A differentiating method for seed bank analysis: validation and application to successional stages of Koerelio-Corynephoretia inland sand vegetation

by Carlsten Eichberg, Christian Storm, Annelin Kratochwil, and Angelika Schwass, Darmstadt and Osnabrück

with 4 figures and 5 tables

Abstract. Sampling of soil seed banks is known to be methodologically difficult, as the spatial distribution in soil is often patchy. Especially rare plant species are inherently difficult to detect. In our study we validated the accuracy of a sampling method which is based on a high number of individual sample units (100 soil cores/plot, altogether 12 plots) gathered by means of a random systematic sampling design. We used this method in the course of a case study on successional stages of endangered inland sand vegetation in two areas of Germany. We analysed seed bank composition, proportion of endangered specis, similarity between seed bank and aboveground vegetation and grazing impact.

1) Methodological approach. The method produced results with high representativeness. On average, about 78% (top soil: 0–5 cm depth) and 72% (subsoil: 11–16 cm) of the species (jackknife estimator) were detected. The mean Sørensen distance between sample units was low (≤ 0.20 topsoil; ≤ 0.3 subsual). Ordination of the topsoil samples revealed a high degree of homogeneity of the composite samples.

(2) Case study. The soil seed banks of mid-successional stages (Diplotnto-Armerietum, Armerio-Festucetum) were significantly richer in species and differed from the associated pioneer stages (Spartulo-Corynephoretion, Koerelion glaucum). The seed banks of the base-rich successional series were significantly richer in plate species (parallel to aboveground vegetation) as well as in diasporas than the seed banks of the acidic series. Diasporas of many pioneer species were found in very low densities (e.g. Corynephorus canescens) in the soils of mid-successional stages or were not found in these stages (e.g. Phleum arenarium). Thelysperms with higher ability to colonize gaps in mid-successional stages accumulated seed banks, albeit mostly in low densities. Among them were two Red List species (Medicago ramosa, Vicia lathyroides). With some exceptions (e.g. Vicia lathyroides) diasporas of Red List species were found in low abundance in the seed banks (≤ 50 diasporas per m² in topsoil as well as in subsual). Among the Red List species detected in the aboveground vegetation one of four species (25%; acidic series) or seven of 12 species (58%; basic series) were detected in the seed banks. Atwoyear period of extensive sheep grazing did not alter seed banks of Koerelion glaucum and Armerio-Festucetum mandas.

Keywords: grazing impact, jackknife estimator, rare species, seed bank versus aboveground vegetation, Sørensen distance, species area curve.

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1 Introduction

Although the importance of soil seed banks for the regeneration of many plant species has long been known (e.g. Brenchley 1918, Major & Prové 1966, Poschlod 1991), sampling methods have not yet been standardised (Thompson et al. 1997, Jentsch & Bleyschal 2002, Jensen 2004). The main problem in estimating soil diaspore densities is the patchy distribution of diaspores in the soil (Thompson 1986). Thus, several authors recommended collecting many small samples, rather than a few larger ones (Roberts 1981, Bigwood & Inouye 1986, Thompson et al. 1997). Especially rare species are inherently difficult to detect (Thompson et al. 1997, Streyker et al. 1998). For this reason, and because endangered habitats are still infrequently studied, there is a considerable gap in knowledge concerning the diaspore persistence of rare and endangered species (Bakker et al. 1996, Streyker et al. 1998, Thompson et al. 1998, Bosuut & Hermey 2004, Hözel & Otte 2004, Jensen 2004). Many studies on a variety of dry (Donelain & Thompson 1982, Milberg 1992, Poschlod et al. 1996, Jentsch 2002) and wet (Mann & Schopf-Guth 1995, Bosuut & Hermey 2004, Schautzer 2004) open ecosystem types in Europe document a low diaspore persistence of rare and endangered plant species in the soil. For wetlands exceptions from this have been found, e.g. by Bekker et al. (1999) for dune slacks in the Netherlands or by Hözel & Otte (2004) for flood-meadows in Germany.

We were able to validate our differentiating method in inland sand eco-
systems, which are among the highly endangered habitats in Europe (Streyker et al. 1998). There is evidence that besides other factors (e.g. airborne nutrient input) sand ecosystems are endangered particularly by fragmentation, often followed by diaspore limitation. Existing data suggest that their potential for regeneration from soil seed banks is limited, for both acidic and base-rich sand vegetation (Kroupper & Schirane 1996, Kratchewi et al. 2002, Stroh et al. 2002, Jentsch 2004). In addition, diaspore dispersal seems to be limited for many key species of the sand vegetation (Stroh et al. 2002, Jentsch & Bleyschal 2003).

It is a generally observed phenomenon that grasslands on calcareous soils are richer in plant species than grasslands on acidic soils; in our study we ask if this holds true for soil seed banks of inland sand vegetation. Studies on annual Mediterranean pastures showed that in early successional stages seed banks accumulate until a maximum is reached within mid-successional stages (Levassor et al. 1992). For nature conservation purposes it is potential to know how well endangered species can persist in the soil seed bank (Streyker et al. 1998).

Many grassland studies found little similarity between the species composition of the seed bank and the aboveground vegetation (Bakker 1989, ...
There are only a few studies analysing the impact of livestock grazing on seed bank composition (Juttila 1998). Results of these studies are inconsistent and difficult to compare, as ecosystem type and grazing regimes (livestock species, intensity of grazing) vary over a broad spectrum. In many cases grazing causes the soil diaspore density of perennial plant species to decrease (Johnston et al. 1969, Bertiller 1996, Ortega et al. 1997, Juttila 1998, Sternberg et al. 2003).

To our knowledge, investigations of successional series of soil seed banks in a similar substrate on a broader spatial scale with a high degree of comparability (same method, same time span) are rare.

In the present study we focus on generative diaspores. We concentrate on the following questions:

A. Validation of the method
- Is the method suggested in this study adequate for assessing soil seed banks of inland sand ecosystems?

B. Application of the method: inland sand ecosystems
- Are there differences of species diversity and diaspore density depending on a) pioneer and mid-successional stages of sand vegetation, b) subalkaline/acidic and subcontinental/primarily base-rich sand ecosystems, and c) soil depth?
- Is there a potential for endangered species of plant communities of inland sand ecosystems to persist in the soil seed bank?
- How are the soil seed banks related to the aboveground vegetation in the two successional stages and two study areas?
- Does a short period (2 years) of extensive sheep grazing suffice to alter the soil seed bank composition?

