

Assessing soil seed bank persistence in flood-meadows: The search for reliable traits

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Abstract. To assess seed bank persistence of target species in endangered flood-meadows (alliances *Cnidion* and *Molinion*), we investigated established vegetation and soil seed bank of 46 plots for 3 yr and 2 yr, respectively. As traits of seed persistence we calculated various continuous indices that refer to the frequency and abundance of species in above-ground vegetation and at different soil depths. Furthermore, we tested the significance and soundness of easily observed traits such as maximum seed density per plot and seed attributes (mass, size and shape) as predictors of soil seed bank features.

In linear regression, SAI, the seed accumulation index, showed the best agreement ($R^2 = 0.64$) with the seed longevity index that was derived from the database by Thompson et al. (1997) for a set of 115 species. The second best predictor ($R^2 = 0.39$) of the seed longevity index was maximum seed density per plot in the lower soil layer (5-10 cm). Depth distribution indices and seed attributes showed weaker but still significant relations. The dynamic character of flood-meadows was reflected by a large proportion of species with a strong tendency to accumulate seeds in the soil relative to their importance in above-ground vegetation. Most of these species have a ruderal strategy, exploiting gaps after flood disturbances, while the dominants of flood-meadows tended to have short-lived seed banks. Compared to other grassland types, a relatively large proportion of rare and endangered target species can be expected to form long-term persistent seed banks. However, only under marginal conditions that facilitate seed survival in the soil (e.g. fallow) are these persistent seed banks likely to contribute to restoration.

We conclude that easily observed traits of persistence such as seed weight, size and shape do not meet the accuracy needed in scientific and practical applications. Thus, there is a crucial demand for further seed bank studies in poorly investigated habitats and of rare species.

Keywords: *Cnidion*; Depth distribution; *Molinion*; Restoration; Seed accumulation index; Seed longevity index; Seed shape; Seed size; Seed weight.

Nomenclature: Wisskirchen & Haeupler (1998).

Abbreviation: SAI = Seed accumulation index.

Introduction

There is an increasing demand for reliable information on seed banks, both for scientific purposes and as a decision tool in habitat and landscape management, particularly restoration projects. The lack of seed sources due to limited dispersal of target species is as a main constraint, even under favourable site and management conditions (Bakker & Berendse 1999). Soil seed banks play an important role in restoring former species diversity (Bakker et al. 1996a). Seeds of target species may have survived beneath degraded plant communities. It has also been shown that the risk of local extinction increases in species with short-lived seed banks, particularly in fragmented landscapes (Stöcklin & Fischer 1999).

Thompson et al. (1997) suggested a classification of seed bank types as to seed longevity: transient: < 1 yr; short-term persistent: 1-5 yr; long-term persistent: > 5 yr. Only the latter category may play a significant role in the restoration of species richness. Thus, soil seed bank persistence is a key factor in the regeneration of plant communities (e.g. McDonald et al. 1996; Bekker et al. 1997) and for the assessment of the local extinction risk (Stöcklin & Fischer 1999). There is a strong bias in seed bank studies for common species of arable land and pastures, and we know less about species that are most relevant in restoration (Bakker et al. 1996a; Thompson et al. 1998). This also applies to flood-meadows of the alliance *Cnidion*, which have a high biodiversity but belong to the most endangered grassland communities in Europe. They are presently the target of large-scale restoration efforts in parts of Central Europe (Seffer & Stanová 1999; Bischoff 2002; Hölzel et al. 2002). However, until recently (Hölzel & Otte 2001), no information was available on seed longevity of their highly threatened species (Schnittler & Günther 1999). Judging from the experience in other dynamic wet habitats (e.g. van der Valk & Davis 1978; Schneider & Sharitz 1986; Bekker et al. 1999; Jutila 2001), one can expect that recruitment from the persistent seed bank may also play an essential role in flood-meadows restoration.

