discussed under Thompson (1993); Poschlod (1993) is not indicated separately, being a variant of Poschlod and Jackel (1993).

set of attributes, would allow prediction of seed bank types for a great number of species without the need for direct experimentation. Once the seed bank types of a critical number of species are known, it may be possible to derive, and to evaluate statistically, taxonomic and evolutionary relationships.

Description of the classification systems

The earliest soil seed bank classification system of which we are aware was proposed by Schafer and Chilcote (1969). They divided the soil seed bank (all seeds in the soil) into four general categories: (1) The first group consists of seeds that are in a dormant state due to exogenic causes, i.e. causes originating from the external environment. [This status is also called enforced dormancy by Harper (1977) and quiescence by Murdoch and Ellis (2000).] The seeds in this category begin to germinate if ideal conditions are provided. (2) The second group consists of seeds that are in a dormant state due to endogenic causes (innate dormancy *sensu* Harper). These seeds are incapable of germination even if ideal conditions are provided. (3) The third group consists of seeds capable of germinating under current conditions, while the fourth group (4) includes the non-viable seeds in the soil.

The first soil seed bank classification system with an ecological approach was proposed a decade later. Based on their extensive studies of various habitats, Thompson and Grime (1979) defined four soil seed bank types. Their system is hierarchical, where the two main groups are created by separating transient and persistent types. They consider a soil seed bank to be transient when the dispersed seeds remain viable for less than 1 year (either germinating or dying during this time). In the case of a persistent soil seed bank, a portion of the seeds remains dormant in the soil for more than 1 year. There is no upper limit to longevity, and seeds remaining viable for 2 years and those remaining viable for 100 years all fall into the persistent soil seed bank behaviour category.

Within the transient type, two other groups are defined: in Type I the seeds germinate in the summer or autumn following seed dispersal, so the seed bank of the species is present in the soil only for a few months. In Type II the seed crop of a given year lies dormant during the winter and then germinates completely in the spring. The seed bank may be present in the soil for several months, but the length of its presence is less than 1 year.

The persistent type is also divided into two groups, although on a different basis. In Type III only a small percentage of the species seed crop remains dormant, with most of the seeds germinating within 1 year. The quantity of soil seed bank shows significant seasonal variability within the year. Finally, in Type IV the great majority of the annual seed crop does not germinate and becomes a part of the persistent soil seed bank, which may become quite large and shows only a slight quantitative variation within the year.

Two years later, Grime (1981) tried to refine this system. He divided Type I into four and Type III into two subtypes, but he kept Types II and IV unchanged. Subtypes were characterized by various combinations of timing of seed release, forms or absence of dormancy, seasonal pattern of germination and light/dark germination requirements. Grime emphasized the adaptive significance of the various seed bank types of plant species that occupy the same habitat, and concluded that a diversity of seed characteristics allow species to exploit different types of habitat disturbances, and that this explains, at least partly, such species coexistence in species-rich plant communities.

In the past few decades, Japanese ecologists have researched soil seed banks intensively and have modified the seed bank classification system of Thompson and Grime (1979). Nakagoshi (1985) merged the two transient categories of Thompson and Grime, but kept the other two categories. Then he combined these three types with the three main life-form categories (herbaceous plants, shrubs and trees). This resulted in nine types, with one more additional possibility for each of the three life forms, namely the case when ‘there is usually no seed production’. Altogether, Nakagoshi worked with 12 types.

It seems that the role of soil seed banks in the life of populations can be more closely connected with the reaction to disturbance than with the life forms, as is discussed by Grubb (1988). Grubb differentiated three types according to environmental effect (disturbance) and characteristics of the related soil seed bank activation (recruitment). These were:

1. Species having a soil seed bank that reacts to disturbances quickly and almost completely (‘disturbance-broken’ type). These species are natural pioneers, appearing first in storm clearings, or are usually short-lived plants occupying disturbed patches in grasslands. Many species of fire-influenced vegetation types are also included.
2. Species that retain a certain percentage of their soil seed bank even under favourable conditions (‘risk-spreading’ type). This is especially important for those species where there is a high, or even full, mortality of the juvenile plants in certain years. The lengthening of the germination period to several subsequent years and the spreading of risk is usually ensured by some kind of innate seed dormancy (Harper, 1977).
3. The seeds await a special signal from the environment, indicating the occurrence of

appropriate weather ('weather-dependent' type). In the semi-arid areas, where this type is quite frequent, the signal is the wetting of the soil. Grubb only mentions this type briefly and does not provide a detailed analysis.