2 Study areas

Our investigations took place in the floodplains of the rivers Ems and Hase in north-western Germany (area 1, data set 1) and in the northern upper Rhine valley in south-western Germany (Hesse, district of Darmstadt) (area 2, data set 2). On sandy soils both areas bear vegetation types (pioneer and mid-successional stages) with a high nature conservation value (FFH directive, Stymann et al. 1998). The mid-successional stages are characterised by a high proportion of perennial grasses (e.g. Agrostis spp., Festuca spp., Poa pratensis agg.). In the study sites a successional increase in the total nitrogen content in the soils from pioneer communities (0.02–0.09%) to grasslands (0.28–0.23%) has been shown (Bergmann 2004, Reay & Menzel, 2004).

Area 1. Study sites were “Hammer Schleife” near Haselünne (ca. 37 ha; 5°26’E/52°39’N) and the nature reserve “Sandroekenrasen am Biener Busch” near Lingen (24 ha; 5°15’E/52°34’N). With a mean annual precipi-
tation of about 800 mm and a mean annual temperature of 9.4°C the cli-
mate is subatlantic. The pH-value in 0–10 cm soil depth (measured in 0.01
mol/L CaCl₂ solution) is 4.1–5.0 in pioneer stages or 4.5–4.7 in mid-succes-
sional stages (REMY & MENZEL 2004). On these sites the pioneer stages
belong to the Spargulo morisonii-Corynephoretum typicum (C) and the mid-successional stages mainly belong to the Diantho-deltoïdii-
Armerietum elongatae (D). Additionally there are stands of Spargulo
morisonii-Corynephoretum cladonietosum/Calluna vulgaris stages
(CC).

Area 2. Study site was the nature reserve "Ehemaliger August-Euler-
Flugplatz von Damstadt" (71 ha; 8°39'E/49°51'N). The climate here is
characterised by subcontinental influences with lower annual precipitation
and higher mean annual temperatures (650 mm, 9.9°C). The pH-values
(measured in 0.01 mol/L CaCl₂ solution) of the soils (0–10 cm depth) of
pioneer stands are 7.4–7.5, those of the mid-successional stages are 5.7–7.4
(BERGMANN 2004). On this site the pioneer stages mainly belong to the
Koelerion glaucae (K), the mid-successional stages mainly belong to the
Armerio-Festucetum trachypyllae (A); transitional stages have also
developed: Koelerion glaucae/Armerion elongatae (KA).

C and K on the one hand, and D and A on the other hand can be
considered as equivalent successional stages in sand ecosystems which differ
in climate and soil pH (BERGER-LANDERFELD & SUKOPP 1965, OBER-
DORFER 1993). Area 1 is a historical grazing area (cattle), whereas in area 2
grazing has been established only since 1999 (sheep). For further informa-
tion about the study areas see SCHWARZ & KRAUCHEL (2004) and SYVOSTI
et al. (2005); for successional studies see SIÖSS et al. (2004).

3 Methods

3.1 Seed bank sampling

Plots representative of the above-mentioned vegetation types were sectected
randomly (split-plots of area 2, see below) or judgemental (all plots of area
1 and plots K/K/A; A3 of area 2). Plot size was 25 m² or, in the case of split-
plots, 2 × 20 m². Split-plots were established to investigate the influence of
sheep grazing; one 24-m² plot had been subject to extensive sheep grazing
(paddock of 2–5 ha grazed by 160–190 sheep for 1–2 weeks per year) for
two years while the other one (distances between centres of plots ca. 4–18
m) had been fenced to exclude sheep (but not rabbits). The numbers of
plots (replicates) were 1 (CC/K/A), 2 (C/E) or 3 (K/A).

A random-systematic sampling took place in March/April 2001. From
each plot 100 primary samples (= individual sample units) were taken. In
order to distinguish the clearly, a 1-m² grid was superimposed on the whole
plot. From each grid cell 4 (or 5) primary samples were taken at random.
Sampling device was an Eijkelkamp "liner sampler". The sampled area for
each plot was 0.1735 m². The primary samples were subdivided into two
(area 1) or three layers (area 2), as follows: layer 0: 0–1 cm mineral soil + litter + complete phytolm of cryptogams and phanerogams (only area 2), layer 1: 1–6 cm, layer 2: 11–16 cm. The term "seed bank" refers only to layers 1 and 2. Because for layer 0 a high proportion of transient diasporas can be expected, this layer is considered separately. Material from layers 1 and 2 but not from layer 0 was sieved (mesh width: 5 mm). The soil of ten primary samples was mixed to give a composite sample (= bulk sample). In total, ten composite samples were retrieved per plot per layer.

The soil seed banks were analysed by means of the germination method (THOMPSON et al. 1997). Layer 0 samples were mixed with subsoil from area 2 (which was treated in moist condition at 90–95°C in order to eliminate diasporas) to give the same volume per tray (about 0.9 l) as in case of layers 1 and 2. To eliminate quantitatively vegetative propagules the samples were stored dry at room temperature for several weeks until exposure. The possible disadvantage of inducing secondary dormancy in diasporas of some species should be compensated by the long exposure time (May/July 2001 to June/August 2003). The samples were exposed outdoors in the botanical gardens of the universities of Darmstadt and Osnabrück. They were placed in a special wooden frame with a platform 0.9 m above the soil and covered with gauze. The frames are rooted at a height of 1.5–2 m by transparent plastic. Ventilation was sufficient to ensure exposition at ambient temperature. Emerging seedlings were identified (CAPOROSI 1968, MULLER 1978, HANF 1990), counted and removed every 4–8 weeks. The soil material in the trays was kept continuously moist and was turned 3–7 times within the exposure period. In control trays with heat-treated subsoil (see above) two seedlings of two species (Parietaria officinalis and an unidentified dicotyledonous species) emerged, which were not found in the sample trays. Poa bulbosa was excluded from the data as it was not possible to distinguish between plant individuals that regenerated from carpopores or from bulbs (evidently bulbs are not killed by the drying procedure and can pass through the sieve). In two cases species were pooled: Myosotis ramosissima, M. stricta, Scleranthus annuus agg./X. perennis.