Methods to measure seed persistence in the soil have not yet been standardized (Thompson et al. 1997). The following approaches are most commonly used to assess seed persistence in the soil: (1) burial experiments (e.g. Jensen 2001); (2) distribution of species in established vegetation and at various soil depths (Thompson et al. 1997); (3) seed attributes such as mass, size and shape (Thompson et al. 1993; Bekker et al. 1998).

Burial experiments require at least 5 yr. They can easily be misinterpreted due to their artificial nature (Bakker et al. 1996a; Thompson et al. 1997). We investigated seed longevity by a refined and extended combination of the approaches 2 and 3. We examined in particular which traits of seed banks and seeds are the most reliable and straightforward to assess seed longevity in a threatened habitat type.

Material and Methods

Study sites

The studied flood-meadows are situated in the Holocene flood-plain of the northern Upper Rhine between the tributaries Neckar and Main (core area: 49°51' N, 8°23' E; 83 - 91 m a.s.l.). In this region flood-meadows occupy fine-grained, calcareous alluvial soils that are irregularly inundated by high water levels of the River Rhine. In conjunction with the comparatively warm and dry climate (mean annual temperature 10.3 °C and annual precipitation 580 mm), the irregularity of flooding results in a high seasonal and inter-annual variation in ecological conditions. The 46 flood-meadows that were analysed represent a broad variety of vegetation types in terms of flooding regime, soil nutrient status and management and cover almost the entire spectrum of possible target species. They range from mown *Magnocaricion* stands at the lowest elevations, over *Cnidion* stands at intermediate levels to alluvial *Arrhenatherion* communities at the rarely inundated highest positions in the flood-plain (Dister 1980; Hölzel 1999). Eight plots originate from former arable fields and poplar plantations that were restored into grassland ca. 10 - 15 yr ago, while six plots comprise strictly oligotrophic alluvial *Molinion* communities that are confined to particularly nutrient-poor sites where the loamy topsoil was removed in the past.

Above-ground vegetation sampling

Species composition of vascular plants in above-ground vegetation was sampled each year from 1998 to 2000 on 46 permanent plots of 200 m². Species cover-abundance was visually estimated on a modified Braun-Blanquet-scale (van der Maarel 1979). The vegetation was usually sampled in June. In 1999,

when the above-ground vegetation of many plots at low elevations was destroyed by heavy flooding in May/June, sampling was performed in August after resprouting of the meadows.

Seed bank sampling

The soil seed banks were sampled in September 1997 and September 1999 to cover two years with contrasting flooding conditions. Whereas the season before the first sampling in 1997 was unusually dry, high and long-lasting flooding events occurred in the winter, spring and early summer of 1999.

Within each of the 46 permanent plots, 20 cores of 3 cm diameter and 10 cm depth were taken at random locations after thoroughly removing living and dead plant material from the soil surface. Thus, the data represent the soil seed bank in the strict sense without the superficial diaspore litter deposited during the sampling year (Urbanska 1992). The soil cores were then divided into 0-5 cm and 5-10 cm sections. The soil samples represent 141 cm² of the soil surface and 1410 cm³ of the soil volume in each plot and were thus well above the minimum requirements given by Oomes & Ham (1983) for studies of seeds in grassland.

We analysed seed banks by the seedling emergence method (Roberts 1981) for 36 months. For further information see Hölzel & Otte (2001).

Seed persistence traits

To achieve formalized seed persistence criteria, we defined various traits that were applied in a modified way in previous studies (Thompson et al. 1997; Bekker et al. 1998). Basically, these traits refer to the relationship between the occurrence of a species in above-ground vegetation and in the soil as well as to the vertical distribution of seeds within the soil profile. To define seed bank types from this kind of data, Thompson et al. (1997) used a simple dichotomous key that only gives a rough estimation of seed longevity, which must be seen as a concession to the highly inconsistent and heterogeneous information compiled in their database. In the present study, we developed several indices of seed persistence that make it possible to allocate species along continuous gradients. Since the application of such indices always depends on extensive seed bank and vegetation studies with a large set of samples, we also tried to assess the reliability of easier traits (Weiher et al. 1999). Thus, besides maximum seed densities per plot at different soil depths, we included seed morphological attributes such as mass, size and shape in the analysis. These parameters are thought to be predictors of depth distribution and seed longevity (Thompson et al. 1993; Bekker et al. 1998; Thompson et al. 1998).