Garwood (1989) proposes an interesting classification system of five categories, based on research carried out in equatorial rain forests. Instead of the transient category, defined for the temperate regions as seeds having less than 1 year viability, she introduces some unique types (1–3):

1. Transient. These are the species with seeds that are viable for a short period only; the seeds begin to germinate immediately and, in some species, long-lived seedling banks are formed.
2. Seasonal transient. The seeds have the ability to go dormant, but this status is held only for a short period of time. These seeds are present in the soil for less than 1 year.
3. Pseudo-persistent. This type can be interpreted among tropical conditions only: the seeds of the species in this category are ripened and dispersed continuously, so they seem to maintain a persistent soil seed bank, although individual seeds are not persistent.
4. In addition to these three categories, she describes a fourth, called 'delayed-transient'; this is similar to 'short-term persistent' according to the recent terminology of Thompson *et al*. (1997). According to Garwood's description, the species in this type have seeds germinating with a delay and often asynchronously, and a part of the seeds may remain in the soil for 1–2 years.
5. Garwood's fifth type is the traditional persistent category where the seeds are long-lived: several kinds of dormancy can be observed and the seeds may remain in the soil for years.

Modified classification systems, like the ones developed by Nakagoshi or Garwood, were not real alternatives to the system published by Thompson and Grime (1979), as these did not intend to be universal. Instead, their purpose was to describe the soil seed bank dynamics of the vegetation studied by the authors.

However, Bakker (1989) tried to revise the Thompson and Grime system on the basis of a large amount of his own research data. During his grassland management studies, Bakker discovered that certain species that would be classified as persistent soil seed bank types (i.e. the seeds of these species can be found in the soil any time of the year) according to Thompson and Grime (1979), can be divided into two groups.

The first group – named the *Bellis perennis* group after its most typical representative – consists of species with seeds that are present in the top 2 cm of soil in a larger amount than in identical volumes excavated from deeper layers. A common characteristic of the species in this group is that they have a well-developed seed bank only when they are represented in the standing vegetation of the studied area. If the populations of these species are destroyed by herbicide treatment, their soil seed bank will disappear from the area in a few years.

The other group – named after *Sagina procumbens* – includes species that have relatively few seeds in the top 2 cm of the soil, but have a well-developed seed bank in the deeper soil layers. It is also a characteristic of the *Sagina* group species that their seed bank is present in the soil even where no standing specimens have been present in the vegetation for several years.

Bakker emphasizes that the population dynamics of the above-mentioned two groups are different and their importance in rehabilitation ecology is not identical. He proposes that the *Bellis perennis* type soil seed banks should be named 'persistent' while the *Sagina*-type, much longer-lived soil seed banks, should be called 'permanent' (Bakker, 1989). He thinks that this latter group has a key role in rehabilitation ecology.

Although Bakker noted several important aspects, he did not address the transient categories. This was done later, through discussion with Thompson, and they merged the two transient categories previously defined by Thompson and Grime (1979). Thompson (1993) explained this by stating that, lacking the data on the seasonal seed bank dynamics of the overwhelming majority of species, it is impractical to separate transient Types I and II, and that these two types have little relevance to regeneration ecology, where the absolute longevity of the seeds matters principally. However, it must be stressed that the distinction between Types I and II could be important in certain cases and should be retained wherever possible.

A further point regarding Bakker's work is related to terminology. We cannot know whether he was aware of Nakagoshi's work (1985), in which the term 'permanent seed bank' was first used, or introduced it independently, but it is not a very good idea to use two quite similar words ('persistent' and 'permanent') together. Furthermore, the latter has some semantic problems, as well, as its closest synonym is 'everlasting', which cannot be true for any soil seed bank. Thompson recognized this and changed the names so that they made more sense in English.

Finally, a three-category soil seed bank system was published by Thompson (1993). Types include:

1. transient – the seeds are viable for a maximum of 1 year;

2. short-term persistent – viability is longer than 1 year but less than 5 years;
3. long-term persistent – viability is at least 5 years.

In 1993, two further classification systems were proposed. Poschlod and Jackel (1993) created four categories for the survival period of the seeds: (1) transient, with viability less than 1 year; (2) transient, with a viability of 1–2 years; (3) persistent with viability ranging from a few years to a few decades; and (4) persistent for several decades.

The first three categories were each divided into two subgroups, on the basis of dormancy: (a) seeds without innate dormancy, and (b) seeds with innate dormancy; thus producing a total of seven categories.