3.2 Aboveground vegetation analysis
In May–July 2001, relevés were made using the cover-abundance scale of BARKMAN et al. (1964). In area 1, five plots of 21–25 m² directly adjacent to the seed bank plots were analysed, while in area 2 the seed bank plots themselves were analysed (whole plot). In previous investigations this technique of seed bank sampling did not alter the vegetation composition (KROHNER & SCHWARTZ 1998). The species Medicago falcata and M. x varia were pooled.

3.3 Data analysis
Whereas the following Section 3.3.1 is based on the data from the individual composite samples, for Section 3.3.2 the ten composite samples of each plot and layer were pooled. The data were analysed by mixed linear models.
(SAS 9.1, Proc Mixed) since the model comprises fixed and random (plots/ blocks) effects due to a split-plot design (Littell et al. 2000). The different soil layers were retrieved from the same soil core and are thus not independent. The same is true for the adjacent grazed/control plot treatments.

### 3.3.1 Assessment of the sampling design
In order to assess whether the sampling design was appropriate to estimate seed bank diversity (number of species) and quantitative seed bank composition (diaspores per species) we applied three methods:

a) Species-sample size curves
Species-area curves have been used in vegetation science to determine the required area of a plot (Greef-Smith 1964), this technique was adopted for seed bank studies (Nümata et al. 1964, Forcella 1984, Gross 1990).

The number of species is displayed against the number of samples (or the sampled surface area). Adapting recommendations for the aboveground vegetation, at least 80% of the species occurring in the seed bank should be detected (Thompson et al. 1997). The software PC-ORD (Version 4.27) allows the construction of specis-area curves on the basis of a subsampling procedure. Thus, uneven curver caused by an arbitrary order of the samples are avoided.

In addition, a jackknife estimator of species richness was applied. According to Palmer (1990, 1991) the first-order jackknife estimator is the most precise estimator: \[ \text{JACX1} = SO + r(1 - n/n) \] (SO: the observed number of species, r: the number of species occurring in only one sample unit, n: the number of sample units). To make the species-sample size curves from different vegetation types comparable, we calculated the percentage of this estimated species richness attained by a certain number of primary samples. This percentage calculated for 100 primary samples was used as dependent variable in two mixed linear models. We tested the influence of the soil layer as independent variable. In the first model we included layers 1 and 2 of areas 1 and 2 (n = 16 per layer), in the second model layers 1 and 2 of area 2 (n = 14 per layer).

b) Dissimilarity measures
In order to take into account the quantitative composition of the samples, PC-ORD calculates the distance between subsamples and the overall species composition, in relation to subsample size. The Sørensen distance (also known as the Czekanowski or Bray-Curtis coefficient) was chosen as a distance measure. The Sørensen distance calculated for 92 primary samples was used as dependent variable in two mixed linear models as described in (a).

c) Ordination
We used detrended correspondence analysis (DCA) to display seed bank composition by means of PC-ORD 4.27. The raw data were log (x + 1)
transformed prior to analysis to avoid undue influence of the dominant species. Ordination without transformation produced essentially the same results in all layers. As most species have only a few occurrences in the data, their influence was reduced by applying downweighting of rare species.

3.3.2 Application in sand vegetation

The data were analysed by two mixed linear models in order to assess the influence of the following independent variables on species number, total diaspore number and, only in case of model b, diaspore number of all individual species: a) study area (1/2), successional stage (pioneer/mid-succes- sional), and soil layer (1/2) and b) successional stage (pioneer/mid-suc- cessional), grazing (0/1) and soil layer (1/2). We regard it as extremely un- likely that soil layer 2 should be influenced by a grazing impact lasting two years. Instead, we argue that an effect of grazing should be restricted to layer 1 and thus result in a significant treatment x soil layer interaction. That is, if both soil layers of a grazed plot are found to be different in the same direction in comparison to those in the control plot, we would regard this as a result of intra-plot differences prior to our experiment. Diaspore numbers were always log or log (x + 1) transformed prior to analyses.

Similarity of seed banks and aboveground vegetation was qualitatively (presence-absence data) analysed using detrended correspondence analysis (DCA) with PC-ORD 4.27. As only phanerogams were investigated in the seed bank analysis, cryptogams of the aboveground vegetation were ex- cluded from ordinations. The same was done with Ps. balsamifera that sprouted vegetatively within seed bank analysis (Section 3.1). Downweighting of rare species was applied to reduce their influence.

Classification of persistence of diaspores that were found in the seed bank follows the key of THOMPSON et al. (1997), which is based on criteria of depth distribution of the diaspores of a species in soil, presence/absence of a species in aboveground vegetation and time span since last record of a species in the vegetation. THOMPSON et al. (1997) distinguish three seed bank types: transient (diaspores viable for  1 yr), short-term persistent (di- aspores viable for 1 yr to < 5 yr) and long-term persistent (diaspores viable for  5 yr).

4 Results

4.1 Assessment of the sampling design

a) Species-sample size curves

Figure 1 shows the species-sample size curves. The percentage of the esti- mated species number of the seed banks attained by 100 primary samples depends significantly on soil layer (layer 1 vs. 2: p = 0.0029; n = 16 per
layer; areas 1 and 2). Layer \( \delta \) differs significantly from layer 2 \((p = 0.0027)\), but not from layer 1 \((p = 0.295; n = 11\) per layer; area 2). The mean percentage decreases in the following order: layer \( \delta \) (83%) > layer 1 (78%) > layer 2 (72%). This is due to the properties of rare species in the layers 0, 1, and 2 and the average proportion of species with occurrence in only 1 of 10 composite samples equals 23%, 33%, and 46%, respectively.

In layer 1 most plots (11/16) reach 82% ± 1% (mean ± SE) of the estimated species number, the other plots, reaching only 69% ± 1%, are plots with a low species number (12–23) and a high proportion of species with occurrence in only one composite sample (42–58%). These plots mainly bear pioneer vegetation.

b) Dissimilarity measures

As Figure 2 shows, 70–90 primary samples are necessary to reach Sørensen distance \(<0.1\), depending on the layer. The mean Sørensen distance calculated for 90 primary samples increases in the following order: layer 2 (0.038) < layer 1 (0.045) < layer 2 (0.074). The difference between layers 1 and 2 is highly significant \((p < 0.0001); n = 16\) per layer, areas 1 and 2).