Seed accumulation index (SAI)

Two indices were created to express the relationship between the presence of a certain species in above-ground vegetation and in the soil seed bank in a continuous way. The first index relates the plot frequency of a certain species in above-ground vegetation (AV_f) with its frequency in the soil seed bank (SB_f):

$$AV/SB_{freq} \text{ index} = (SB_f / (SB_f + AV_f)) * 100 \quad (1)$$

The second index relates cumulative cover of a certain species over all plots (AV_q) to the total number of seeds recorded in the seed bank over all plots in both years of sampling (SB_q):

$$AV/SB_{quant} \text{ index} = (SB_q / (SB_q + AV_q)) * 100 \quad (2)$$

Since there was considerable flood-induced inter-annual variation in species dominance, cover in a certain plot was calculated as an average of three years with contrasting flooding conditions namely: 1998 = very dry; 1999 = very wet; 2000 = medium. Both indices range between 0 (only present in above-ground vegetation and therefore strictly transient) and 100 (only present in the soil seed bank and therefore strictly persistent).

To integrate quantitative aspects of species occurrence in above-ground vegetation and seed bank, we merged the two indices into a single one by the addition of both values and division by two. We call this complex index 'seed accumulation index' (SAI), since it expresses the tendency in a certain species to accumulate seeds in the soil, rather than the potential seed longevity.

Depth distribution indices

A large proportion of deeply buried seeds is regarded as an indicator of persistent seed banks (Thompson et al. 1997; Bekker et al. 1998). To describe depth distribution of seeds in the soil we used indices similar to those described above. One describes plot frequencies of a certain species in the lower layer of 5-10 cm (LL_f) in relation to those in the upper layer of 0-5 cm (UL_f):

$$DD_{freq} \text{ index} = (LL_f / (LL_f + UL_f)) * 100 \quad (3)$$

A second depth-distribution index refers to the relationship between the total number of seeds in a certain species over all plots in both years of sampling in the lower (LL_q) and in the upper layer (UL_q), respectively:

$$DD_{quant} \text{ index} = (LL_q / (LL_q + UL_q)) * 100 \quad (4)$$

Both indices also range from 0 (only present in upper layer) to 100 (only present in the lower layer).

Maximum seed densities

Additionally, we chose maximum seed density in a certain species per plot during a single sampling occasion in the lower layer of 5-10 cm (LL_{max}), and in the

entire profile depth of 0-10 cm (T_{max}) as an indicator of persistence. We expected these traits to be particularly useful in assessing the potential for seed accumulation in the soil within a particular species.

Seed attributes

Physical seed attributes such as mass (M), size (S) and shape (SH) are thought to be major determinants for depth distribution of seeds in the soil and therefore also play a significant role in estimating seed longevity (Thompson et al. 1993; Bekker et al. 1998; Moles et al. 2000). Light, small and round seeds will penetrate the soil more readily, facilitating the creation of long-term persistent seed banks due to dark dormancy and escape from predation (Grime et al. 1981, Thompson 1987).

Seed mass was measured as a mean for at least 1000 seeds, length and breadth were calculated as the median of 20 grains. Additional data on common species were derived from Grime et al. (1988), Korsma (1930) and Jensen (unpubl.). Based on the assumption that the maximum surface area of seeds determines the probability of burial, we defined size as the product of length and breadth. In contrast to Thompson et al. (1993), Bekker et al. (1998) and Moles et al. (2000), who used a three dimensional approach, shape was defined by us as the ratio of length and breadth. Given the same volume, spherical to lens-shaped seeds are considered to be more easily buried than slim elongated seeds.