A modified version of the above classification was reported for habitat conservation purposes and possible use in restoration ecology (Poschlod, 1993). For species in the 'Red Data' books of endangered species (e.g. Wigginton, 1999), it was also proposed that this classification should be considered. The categories presented were: (1) transient (<1 year); (2) transient (1–2 years); (3) persistent (few years); (4) persistent (several years to few decades); (5) persistent (several decades). In comparison to the Poschlod and Jackel (1993) system, the subtypes based on dormancy were omitted and the number of categories based on persistence increased.

Discussion

It is clear that Schafer and Chilcote based their system primarily on the seed dormancy types. However, as discussed by Thompson (2000), many species persist in the soil for years or decades in a non-dormant state, and dormancy is neither a necessary nor a sufficient condition for persistence in the soil. Thus, there is no simple relationship between persistence and dormancy (Thompson *et al*., 2003). Another point in which Schafer and Chilcote's work differs from modern seed bank ecology is that they included the non-viable seeds. Additionally, at that time, the number of publications about soil seed banks from the viewpoint of ecology was relatively few, since even the term 'seed bank' was not coined until the mid-seventies (by van der Valk and Davis, 1976). (Formerly, the rather long expression 'buried viable seed content of the soil', or its alternatives were used.) These are probably the main reasons why this system did not become more widespread in the seed bank ecology literature.

From these classification systems, seed bank survival in time proved to be the main feature by which to set up types. Most of the authors agree that a distinction of transient (short-lived) and persistent (long-lived) seed banks is important. In this respect, the 1-year survival seems to be the most natural dividing value between the two types, at least when seasonal dynamics of vegetation prevail. Thus, the transient seed bank always consists of the seeds formed in the same year, i.e. the seed bank generations never overlap, whereas for species with persistent seed banks, several seed generations may be stored in the soil, which may have consequences for the population dynamics and genetics of the species (Brown and Venable, 1986; Baskin and Baskin, 1998).

Further divisions based upon survival time can be an obvious way for refinement of the system. Garwood (1989) and Thompson (1993) distinguished three different categories in time, Poschlod and Jackel (1993) established four, while Poschlod (1993) worked with five.

When a continuous variable, such as seed persistence, is divided into categories, there is a trade-off between number of categories and reliability of placing the species into categories. In other words, if the number of temporal categories increases, the number of species having contradictory data (referring to two or more neighbouring classes) will also increase. Alternatively, too few categories could make the system too coarse, thus allowing only rough conclusions to be drawn. This is the reality that we have to live with when establishing categories.

However, establishing categories without exact definitions should be avoided. Researchers certainly have different ideas about the dividing line between 'few' and 'several' years/decades of longevity, as this may be seriously affected by the vegetation type with which they are working, and by their previous experience with seed survival. Therefore, the exact time-span of each category should be given, even if the underlying ecological reason is missing. Such an arbitrary cut-off point was successfully introduced by Thompson *et al*. (1997), who separated short-term and long-term persistence at 5 years. This is because 5 years is the end point of a significant number of burial experiments (e.g. Roberts and Bodrell, 1983, 1985; Roberts, 1986).

Based on the fact that a seed cohort of a species can be composed of seeds with different potential longevities, a question may be posed: How many persistent seeds of a seed cohort are required for classifying the species into the group having a persistent seed bank? Is a single seed sufficient, are a dozen seeds needed, or more than 50% of the cohort? For example, the Beal experiment is often cited as proof for more than 100-year seed survival of *Verbascum thapsus* and *Malva rotundifolia*, although this status was fulfilled by a single seed (2% of the buried seeds) for the mallow (Telewski and Zeevaart,

[1]If anyone knows of the use of the term 'seed bank' prior to 1976, we would very much appreciate being informed.

2002). A quantitative approach, instead of rough categorization, would resolve the problem.

Even if individual papers have well-founded conclusions about longevity categories, the behaviour of species may remain obscure, because individual experiments may support different conclusions about longevity of the same species (cf. Thompson *et al.*, 1997). This may be caused by the altered behaviour of species under various habitat conditions, or by differences in the methods applied. For example, 2-year-long survival of seeds is considered short-term persistent according to Thompson (1993), but it falls under the transient category in the system of Poschlod and Jackel (1993).