Again, layer \( \delta \) differed significantly from layer 2 \((p < 0.0001)\), but not from layer 1 \((p = 0.3352; n = 11\) per layer, area 2). Even though the curves do not reach a clearly visible plateau, the low indices indicate that for all layers a high degree of representativeness is attained by 100 primary samples.

c) Ordination

Ordination analysis (DCA) of species composition in the composite samples of layer 1 of areas 1 and 2 reveals the high degree of homogeneity of the composite samples of each plot (Fig. 3). Samples of pioneer stages (C/K) are clearly separated from the corresponding mid-successional stages (D/A), while CC and KA occupy intermediate positions. This is even true for separate ordination analyses of the two areas in an exception, the position of CC is more discrete within data set 1 with close relation only to C5, but not D1; DCA, not shown). Moreover, even the composite samples from the replicates (D1/D2, K1/K2/K3, A1/A2/A3) are more or less apart. An exception is the Spergula-Corynephoretum typicum (C1/C2), which is widespread along axis 1. Generally, the seed banks of the pioneer stages are more inhomogeneous than those of the mid-successional stages. Most composite samples from layer 1 allow identification not only of the vegetation complex but also of individual plots — even if the plots were separated by only a slight distance in the field, as in the cases of the two plots of a split-plot (Section 3.3).

Analyses of layer 2 and layer 2 composite samples are not displayed here, results are as follows: the segregation in layer 0 is very clear as in layer 1 (DCA, data set 2). Due to low diaspore densities and species numbers (C5: 5, CC: 8, D1: 12, K7: 7, KA: 15, A1: 17) and a mean percentage of 58% (area 1) or 41% (area 2) of species with occurrence in only one composite sample
Fig. 1. Species—sample size curves: mean percentages (with standard errors) of the total species number of seed bank plots of Koeleria-Carex sphagnorum sand vegetation depending on the number of primary soil samples for three soil layers: L0: 0—1 cm mineral soil layer; L1: complete phytomass of cryptogams and pteridophytes (11 plots); L1: 1—6 cm (16 plots); L2: 11—16 cm (16 plots). ACKNOWLEDGMENT: first-order jackknife estimator of species richness (see text).

Fig. 2. Distance curves: mean distances (with standard errors) of seed bank plots of Koeleria-Carex sphagnorum sand vegetation depending on the number of primary soil samples for three soil layers (for abbreviations and number of plots per layer see Fig. 1).
Fig. 3. Detrended correspondence analysis (DCA) of species composition in the composite soil (50 cm depth) based on log(x + 1) transformed biomass numbers (158 composite samples, 92 species; two composite samples of C containing no seedlings were excluded). The DCA procedure was adjusted to 26 segments, scaling of axes, downweighting of rare species. The eigenvalues of axes 1, 2 and 3 are 0.674, 0.314 and 0.181, respectively. The same symbol was used for all composite samples of each plot. The two plots of a split plot used to estimate grazing effects are indicated by symbols with the same shape/filled: grazed, empty: not grazed. Vegetation types: C: Spargano-Carpophytorum typicum, CC: Spargano-Carpochno-Sphagnetum uliginosum, C: Carphano-Sphagnetum uliginosum, D: Ðiansky-Armerietum, K: Kotselion glaucæ/Armerion elatigæ; A: Armerio-Festucetum.

Table 1a. Mean species numbers and diaspores densities per soil layer (diaspores m⁻²) with standard errors (n=2) of area 2 (split plot). Soil layers: L0: 0–1 cm quarto, soil + litter ± composite phytosan of crypogams and planograus, L1: 1–6 cm, L2: 7–16 cm. g: grazed, c: control.

<table>
<thead>
<tr>
<th></th>
<th>Number of species</th>
<th>Diaspores m⁻²</th>
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<tbody>
<tr>
<td></td>
<td>L0</td>
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</tr>
<tr>
<td>Kotselion glaucæ</td>
<td>52 ± 6.5</td>
<td>35 ± 6.5</td>
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<tr>
<td>Armerio</td>
<td>28 ± 6.5</td>
<td>21 ± 6.5</td>
</tr>
<tr>
<td>Festucæ</td>
<td>27 ± 6.5</td>
<td>31 ± 6.5</td>
</tr>
</tbody>
</table>
Table 3b. Tests of fixed effects on soil seed bank data (species numbers, diaspore numbers) of the data set of 1a (excluding 1.2) by mixed linear models (SAS 9.1, Proc Mixed). Significant results (p < 0.05) are displayed in bold type. Nd.f.: numerator degrees of freedom, Dd.f.: denominator degrees of freedom.

<table>
<thead>
<tr>
<th>Nd.f.</th>
<th>Dd.f.</th>
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<th>Number of diaspores</th>
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</table>

per plot, the composition of the seed bank in layer 2 is influenced by random variation. This leads to outliers with erratic position in the ordination diagrams of data sets 1 and 2 (DCA).

4.2 Grazing effects

Mean species numbers and diaspore numbers of grazed and not grazed vegetation types (split-plots) are shown in Table 1a. In the mixed linear model of the total diaspore densities of layers 1 and 2 of area 2, only the variable soil layer is significant (p = 0.0002), but not successional stage (K/A), treatment (grazed/control) or any of the interaction terms (Table 1b). With respect to the species number, soil layer (p < 0.0001) and treatment (p = 0.0209) are significant, but again no interaction terms. Thus, we conclude that grazing had no effects so far on either of the dependent variables (cf. Section 3.3.2).

The same is true for the diaspore densities of the individual plant species, as no significant (p > 0.05) interaction effects (treatment x soil layer) were revealed. Diaspore density of Agritris capitata is twofold lower in grazed plots (15% ± 40 diaspores m⁻², mean ± SE) than controls (357 ± 17 of layer 1 of A (layer 2: 23 ± 0 grazed/5 ± 35 control) but due to the low replicate number (n = 2) this tendency is not significant.

For layer 2, which is a special diaspore pool (Section 3.1), Table 1a shows that grazing had no obvious influence since mean values of species numbers and diaspore densities of grazed and not grazed plots are very similar.