Data analysis

Trees and shrubs, and herbaceous species with less than three occurrences either in above-ground vegetation or in the seed bank, were omitted from the data set. For 27 species, no data on seed attributes were available, which left 152 species for the final analysis. The values of LL_{max} and T_{max} and those of mass (M), size (S) and shape (SH) were log-transformed prior to analysis.

To evaluate the reliability of SAI and its two components as a measure of persistence, we used the seed longevity index of Bekker et al. (1998) for a set of 115 species:

$$\text{Longevity index } (L) = ((SP + LP) / (T + SP + LP)) \quad (5)$$

where (SP + LP) is the total number of short-term and long-term persistent records, and (T + SP + LP) the total number of transient plus short-term plus long-term persistent records in the database of Thompson et al. (1997).

The underlying correlation structure of seed longevity traits was explored in a Principal Component Analysis (PCA). Simple and multiple linear regression models were used to check the predictive power of seed longevity traits. In multiple regressions we applied the more robust stepwise backward selection (Zar 1999). All analyses were carried out with STATISTICA 6.0.

Results

Variation structure of traits

The principal-component analysis (PCA) revealed the correlation structure of the longevity traits calculated from our data set. The first three axes of the PCA ordination explained 56%, 18% and 11%, respectively, of the variation in the data set (Table 1). There was a very close negative correlation between the first axis and the traits AV/SB_{freq} , AV/SB_{quant} , $\log T_{\text{max}}$ and $\log LL_{\text{max}}$ and to a lower degree DD_{freq} and DD_{quant} indicating a significant interdependence between all these traits directly calculated from our data. In contrast, log seed mass (M) and log seed size (S) loaded strongest on axis two and log seed shape (SH) on axis three. Thus, the variation structure of these seed attributes differed from those of the other traits.

Performance of seed persistence traits

Simple linear regression analysis for a set of 115 species between the seed longevity index of Bekker et al. (1998) as dependent variable and the various traits of persistence as predictor variable resulted in each case in a highly significant correlation (Table 2).

The indices that relate frequency (AV/SB_{freq}) and abundance (AV/SB_{quant}) of a certain species in the above-ground vegetation and in the seed bank exhibited the best correlation with a large proportion of explained variance (R^2 of 0.60 and 0.58, respectively). An even higher correlation ($R^2 = 0.64$) was achieved with the seed accumulation index (SAI) (Fig. 1), which combines both indices.

Seed densities per single plot in the lower layer ($\log LL_{\text{max}}$) and the entire sampled profile ($\log T_{\text{max}}$) gave the second best correlation with the seed longevity index (R^2 of 0.39 and 0.34, respectively). In contrast, the predictive power of the depth distribution indices DD_{freq} and DD_{quant} was considerably lower ($R^2 = 0.21$ and 0.20, respectively). An identical proportion of variance was

Table 1. Explained variance and correlation structure of seed longevity traits in PCA ordination (first three axes). High correlations are given in bold.

$n = 152$	Axis 1	Axis 2	Axis 3
Explained variance (%)	59.12	15.46	10.63
AV/SB_{freq} index	-0.88	0.01	0.12
AV/SB_{quant} index	-0.90	-0.01	0.18
DD_{freq} index	-0.81	-0.36	-0.32
DD_{quant} index	-0.72	-0.40	-0.36
$\log(T_{\text{max}})$	-0.88	-0.09	0.10
$\log(LL_{\text{max}})$	-0.92	-0.16	-0.08
$\log(M)$	0.63	-0.72	0.11
$\log(S)$	0.63	-0.70	-0.02
$\log(SH)$	0.37	0.24	-0.80

explained by the seed attributes log mass (M) and log size (S), while log shape (SH) showed the poorest ($R^2 = 0.09$) correlation. In multiple linear regression with stepwise backward selection including the easily observed traits 'maximum plot density' and 'seed attributes', only maximum density in the lower layer ($\log LL_{\text{max}}$) and log mass (M) were added to the model, which resulted in an $R^2 = 0.44$. Thus, the addition of log (M) to the model led to an increase in explained variance of only 5%.