Beyond the different judgements on the same survival length by different classification systems, there are cases when the survival length of seeds is directly altered by the methods used. Natural potential longevity may be wrongly classified when dry-stored seeds are investigated (Kjaer, 1940; Garwood, 1989; Bonner, 1994). Care should also be taken regarding longevity data from experiments with artificially buried seeds. Burial depth affects seed longevity, with the result that, in most cases, longer survival occurs in deeper soil layers (Toole and Brown, 1946; Kropać *et al.*, 1986; Baskin and Baskin, 1998). Of course, different species are not equally sensitive to burial depth. For example, *Ulex europaeus* proved to be weakly influenced (Hill *et al.*, 2001), whereas no effect of burial depth on longevity was found with *Centaurea solstitialis* (Callihan *et al.*, 1993). The best estimation of seed longevity in burial experiments can be achieved if the native soil type of the species is considered (not always the case when seeds are buried in experimental gardens). Detailed studies underline that groundwater level may also influence the survival of seeds in the soil, and that it is especially important when species of waterlogged habitats and wetlands are investigated (Leck, 1989; Bekker *et al.*, 1998c; Collins and Battaglia, 2001).

Since the improved dichotomous key for identification of seed bank types was published (Thompson *et al.*, 1997), germination tests of layered soil samples play an increasing role in seed bank classification of species (Funes *et al.*, 1999a; Sendtko, 1999; Matus *et al.*, 2001). However, the depth distribution of seeds of the same species may vary between sites, potentially supporting different conclusions about longevity (Bekker *et al.*, 1998a).

Whatever the reason for ambiguity, ecologists face the problem of providing a definite classification of species. This problem is resolved by the proposed longevity index (L) that arranges the species along a continuum of seed persistence:

$$L = (SP + LP)/(T + SP + LP),$$

where T, SP and LP represent the number of transient, short-term persistent and long-term persistent records, respectively (Thompson *et al.*, 1998).

Probably the main advantage of the longevity index is that it transforms records of persistence to data suitable for advanced statistical analyses, as was clearly demonstrated regarding various vegetation types and ecological phenomena (Bekker *et al.*, 1998a, b; Thompson *et al.*, 1998). The only limit for its application seems to be that using at least five categorized records (or three unanimous categorized records) is recommended for calculating the L-value of a particular species (Bekker *et al.*, 1998b).

For some species an exact classification into survival time categories is intrinsically impossible because their seeds are physiologically (often also morphologically) heterogeneous (Baskin and Baskin, 1998; Mandak and Pysek, 2001). For such species, after gathering the necessary amount of seed longevity data, the percentage distribution into survival length classes could be given. Of course, the ratio of seeds falling into different classes may vary among populations due to genetic differences and also may depend on habitat variables (Tóthné *et al.*, 1996; Dao *et al.*, 1999; Kebreab and Murdoch, 1999). However, for a basic survey, following the tradition of long-term seed burial experiments (Toole and Brown, 1946; Egley and Chandler, 1983; Burnside *et al.*, 1996; Telewski and Zeevaart, 2002), further investigations could be recommended involving species not yet tested.

Besides distinctions based on longevity, dormancy type is often used as a criterion for seed bank classification (Grime, 1981; Grubb, 1988; Poschlod and Jackel, 1993). In this respect, Grime (1981) developed the most detailed system, combining dormancy types with timing of seed release and seed germination, and interpreted these seed bank types as adaptations for various disturbance regimes and in connection with the role of a species in plant communities. There is no doubt that it would be quite promising to use either the Grime diversified classification or the Poschlod and Jackel more regular system (with and without innate dormancy bifurcation within main types). However, it would require much greater knowledge about dormancy characteristics of wild species. It is likely that lack of dormancy data in this field restricts the use of these systems to some well-studied local floras. To widen their successful applicability, future seed bank studies should be complemented with germination ecophysiology investigations. In this respect, even the re-investigation of already studied species could provide new information, because seed cohorts of different years could show different types of annual dormancy cycles in the same species, as demonstrated for *Viola arvensis* (Baskin and Baskin, 1995).

In some cases the ratio of yearly input and total amount of seed bank is also considered for seed bank type classification (Thompson and Grime, 1979; Nakagoshi, 1985; see Table 1). It is easy to see that a series of transitional states can be found between the third and the fourth groups of Thompson and Grime, as the defined categories represent only the extremes of a continuum (Thompson *et al.*, 1997). (Of course, the same is valid for the corresponding groups of Nakagoshi.) Even for a single species, this ratio may be changed through modification of the seed input, seed survival in soil or both, governed by gradual change of the habitat type (Thompson, 1985). Provided that accumulated change is large enough along altitude, latitude, or other environmental gradient, it may lead to the change of the species seed bank type itself. For example, regarding latitude, a 'switch' of germination time between autumn and the following spring is discussed by Grime (1981; types 1a and 1b). Future results in this field of study may highlight spatial relationships of seed bank types.