4.3 Seed bank composition

The soil seed bank data and the vegetation data are shown in Table 2 (area 1) and Table 3 (area 2). As we could detect no grazing effects (Section 4.2),
Table 2. The data from the soil seed bank analysis (number of seedlings) and the above- 
ground relevés of the Emer area (area 1). Species detected in the seed bank are ordered 
block-wise according to decreasing presence in the seed bank. In area 1, the plots of 
the relevés were located directly adjacent to the respective seed bank plots (see text). 
Characteristic species of inland sand vegetation belong to the phytosociological classes 
Koellerio-Corynephorosereae (R-C) and (in Table 3) Patricio-Brometum (P-B), 
as indicated behind the species names. Species that were detected in the seed banks (SB) 
of area 2 are designated (s) (cf. Table 3). The seeding of Agrostis ap, stands with high 
probability so one of the two identical Agrostis species (A. capillaris, A. vinosus), but 
could not be definitely classified as a particular one; thus, Agrostis ap. was not counted 
as an individual taxon. Vegetation types C. Spargano-Corynephorosereae typicum, 
CC. Spargano-Corynephorosereae cladozonion (C. Cladorrhidion, D. Di-
antho-Armerietum. Red List (RI): G (Germany) according to Kormeck et al. 
1996/97. Lower Saxony (according to Gartz 2004).) It vulnerable, NE near threatened 
in the (lowland). * only concern juveniles.

<table>
<thead>
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<th>Stratum</th>
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<th>Seed bank, 1-2 m deep</th>
<th>Aboveground vegetation</th>
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<td>Pot parts</td>
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<tr>
<td>Grass species (R)</td>
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- Present in the soil seed bank and in the aboveground vegetation:
  - Tectoria cinerea var. (R-C)
  - Tectoria rutila var. (R-C)
  - T. ciliata (R-C)
  - T. imbricata (R-C)
  - T. ciliata (R-C)
  - T. imbricata (R-C)
  - T. ciliata (R-C)
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  - T. imbricata (R-C)
  - T. imbricata (R-C)
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<thead>
<tr>
<th>Species</th>
<th>Seed bank</th>
<th>Soil bank</th>
<th>Abundance vegetation</th>
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</tbody>
</table>

Species numbers and dispersal numbers of grazed plots and control plots of split-plots were averaged for analyses, respectively.

In total, 99 phanerogam taxa (mostly species; area 1; 40, area 2; 73) were detected in the soil seed banks; 12 species additionally in Saver 0 (area 2). In area 1, the five most abundant species in the soil seed banks were (in order of decreasing abundance): Rumex acetosella s.l., Caltha palustris, Carex pseudopurpurea, Euphorbia cyparissias agg., and Polygonum aviculare agg.; in area 2: Potentilla argentea agg., Rumex acetosella s.l., Viola latifolia, Saxifraga tridactylites and Veronica arvensis. Only Rumex acetosella s.l. was detected in the seed banks of all investigated vegetation types. In mid-successional stages and in the stages CC and KA Rumex acetosella s.l. was one of the three dominating species of the seed bank.

Mean species numbers and dispersal densities in each vegetation type are shown in Table 9a. Data analyses by mixed linear models revealed that
Table 3. The data from the soil seed bank analysis (number of seedlings) and the above-ground relevés of the northern upper Rhine area (area 2). Species detected in the seed bank are ordered block-wise according to decreasing presence in the seed bank. Species that were detected in the seed banks (1B) of area 1 are designated (·) (cf. Table 2). The seedlings of Veronica sp. belong with high probability to one of the three identified Veronica species (V. arvensis, V. praecox, V. serpyllifolia), but could not be definitely classified as a particular one; thus, Veronica sp. was not counted as an individual taxon.  

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed bank (B)</th>
<th>Above-ground relevés (A)</th>
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<tr>
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Abiotic vs. biotic environment

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<tr>
<td>90</td>
<td>100</td>
<td>110</td>
<td>120</td>
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</table>

Vegetation types: K - Koeleria glauca, A - Agropyron/A. elongatum, B - A. armerio-Festucetum, E - E. inaequalis, P - P. glauca. For further abbreviations see Table 2.
<table>
<thead>
<tr>
<th>Species</th>
<th>Legend</th>
<th>X</th>
<th>XAI</th>
<th>XAI A</th>
<th>Total (x 10 cm)</th>
<th>X</th>
<th>XAI</th>
<th>XAI A</th>
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<tbody>
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</table>

**Notes:**
- X: Presence in the study area (%)
- XAI: Area in which the species was observed (%)
- XAI A: Area in which the species was observed in absolute terms

**Key:**
- Hummingbird: *Mellisuga hummmingbird*
- Tumbleridge: *Calliope calliope*
- Silvershanks: *Heliophorus argentatus*
- Yellow-bellied: *Zonotrichia capensis*
- Hummingbird: *Selasphorus sp.*

**Legend:**
- X: Presence in the study area (%)
- XAI: Area in which the species was observed (%)
- XAI A: Area in which the species was observed in absolute terms

**Table 3 (cont.)**
### Differentiating method for seed bank analysis

#### Table 1: Seed Bank Development

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<th>Week</th>
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#### Table 2: Seed Bank Composition

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### Notes:

- All seed banks were analysed for the following composition: MA, KA, and A.
- The development stage was determined based on the composition analysis.
- The results show a significant increase in the composition of MA and KA over the weeks.
- The final result indicates that the seed bank analysis was successful.

(Copyrigh 2023)
Table 4a. Mean species numbers and diaspore densities per soil layer (diaspores m⁻²) with standard error of the soil seed banks of areas 1 and 2. Values of grazed and not grazed plots of K. glutinosa glaucae and Armeria-Festucetum stands were pooled prior to analysis (no grazing effect [grazing x soil layer] detectable, see text). Soil layers: L0: 0–1 cm mineral soil + litter + complete phytosociology of cryptogams and phanerogams, L1: 1–4 cm, L2: 11–16 cm. – no data.

<table>
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<th>n Number of species</th>
<th>Dianese m⁻²</th>
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<td>L0</td>
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<tr>
<td>Vegetation types on acidic sand</td>
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</tr>
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<td>Spergula-Corynephor- etum typicum</td>
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<tr>
<td>S.-C. cladoniasorum/ Calysis rupestris stage</td>
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<tr>
<td>Diatomo-Armerietum</td>
<td>2 18 ± 2 10 ± 3</td>
</tr>
<tr>
<td>Vegetation types on primarily calcareous sand</td>
<td></td>
</tr>
<tr>
<td>Koeleria glauca/</td>
<td>3 25 ± 3 20 ± 3 7 ± 2</td>
</tr>
<tr>
<td>Koeleria glauca/</td>
<td>1 31 31 15</td>
</tr>
<tr>
<td>Armeria-Festucetum</td>
<td>3 26 ± 2 31 ± 2 17 ± 2</td>
</tr>
</tbody>
</table>

Table 4b. Test of fixed effects on soil seed bank data (species numbers, diaspore numbers) of the data set of 4a by mixed linear models (SAS 9.3, Proc. Mixed). Significant results (p < 0.05) are displayed in bold type. N.d.f.: numerator degrees of freedom, D.l.f.: denominator degrees of freedom.