Influence of seed traits on seed accumulation and depth distribution

As already indicated by the PCA ordination (Table 1) there was a strong intercorrelation between the seed attributes mass and size. Consequently, in multiple regression with stepwise backward selection ($n = 152$) only log mass (M) and log shape (SH) were added to the model (Table 3). Explained variance was highest for the SAI ($R^2 = 0.38$) and maximum densities at both measured soil depths ($R^2 = 0.27$). In contrast, there was a much lower but still significant correlation between log mass (M) and the two depth distribution indices (R^2 of 0.10 and 0.06, respectively).

Species patterns of seed accumulation

Due to its high correlation with the seed longevity index we used the seed accumulation index (SAI) to assess seed persistence in the studied flood-meadows. The application of the SAI to our data set resulted in a continuous and very differentiated ranking of species (App. 1). Species with high index values were predominantly therophytes or perennials that follow a ruderal life strategy. With few exceptions, such as *Potentilla reptans*, *Ranunculus repens*, *Lysimachia vulgaris*, *Poa trivialis* and *Agrostis stolonifera* species with high scores were scarce or completely absent in above-ground veg-

Table 2. Simple linear regression models with the seed longevity index (Bekker et al. 1998) as dependent variable and various traits of seed persistence calculated from the flood-meadow dataset as predictor variables. All values are significant at $P < 0.001$

$n = 115$	Longevity index (L)	R^2
SAI	$L = 0.0077 \times \text{SAI} + 0.0797$	$R^2 = 0.64$
AV/SB_{freq}	$L = 0.009 \times AV/SB_{\text{freq}} + 0.112$	$R^2 = 0.60$
AV/SB_{quant}	$L = 0.0059 \times AV/SB_{\text{quant}} + 0.0952$	$R^2 = 0.58$
DD_{freq}	$L = 0.0057 \times DD_{\text{freq}} + 0.2468$	$R^2 = 0.21$
DD_{quant}	$L = 0.056 \times DD_{\text{quant}} + 0.2785$	$R^2 = 0.20$
$\log(T_{\text{max}})$	$L = 0.0849 \times \log(T_{\text{max}}) + 0.2984$	$R^2 = 0.34$
$\log(LL_{\text{max}})$	$L = 0.0927 \times \log(LL_{\text{max}}) + 0.3905$	$R^2 = 0.39$
$\log(M)$	$L = -0.0903 \times \log(M) + 0.3555$	$R^2 = 0.22$
$\log(S)$	$L = -0.1204 \times \log(S) + 0.4939$	$R^2 = 0.21$
$\log(SH)$	$L = -0.2302 \times \log(SH) + 0.5363$	$R^2 = 0.09$

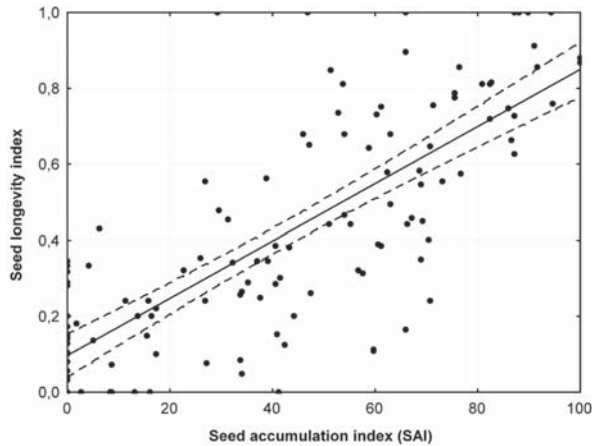


Fig. 1. Correlation between the seed longevity index of Bekker et al. (1998) and the seed accumulation index for 115 species. Regression line and 95 % confidence intervals are shown.