Although neither Bakker (1989) nor Thompson (1993) emphasize them, certain relationships may be noted between the two persistent categories of the Thompson–Grime (1979) system and the short-term and long-term categories of Thompson (1993). With regard to the third Thompson–Grime category, the seasonal fluctuation of seed bank density may be caused by relatively short longevity (at least for certain species). Alternatively, if seeds of a species are long lived, then irrespective of the portion of immediately germinating seeds, its seed bank will certainly be large enough, under populations setting seeds for several years, to make the yearly seed input relatively insignificant. Studies about the validity of this relationship between the two systems would increase our understanding of soil seed banks. Including criteria other than longevity and dormancy types of seeds for construction of seed bank classification systems was first attempted by Nakagoshi (1985), who considered the life form of plants.

The interrelationship between life forms and seed bank types was recognized in many studies, indicating the low representation of woody species in the persistent fraction of the seed bank (Leck *et al*., 1989; Thompson *et al*., 1997, 1998; Cao *et al*., 2000), and this issue seems to be worthy of further studies. However, it would make a seed bank classification system more coherent if further attributes of the seeds themselves are considered (instead of attributes of the established plants).

Correlations between the main life forms, or plant size and seed size have long been known (Salisbury, 1942; Baker, 1972; Thompson and Rabinowitz, 1989). The recognized trend is based on large data sets, but individual species do not necessarily follow the rule. Seed size has also been suggested as a predictor of seed bank type (Thompson *et al*., 1993, 2001; Bekker *et al*., 1998a). A quantitative analysis of the relationship of seed weight categories and three seed bank types (*sensu* Thompson, 1993) is also given in Fig. 1. It is apparent from both the literature and the figure that large-seeded species tend to form transient seed banks, and vice versa. However, it is also important to note that this rule is not exclusive. Thus, for example, a seed bank classification based on the transient, short-term persistent and long-term persistent longevity categories, in combination with three seed weight categories, seems to be worthy of consideration.

A further seed attribute that has ecological significance is dispersal type. Combining the three main seed bank types mentioned with anemochory, epizoochory, endozoochory, etc. would result in a new classification system. Its applicability to ecological research would be interesting to test, because recent studies show that the relationship between dispersal capacity and seed persistence is not yet fully understood (cf. Thompson, 2000).

Considering the Garwood (1989) study, it is apparent that, in the climate of the equatorial areas where the vegetation has no unfavourable period for plant growth, the transient seed bank types dominate. It draws attention to the importance of habitats to seed bank characteristics of the vegetation. The data on persistence of tropical seeds (the highest values are about 10–14 years) show, for areas without a dry season, that it is likely that there is no extreme persistence, but instead the seed bank is often replaced by a seedling or sapling bank. Under extremely dry conditions, often coupled with fire-prone vegetation, the canopy-stored seed bank (also called an aerial seed bank) becomes strikingly frequent (Zammit and Westoby, 1988; Pannell and Myerscough, 1993). This seed bank type seems to have special advantages when there is a high probability of seed loss on the soil surface (either by predation or fire) and the humid periods favourable for germination are short and unpredictable in time (Narita and Wada, 1998). Based on numerous studies during past decades, seed ecologists have come to the general conclusion that woody species usually make a minor contribution to the composition of the persistent fraction of soil seed banks. More recently, as the numbers of studies on Mediterranean and subtropical areas have increased, evidence of the opposite was also found (Arianoutsou and Thanos, 1996; Witkowski and Garner, 2000). Although, in the latter cases, the effect of habitat on the increase of woody species in the soil seed bank is difficult to separate from taxonomic relations, i.e. hard-coated *Fabaceae* species often dominate in the above-mentioned vegetation types, still, these findings demonstrate the limits of generalization and underline the need for seed bank studies on habitats