<table>
<thead>
<tr>
<th>d.f.</th>
<th>n.d.f.</th>
<th>Number of species</th>
<th>Number of diaspores</th>
</tr>
</thead>
<tbody>
<tr>
<td>F value</td>
<td>p</td>
<td>F value</td>
<td>p</td>
</tr>
<tr>
<td>Area</td>
<td>1 6</td>
<td>17.07</td>
<td>0.0061</td>
</tr>
<tr>
<td>Succession</td>
<td>1 6</td>
<td>17.44</td>
<td>0.0058</td>
</tr>
<tr>
<td>Soil layer</td>
<td>1 6</td>
<td>124.95</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Area x Succession</td>
<td>1 6</td>
<td>2.20</td>
<td>0.1489</td>
</tr>
<tr>
<td>Area x Soil layer</td>
<td>1 6</td>
<td>5.99</td>
<td>0.0282</td>
</tr>
<tr>
<td>Succession x Soil layer</td>
<td>1 6</td>
<td>0.51</td>
<td>0.4331</td>
</tr>
<tr>
<td>Area x Succession x Soil layer</td>
<td>1 6</td>
<td>0.02</td>
<td>0.9300</td>
</tr>
</tbody>
</table>

all independent variables that were tested—area (1/2), successional stage (pioneer/mid-successional) and soil layer (1/2)—had significant influence on species number and total diaspore number (Table 4b).

a) Area. The soil seed banks (layers 1 and 2) of area 1 are richer in species and diaspores than the soil seed banks of area 2. The mean species diversity of layer 1 in area 2 is 1.7-fold higher than that of area 1 (pioneer stages: factor 1.6, mid-successional stages: 1.8). The mean diaspore densities
in layer 1 of area 2 are higher than those of area 1 by the factors 2.9 (pioneer stages) and 5.7 (mid-successional stages).

In Successional stage, the seed banks of pioneer stages are poorer in species than the seed banks of the associated mid-successional stages by the factors 1.5 on 1.9 (C/D, layer 1 or layer 2) and 1.6 or 2.3 (K/A, layer 1 or layer 2). Again, diapause densities show the same interaction with the factors 3.1 or 2.3 (C/D, layer 1 or layer 2) and 6.2 or 6.9 (K/A, layer 1 or layer 2). The mean diapause density of the pioneer vegetation on low-rich soils (K) was approximately as high as the diapause density of the mid-successional vegetation on acidic soils (D). Layer 1 of Armerio-Festucetum showed the highest diapause densities (on average 12,217 diaspores m\(^{-2}\)) and species numbers (on average 51 species). Potentilla argentea agg., Romex acetosella s.l. and the endemically therozylite Vicia lathyroides constitute 68% of the diapause pool in both layers 1 and 2 of Armerio-Festucetum.

c) Soil depth. All seed banks show a clear decrease of species richness and diapause density with soil depth. Layer 1 is richer in species than layer 2 by the factors 1.8 to 2.7 and richer in diaspores by the factors 6.8 to 12.3, depending on the vegetation type.

In case of Koelerion stands the diapause reservoir of layer 0 was richer in species than that of layer 1 by the factor 1.7; in case of Armerio-Festucetum is the opposite: layer 0 being poorer in species than layer 1 by the factor 1.2. Moreover, layer 1 of Armerio-Festucetum is 2.9-fold richer in diaspores than layer 0 of Armerio-Festucetum.

4.4 Rare and endangered species in the soil seed banks

Two Red List species (Red List incl. near threatened species; according to Garske 2004) were detected in the soil seed banks of area 1 (Table 5), of which one was found both in the soil and in the vegetation (Santbus deltoides, in D) (corresponding to 25% of the Red List species that were detected in the aboveground vegetation; Table 2). One Red List species (Sedum saxatile, in CC) was present exclusively in the seed bank. In 2000, some individuals of Sedum were recorded in the aboveground vegetation of permanent plots of C not far from plot CC (Strohs & Kräuchi, 2004).

In area 2, seven Red List species (according to Korneck et al. 1996) were found both in the soil seeds and in the vegetation, corresponding to 58% (7/12) of the Red List species present in the aboveground vegetation. Two further Red List species were detected exclusively in layer CC: Armeria maritima ssp. elongata and Helichrysum arenarium.

Three Red List species (Sedum saxatile, Vicia lathyroides, Medicago minima) were found in layer 1 and layer 2 and fulfill the criteria of at least short-term persistence according to the key of Thompson et al. (1997). With the exceptions of Vicia lathyroides (799 ± 334 diaspores m\(^{-2}\) in layer 1 of A1 mean ± SE) and Sedum saxatile (236 diaspores m\(^{-2}\) in layer 1 of CC), the mean diapause density of the detected Red List species is < 50
Table 5. Mean diaspore densities per soil layer (diaspores m⁻²) with standard errors and presence (Pres.) of endangered species detected in soil seed banks of acid vegetation types in (a) the Etsu area (5 plots) and (b) the northern upper Rhine area (7 plots). Bracketed figures behind the species names denote their Red List status in Germany (according to Kosniwets et al. 1996) and Lower Saxony (De Groot 2004) or Hesse (He; Kosniwets et al. 1996): 2: endangered; 3: vulnerable; NT: not threatened in the lowland; *: least concern. Vegetation types: C: Spargel-Corynephorus typicum; GC: Spargel-Corynephorus cladoni- etum/Galega vulgaris stage; D: Diacho-Armerietum; K: Koeleria glaucescens; KA: Koeleria glaucescens/Armerion elongatae; A: Armerio-Festucetum; soil layers 1.1: 1–6 cm, 1.2: 11–16 cm; time span (months) between the date of soil sample exposition and the last seedling emergence record; see text.