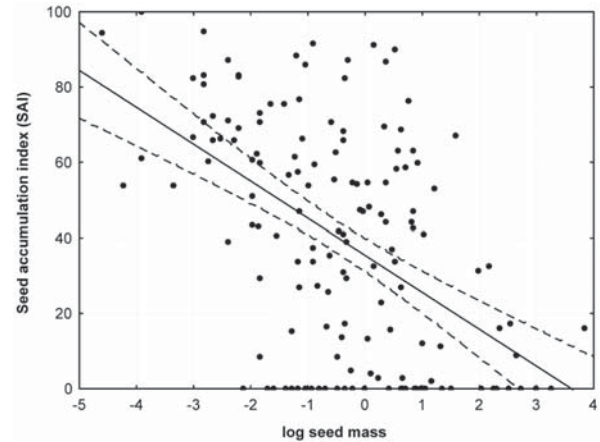


Fig. 2. Correlation between the seed accumulation index (SAI) and log seed mass for a set of 152 species. Regression line and 95 % confidence intervals are shown.

etation. In contrast, most of the dominant grasses and forbs of flood-meadows, such as *Alopecurus pratensis*, *Elymus repens*, *Festuca arundinacea*, *Carex disticha*, *Lathyrus pratensis* and *Vicia cracca* had very low index values. Among the target species of flood-meadows only a limited proportion of about 40% reached high index values of more than 50.

Discussion

In our study the tendency of a species to accumulate seeds in the soil relative to cover in the established vegetation, expressed by the SAI, appeared to be the best predictor of seed persistence among all tested traits. The good agreement ($R^2 = 0.64$) with the seed longevity index of Bekker et al. (1998) is at first surprising, since theoretically considerable flaws can be expected. Potentially, SAI may be strongly influenced by seasonal seed production causing misinterpretations in seed longevity. However, due to the exclusion of superficial diaspore litter during sampling this effect was obviously largely eliminated. This is evident in some abundant species with massive seed production but short-lived seeds, e.g.

Alopecurus pratensis, *Arrhenatherum elatius* which were absent from the soil seed bank samples. Nevertheless, differences in seed production among species with persistent seeds may lead to misinterpretations. However, due to the combination of a frequency index with a quantitative index within the SAI, this problem seems to be at least partially diluted.

With the application of SAI to our data set it was possible to express the tendency in a certain species to accumulate seeds in the soil in a continuous and differentiated way. In comparison to the strictly dichotomous classification of Thompson et al. (1997), allocating species along a gradient of seed persistence is an improvement. As with the seed longevity index SAI will perform better with more records of a certain species. SAI may be applied to other data sets if the relevant vegetation and seed bank data are available. As indicated by the performance of AV/SB_{freq} , presence-absence data may be sufficient to obtain reasonable results.

Depth distribution, highly ranked by other authors (e.g. Thompson et al. 1997), was a significant but comparably weak predictor of seed persistence in the soil ($R^2 = 0.21$). Our results were in line with those obtained by Bekker et al. (1998). Judging from our results, we believe that the vertical distribution of seeds in the soil (in our example DD_{quant}) as a trait of persistence may cause serious flaws and contradictions. Even in species with large long-term persistent seed banks we usually found a steep decrease in seed densities from the upper to the lower layer (App. 1). In contrast, higher concentrations in the lower layer are largely confined to particular situations: typically they occur at sites where singular disturbances or changes in management (e.g. conversion of arable land into grassland, afforestation)

Table 3. Multiple linear regression models with stepwise backward selection of various traits of seed accumulation and depth distribution as dependent variable and seed mass (M), size (S) and shape (SH) as predictor variables.