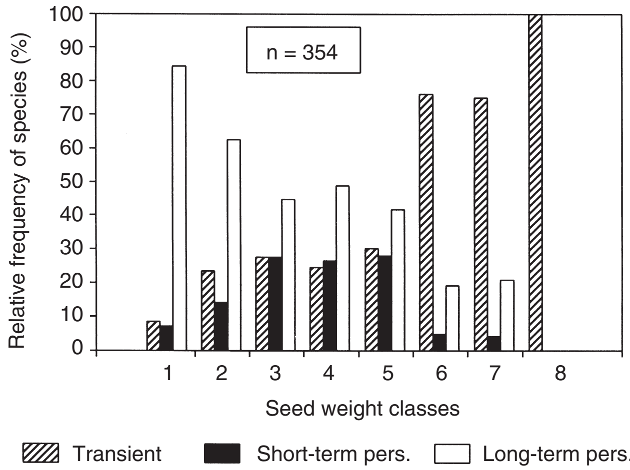

Figure 1. Proportional distribution of seed bank types of 354 species from the Hungarian flora among thousand-seed-weight classes (1 = –0.20 g, 2 = 0.21–0.50 g, 3 = 0.51–1 g, 4 = 1.01–2 g, 5 = 2.01–4 g, 6 = 4.01–10 g, 7 = 10.1–50 g and 8 = above 50 g). Data from Thompson *et al.* (1997) for seed bank types, and from Csontos (1998, 2001) for seed weight.

not yet sufficiently studied. The benefits of geographically extended surveys have been well demonstrated for prediction of seed persistence using seed size and shape (Thompson *et al.*, 1993). Recent studies in Australia, Argentina, Italy, New Zealand and Spain (Leishman and Westoby, 1998; Funes *et al.*, 1999b; Moles *et al.*, 2000; Cerabolini *et al.*, 2003; Peco *et al.*, 2003) have highlighted new aspects of the topic and opened new lines for further research.

Conclusions

Looking over the seed bank classification systems discussed here, none of the ten can be designated as being the best. Most probably such a 'best system' will never be completely accepted because of the wide variety of aims and purposes of studies. For example, an analysis of the restoration potential of a vegetation unit requires a different view of seed banks than one that attempts to relate seed banks with *in situ* vegetation dynamics or the population dynamics of a species.

The search for the best system is made somewhat easier if the two main approaches of research are distinguished. For the case when results are needed in a short time and relatively rough conclusions are adequate to serve the purpose of the study, the most useful classification systems seem to be those of Thompson and Grime (1979) and Thompson (1993), in which he modified and completed the Bakker proposal. The former quickly became popular; the model was used in many books and reviews (Roberts, 1981; Fenner, 1985; Leck *et al.*, 1989), and even today, it is frequently cited (Thompson *et al.*, 1997). The latter seems to receive increasing interest, as well. The usefulness of these systems probably owes much to their simplicity. The 'classic' Thompson–Grime system distinguishes two transient and two persistent types; then further division is made by dormancy type for the transient group and by amount of long-lived seeds for the persistent group. The Thompson (1993) system, with three types, is based on longevity only, and it has a single transient type. In the division of the persistent group, two types are defined according to survival time: short-term persistent (when seeds live longer than 1 year but shorter than 5) and long-term persistent (when seeds live for at least 5 years). These two systems were developed principally for species living under temperate climates. However, the Thompson three-category system seems to be easily applicable to a wider range of species and a wider range of climatic regions.

For cases where detailed studies are required, one can hardly develop a general system that would be applicable everywhere. This is hindered by great differences in the vegetation due to geography and climate. Various viewpoints of different researchers could also produce classification systems that are sensitive to different characteristics of the seed bank. A good example for vegetation-type-induced systems was developed by Garwood (1989), who successfully applied her five-category system to describe seed bank characteristics of equatorial rain forests. For detailed seed bank studies in the temperate region, Grime (1981) and Poschlod and Jackel (1993) proposed their elaborate systems. As an expected outcome, the refinement of seed bank classification systems caused an increase in the number of seed bank types within a system. However, if one considers the frequency of application of the known systems, it becomes obvious that systems involving numerous categories have attained only limited acceptance, because they usually require extensive knowledge of the ecology and dormancy of individual species. Therefore, extensive germination ecophysiology studies are needed to enhance further improvement of seed bank classification systems.

An alternative way to improve the applicability of the classification systems could be achieved by introduction of new variables, especially those where character states can be defined relatively quickly and easily for a large number of species. The Nakagoshi concept is a typical example of this, with the introduction of plant life-forms into his system (Nakagoshi, 1985).

We suggest seed size and seed dispersal mechanism as possible variables for further enrichment of seed bank classification systems. We think that attributes directly related to seeds (as opposed to those derived from the whole plant) are more relevant in construction of systems, and are expected to provide more information about, and better understanding of, seed bank ecology. Application of seedling attributes may also deserve consideration, since the ultimate role of a seed bank, i.e. a regeneration source for the standing vegetation, is realized through the seedling phase.

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