<table>
<thead>
<tr>
<th></th>
<th>C (n = 2)</th>
<th>CC (n = 3)</th>
<th>D (n = 2)</th>
<th>Pres. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L1</td>
<td>L2</td>
<td>L1</td>
<td>L2</td>
</tr>
<tr>
<td>Sedum sexangulare</td>
<td></td>
<td></td>
<td>216</td>
<td>248</td>
</tr>
<tr>
<td>(*/NT)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diathanus delicatus</td>
<td></td>
<td></td>
<td></td>
<td>29 ± 12</td>
</tr>
<tr>
<td>(*/5)</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>K (n = 3)</th>
<th>KA (n = 1)</th>
<th>A (n = 3)</th>
<th>Pres. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L1</td>
<td>L2</td>
<td>L1</td>
<td>L2</td>
</tr>
<tr>
<td>Medicago minima</td>
<td>6 ± 2</td>
<td>3 ± 2</td>
<td>35</td>
<td>6</td>
</tr>
<tr>
<td>(*/2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vicia lathyroides</td>
<td></td>
<td></td>
<td>98</td>
<td>6</td>
</tr>
<tr>
<td>(*/2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Silene coerulea</td>
<td>17 ± 10</td>
<td>12</td>
<td>12</td>
<td>5 ± 3</td>
</tr>
<tr>
<td>(5/2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Silene cotula</td>
<td>7 ± 7</td>
<td>12</td>
<td>9 ± 2</td>
<td>45</td>
</tr>
<tr>
<td>(5/2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corynephorus</td>
<td>13 ± 7</td>
<td>1 ± 1</td>
<td>1 ± 1</td>
<td>45</td>
</tr>
<tr>
<td>canescens (*/3)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phleum arenarium</td>
<td>4 ± 2</td>
<td></td>
<td></td>
<td>19</td>
</tr>
<tr>
<td>(2/2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Veronica prostrata</td>
<td>13 ± 3</td>
<td></td>
<td></td>
<td>14</td>
</tr>
<tr>
<td>(*/5)</td>
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</table>

diaspores m⁻² per plot per seed bank layer. As derived from our data, the soil seed banks of six Red List species (Corynephorus canescens, Dianthus deltoides, Phleum arenarium, Silene coerulea, S. cotula, V. prostrata) were transient (Thompson et al. 1997). In type C and CC of area 1, Corynephorus canescens was detected with higher seed densities than in type K of area 2 and with presence also in layer 2, whereas occurrence in the aboveground vegetation was roughly similar in 2001 (Tables 2 and 3).

The time span between the date of soil sample exposition and the last seedling emergence record of a species gives further hints regarding a species' capacity to persist in the stage of diaspore in soil (Kunzmann 2000). For most of the detected Red List species, apart from Sedum, this time span was 11/2 to 2 yr (Table 5).
4.5 Comparison of soil seed banks and aboveground vegetation

In areas 1 and 2, 69 or 91, respectively, (in total 129) phanerogam taxa (mostly species) were recorded in the soil seed banks and the associated vegetation: 25 (36%) or 50 (55%) of the taxa were detected in both the seed banks and the vegetation, 29 (42%) or 18 (22%) only in vegetation and 15 (22%) or 23 (25%) only in seed banks (Tables 2 and 3). The proportion of target species (Koeleria-Corynephoretea, Festuco-Brometea) among species which occurred exclusively in the seed bank was low (22% or 13%), whereas their proportion among species occurring in seed bank and vegetation was much higher (44% or 56%). Pioneer species with a narrow successional amplitude showed a decrease in soil diaspore density in mid-successional vegetation (e.g. Corynephorus canescens in areas 1 and 2) or were not found in these stages (e.g. Phleum arenarium in area 2), whereas some annual pioneer species with a broader amplitude had higher mean diaspore densities in the seed banks of mid-successional stages (e.g. Aira praecox in area 1, Arenaria serpyllifolia agg, Cerastium semidecandrum and Medicago minima in area 2).

DCA of the complete data set (presence-absence data) showed that the species composition of the aboveground vegetation is relatively closely related to the associated soil seed banks (Fig. 4). The ordination diagram shows a shift of the contrasted strata (three soil layers, vegetation) along the second axis: the deeper the soil layer, the higher the dissimilarity of diaspore pool and vegetation. The second axis reflects the successions gradient and the specific character of seed banks and vegetation due to species occurring only in one of the two types. While the samples of RA occupy intermediate positions between R and A, the samples of CC have more discrete positions with close relation only to C, but not D. As an exception, the seed bank layers of one mid-successional plot (A3) were more similar to the aboveground vegetation of pioneer stages (K) than to its own associated vegetation. The first axis reflects the fact that the qualitative species compositions of the seed banks of the study areas are less similar to each other (15% overall similarity) than is the aboveground vegetation of these areas (24%).

5 Discussion

5.1 Assessment of the sampling design

The analysis of the sampling procedure revealed that the method produced reliable results for the study communities. A higher degree of species list completeness would require a disproportionate sampling effort, because many of the species were present in only one composite sample (especially in the subsoil samples). More important than a greater completeness is the representativeness of the results. In this respect the method works excellently: 7–9 composite samples were sufficient to reach a low Sørensen
distance (< 0.1). This indicates that the quantitative composition of the ten composite samples reflected properly the composition of the soil seed bank. This is documented also by the ordination analyses: almost every single composite sample of layer 0 or layer 1 is sufficient to determine the vegetation complex and even more accurately reflects individual plots.

Some 102 primary samples have been established as a sufficient number for seed bank analysis in various ecosystems by Champness (1949), Forcella (1984), Bendit et al. (1989), Gross (1990), Ten Heerdt et al. (1996) and Jones (1998).
5.2 Grazing effects

We found that species diversity and diaspore density of the soil seed banks of inland sand vegetation were not altered by the initiation of extensive sheep grazing after a 2-year grazing period. For the converse case of an experimental cessation of established sheep grazing by fencing plots in pastures of annual plant communities in Australia, Maronier & Facelli (1999) found no significant change in the soil seed banks even after a 7- to 12-year period. Of course, besides ecosystem type, grazing influence depends to a great extent on grazing intensity and the overall time span of grazing. This is especially true for the strata of soil seed banks, as it takes some time for diaspores to be incorporated into the soil and move down through it (Van Tooren '88). On the other hand, livestock trampling can enforce diaspore incorporation (seed bank replenishment; Eichberg et al. 2005) or, conversely, uncover buried diaspores and stimulate them to germinate (seed bank depletion). In the case of area 2 aboveground-vegetation changes due to grazing were also slight in 2001.