$n = 152$	Seed attributes (M), (S), (SH)	Significance
SAI	$= -9.59 \times \log(M) - 26.0 \times \log(SH) + 50.78$	$R^2 = 0.38^{***}$
DD_{freq}	$= -4.95 \times \log(M) + 24.1$	$R^2 = 0.10^{***}$
DD_{quant}	$= -3.78 \times \log(M) + 19.03$	$R^2 = 0.06^{**}$
$\log(T_{max})$	$= -0.58 \times \log(M) - 1.60 \leftrightarrow \log(SH) + 1.77$	$R^2 = 0.27^{***}$
$\log(LL_{max})$	$= -0.57 \times \log(M) - 1.28 \leftrightarrow \log(SH) + 0.52$	$R^2 = 0.27^{***}$

have led to a drastic decline or complete disappearance of formerly common species in above-ground vegetation (e.g. arable weeds). This means that in most other cases depth gradients will lead to an underestimation of persistence. Equal or higher concentrations in the lower layer are surely a good indicator of persistence but not necessarily *vice versa*.

Maximum seed concentrations per plot in the lower layer were better correlated with the seed longevity index ($R^2 = 0.39$), which was also true for the entire measured soil profile ($R^2 = 0.34$). Potentially, maximum seed densities including the upper part of the soil profile (in our case 0-10 cm) may yield flawed estimations of longevity due to the regular input of short-term persistent seeds (e.g. Thompson & Grime 1979). As already mentioned this effect was largely reduced by the exclusion of superficial diaspore litter during sampling. In contrast, lower soil layers (in our case 5-10 cm) are usually insignificantly affected by seasonal seed rain (e.g. Poschlod & Jackel 1993), indicating that the burial of seeds is a time-consuming process (Thompson et al. 1997). Thus, the likelihood that short-term persistent seeds will reach deeper soil layers in high quantities is low. A more serious problem is related to differences in seed production among species with long-term persistent seed bank. Species with small seeds and therefore usually heavy seed production (e.g. *Veronica* and *Juncus* species) are more likely to reach high concentrations in lower layers than those with relatively large seeds and/or low and irregular seed production (e.g. *Carex*). This may easily lead to an underestimation of seed longevity in the latter. Principally, the same problem as in depth distribution can occur: High seed concentrations in the lower layer are a good trait of seed longevity but not necessarily *vice versa*. Particularly in studies with poor documentation of established vegetation, high maximum seed densities in the lower layer may give a relatively sound assessment of long-term persistence. They are also particularly relevant for restoration practices, since the likelihood that buried seeds will be exhumed e.g. by earthworm, rodent or mole activity, increases with density.

In accordance with Thompson et al. (1993), Bekker et al. (1998), Hodkinson et al. (1998) and Funes et al. (1999), we found a significant negative correlation between seed mass and shape and the seed longevity index. The predictive power of seed attributes was even higher when SAI and maximum densities per plot were used as the dependent variable. In line with Bekker et al. (1998) seed attributes were revealed to be relatively poor predictors of depth distribution, which reflects the general problems of depth gradients as a seed persistence trait, as discussed above. Although we used a two-dimensional approach to describe seed shape, our

correlations were even better than those obtained by Bekker et al. (1998). Generally, seed shape was a less significant predictor of seed accumulation and persistence than seed mass, as found by other authors (e.g. Moles et al. 2000).

Our results confirm that small and evenly shaped seeds tend to be incorporated into the soil more easily. However, we question the usefulness of this relationship, since the overall variation between seed attributes and persistence is still far too large to give a sufficient accurate assessment for a particular species (Fig. 2). Species with a seed mass < ca. 0.14 mg almost generally exhibit a strong tendency to accumulate seeds in the soil whereas seeds with a mass > 2.7 mg are mostly completely absent from the soil seed bank. Between these thresholds, however, all kinds of variations may occur (Fig. 2).

Significance of seed bank persistence in flood-meadows

In flood-meadows of the type studied, seasonal and inter-annual variations in flooding height and frequency cause distinct vegetation dynamics along elevation gradients. According to the SAI results (App. 1), this particular disturbance regime is reflected by a relatively high number of species with large persistent seed banks compared to other, more stable grassland types (Grime 2001). Typically, these species play a subordinate role in established vegetation. Their existence is strongly facilitated by regular disturbances of the turf in the course of flooding events and following draw-down that weaken dominant grasses and create gaps with low competition (Hölzel unpubl.). Besides annuals such as *Centaureum pulchellum* and *Veronica peregrina*, short-growing carpet-forming ruderals such as *Glechoma hederacea*, *Poa trivialis*, *Potentilla reptans* and *Veronica serpyllifolia* are most common and characteristic among the species with persistent seed banks in flood-meadows. In contrast, the highly competitive dominants of flood-meadows tend to have transient or short-lived seed banks (App. 1).

Our findings are in accordance with theory (Thompson & Grime 1979; Thompson et al. 1998; Grime 2001) that predicts a close relation between the degree of disturbance in a habitat and the tendency in species to form long-term persistent seed banks.

In comparison with other threatened grassland types such as dry chalk grasslands (Poschlod & Jackel 1993; Hutchings & Booth 1996; Bakker et al. 1996b; Stöcklin & Fischer 1999) many target species of flood-meadows, such as *Allium angulosum*, *Arabis nemorensis*, *Cardamine parviflora*, *Carex tomentosa*, *Cerastium dubium*, *Pseudolysimachion longifolium*, *Thalictrum flavum*, *Viola elatior*, *V. persicifolia* and *V. pumila* accumulate persistent seed banks (App. 1). Most of these species are

relatively weak competitors and tend to exploit gaps created by flood-induced disturbances. However, as many as ca. 60% of the target species showed no or only a minor tendency to accumulate seeds in the soil, among them many *Apiaceae* (e.g. *Cnidium dubium* and *Selinum carvifolia*) and *Asteraceae* (e.g. *Cirsium tuberosum* and *Serratula tinctoria*). Generally, seed accumulation and persistence was much lower in character species of *Molinion* meadows (e.g. *Gentiana pneumonanthe*, *Succisa pratensis*), which usually exist under more stable conditions than those of *Cnidion* meadows, which are subject to regular flood disturbance. A relatively large proportion of the target species in the studied flood-meadows can be expected to emerge from the persistent soil seed bank in the course of restoration measures. Indeed, we often observed a sudden re-appearance of target species such as *Arabis nemorensis*, *Cerastium dubium*, *Viola elatior* and *V. persicifolia* at locations where these species have been absent from established vegetation for years and decades, after clear-cutting of shrubbery and poplar plantations or after reintroduction of mowing to fallows and reeds (Hölzel et al. 2002). However, such positive examples seem to be largely restricted to situations that benefit the preservation of persistent seeds in the soil (Milberg 1995; Bekker et al. 1997; Falińska 1999). In contrast, arable cultivation usually leads to a rapid depletion in the persistent seed banks of the former plant communities (e.g. McDonald 1993; Hutchings & Booth 1996; Bischoff 2002; Donath et al. 2003). Under such circumstances, the contribution of buried viable seeds to the restoration of former species richness will often be of low significance (e.g. McDonald et al. 1996; Smith et al. 2002; Vécrcin et al. 2002).

Conclusions

Seed attributes such as mass, size and shape generally showed the same relatively poor performance in predicting seed bank characteristics as in previous studies. We believe that 'easy' traits will not meet the increasing requirements for solid autecological information from those concerned with plant functional theory, modelling, or management and conservation issues. As in the case of data on seed longevity purely derived from artificial burial experiments, too many flaws and contradictions occur. Doubtless, seed attributes cannot substitute further empirical seed bank studies in poorly investigated vegetation types and rare species.

Despite the good agreement between seed longevity index and seed accumulation index, neither index can be expected to be perfectly correlated with the actual or potential seed longevity. An 'exact' determination of

longevity is often frustratingly specific, due to the dominance of marginal conditions and the fuzzy nature of seed persistence in the soil. In contrast, indices based on broad empirical evidence may give an average assessment for the tendency in a particular species to accumulate seeds in the soil, which is often much more relevant for scientific and practical applications.

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