The finding of Jutis (1999) that the seed bank of Agrostis capillaris was significantly reduced on cattle-grazed seashore meadows compared with non-grazed seashore meadows in Finland is not in contradiction to our data. Agrostis capillaris showed consistently (but not significantly) lower diaspore numbers in layer 1 seed banks of sheep-grazed Armerio-Festucetum stands than in not grazed Armerio-Festucetum stands, and inconsistent treatment effects in layer 2 (Section 3.3.2). In Diantho-Armerietum stands of area 1, Kratochwil et al. (2002) found that extensive cattle grazing caused a severe reduction of the numbers of inflorescences and intraspecífic differences of Agrostis capillaris by 71% and 72%, respectively.

5.3 Seed bank composition

We found a species and diaspore enrichment of the soil seed bank from pioneer to mid-successional stages of inland sand vegetation. Alteration of seed bank diversity and density during the course of succession depends mainly on the investigated section of a successional series. After an early phase of species and diaspore enrichment due to colonising processes (e.g. Levavassor et al. 1990), seed bank diversity and density typically decline due to competitive exclusion processes in the aboveground vegetation since a stage of wood is reached (e.g. Donelan & Thompson 1980).

The two investigated successional stages are richer in species and diaspores in the subcontinental area with primarily calcareous soils, corresponding to the higher diversity of the associated aboveground vegetation. Grasslands on calcareous soils are known to be richer in species than grasslands on acidic soils (Regon et al. 1996). There are some indications that the associated seed banks behave the same. Knolupper & Schwar (1998), using the same sampling method as in the present study, found a species number (topsoil: 11 ± 5, subsoil: 3 ± 1; mean ± SE; n = 3) and diaspore density (1259 ± 320, 49 ± 27 diaspores m⁻²) for soil seed banks of Sper-
Rare and endangered species in the soil seed banks

In our data the diaspore densities of endangered species in soil were mostly low (<50 diaspores m⁻²) in layer 1 as well as in layer 2, except Sedum exangulare and Vicia lathyroides. From our data the best evidence of a pronounced capacity for diaspore persistence in soil among the Red List species can be derived for the annual Fabaceae species Vicia lathyroides and Medicago minima, which were present frequently in the soil layers 1 and 2 in the northern upper Rhine area. Both species were more abundant in the vegetation of pioneer stages and, in stage of diaspore, more abundant in the seed banks of mid-successional stages. Thus, some endangered species do accumulate seed banks in the course of early to mid succession. However, the percentages of Red List species of the aboveground vegetation that were detected also in the soil seed bank were low (25%, acidic series) or moderate (58%, basic series). Most of the endangered species seem to be dependent on a more or less constant supply of diaspores by plant individuals growing in the aboveground vegetation. Thus, acquiring more knowledge about the minimum diaspore density a species requires to re-establish itself successfully after a time of absence from aboveground vegetation could be an important objective for future research (Thompson & Birkner 2004).

In previous investigations stir further Red List species were found in low densities in soil seed banks of our study areas (area 1); Ranunculus bulbosus in 1–6 cm depth, Kranzochloa et al. 2002; area 2: Alyssum montanum, spp. gmelini, Pae rodendron and Vesicularia rivularis in 1–6 cm depth, Euphorbia seguieriana and Mitracentron minima in 1–6 cm and 11–16 cm depth, Kranzochloa

Comparison of soil seed banks and aboveground vegetation

Ordination of the presence-absence values of soil seed banks and aboveground vegetation showed a shift of the seed bank samples of mid-succes-
sional stages towards earlier successional stages for both areas. The absence of mid-successional (mostly perennial) species from soil seed banks although they occurred in the aboveground vegetation, such as Ranunculus bulbosus (area 1), Hieracium pilosella (area 2) and Bromus berteronius (areas 1 and 2), as well as the occurrence of some pioneer species in the x.d. banks but not the vegetation of later successional stages, such as Alnus glutinosa (area 1), Sisymbrium triquetrifolium (area 2) and Carex buxbaumii canescens (areas 1 and 2), can be considered as important reasons for the dissimilarity shift between seed banks and vegetation. However, the occurrence of these pionee species in the seed banks of later successional stages was more an exception than the rule, and their dispor density were mostly low. A decrease of seed banks of early successional species in the course of succession has also been shown by Mikkelsen et al. (2000) for hayfields in the Netherlands, Matos et al. (2003) for sandy steppe-meadows in Hungary and Bossuyt & Hermans (2004) for dune slacks in Belgium.

In contrast, some annual pioneer species with a broader successional amplitude showed an accumulation of diasprores in the soil during early to mid succession (e.g. Chenopodium serpyllifolia agg., Cerastium semidecandrum and Medicago minima in area 2). These subordinate herbs are well-adapted to colonize gaps in grass-dominated communities, e.g. livestock trails of sheep (Schwarz et al. 2004).

6 Conclusion

According to our results we recommend the applied method of seed bank sampling. The sampling design can easily be modified for usage at different spatial scales according to the vegetation type of research interest.

Proceeding from the results of our case study, we conclude that the populations of many species of open sand vegetation can endure a few years of severely reduced diaspro production because the diasprores survive in the soil, but these diasprores are not able to hofer long periods during which the species have disappeared from the aboveground vegetation. Thus, continuous disturbance dynamics, which lead to an activation and a replenishment of soil seed banks (e.g. by herbivore activity, selection processes), are essential for many sand species. Especially stenoecious therophytes of initial colonisation stages (e.g. Phleum arenarium) are highly endangered by abandonment. Species capable of growing in a longer (early to mid) successional time sequence, known as effective gap colonisers, are less vulnerable to short-term phases of dedynamisation. Among them are common sand species (e.g. Cerastium semidecandrum), but also endangered ones (e.g. Medicago minima). The question whether primarily diaspro persistence in soil enables these species to colonize gaps efficiently or other mechanisms (e.g. high annual diaspro production, effective diaspro dispersal) are more important, or whether it is the combination of many processes, seems to be a worthwhile issue for future research.


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Addresses of the authors:
Dr. Christian Eschenburg, Dr. Christian Stock and Prof. Angelika Schwarz, Darmstadt University of Technology, Department of Biology/Vegetation Ecology, Schnittmühlenstr. 6, 64287 Darmstadt, Germany. E-mail: christian.stock@bio.tu-darmstadt.de
Prof. Dr. Amelie Kästlin, University of Osnabrück, Department of Ecology, Bar-
barastr. 11, 49069 Osnabrück, Germany. E-mail: krautkiewicz@biologie.uni-osnabrueck.de