| Phytocoenologia | 36 (2) | 161–189 | Berlin–Stuttgart, June 14, 2006 |
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# A differentiating method for seed bank analysis: validation and application to successional stages of Koelerio-Corynephoretea inland sand vegetation

by Carsten EICHBERG*, Christian STORM*, Anselm KRATOCHWIL** and Angelika SCHWABE*, Darmstadt* and Osnabrück**

with 4 figures and 5 tables

**Abstract.** Sampling of soil seed banks is known to be methodologically difficult, as diaspore 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 species, similarity between seed bank and aboveground vegetation and grazing impact.

**(1) Methodological approach.** The method produced results with high representativeness. On average, about 78 % (topsoil: 1–6 cm depth) and 72 % (subsoil: 11–16 cm) of the species (jackknife estimator) were detected. The mean SØRENSEN distance between 9 and 10 composite samples (each consisting of 10 soil cores) was low (< 0.05 topsoil, < 0.1 subsoil). 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 (Diantho-Armerietum, Armerio-Festucetum) were significantly richer in species and diaspores than the associated pioneer stages (Spergulo-Corynephoretum, Koelerion glaucae). The seed banks of the base-rich successional series were significantly richer in plant species (parallel to aboveground vegetation) as well as in diaspores than the seed banks of the acidic series. Diaspores 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*). Therophytes with higher ability to colonise gaps in mid-successional stages accumulated seed banks, albeit mostly in low densities. Among them were two Red List species (*Medicago minima, Vicia lathyroides*). With some exceptions (e.g. *Vicia lathyroides*) diaspores of Red List species were found in low abundances in the seed banks (< 50 diaspores $m^{-2}$ in topsoil as well as in subsoil). 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. A two-year period of extensive sheep grazing did not alter seed banks of Koelerion glaucae and Armerio-Festucetum stands.

**Keywords:** grazing impact, jackknife estimator, rare species, seed bank versus aboveground vegetation, SØRENSEN distance, species-area curves.

DOI: 10.1127/0340-269X/2006/0036-0161 0340-269X/06/0036-0161 $ 7.25

**Nomenclature:** The nomenclature follows Wisskirchen & Haeupler (1998) for phanerogams (in case of *Elymus campestris*: Oberdorfer 2001), Koperski et al. (2000) for bryophytes and Scholz (2000) for lichens.

## 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 & Pyott 1966, Poschlod 1991), **sampling methods** have not yet been standardised (Thompson et al. 1997, Jentsch & Beyschlag 2003, Jensen 2004). The main problem in estimating soil diaspore densities is the patchy distribution of diaspores in the soil (Thompson 1986). Thus, several authors recommend collecting many small samples, rather than a few larger ones (Roberts 1981, Bigwood & Inouye 1988, Thompson et al. 1997). Especially rare species are inherently difficult to detect (Thompson et al. 1997, Strykstra 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, Strykstra et al. 1998, Thompson et al. 1998, Bossuyt & Hermy 2004, Hölzel & Otte 2004, Jensen 2004). Many studies on a variety of dry (Donelan & Thompson 1980, Milberg 1992, Poschlod et al. 1996, Jentsch 2004) and wet (Maas & Schopp-Guth 1995, Bossuyt & Hermy 2004, Schrautzer 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 Hölzel & Otte (2004) for flood-meadows in Germany.

We were able to validate our differentiating method in **inland sand ecosystems**, which are among the highly endangered habitats in Europe (Ssymank 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 (Krolupper & Schwabe 1998, Kratochwil 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 & Beyschlag 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. 1990). For nature conservation purposes it is essential to know how well endangered species can persist in the soil seed bank (Strykstra et al. 1998).

Many grassland studies found little similarity between the species composition of the seed bank and the aboveground vegetation (Bakker 1989,

BEKKER 1998, EDWARDS & CRAWLEY 1999, TOUZARD et al. 2002, JENTSCH 2004).

There are only a few studies analysing the impact of livestock grazing on seed bank composition (JUTILA 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, JUTILA 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) subatlantic/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, SSYMANK 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 (0.08–0.23 %) has been shown (BERGMANN 2004, REMY & MENZEL 2004).

**Area 1.** Study sites were "Hammer Schleife" near Haselünne (ca. 37 ha; 7°26′E/52°39′N) and the nature reserve "Sandtrockenrasen am Biener Busch" near Lingen (24 ha; 7°15′E/52°34′N). With a mean annual precipitation of about 800 mm and a mean annual temperature of 9.4 °C the climate is subatlantic. The pH-value in 0–10 cm soil depth (measured in 0.01 mol/l $CaCl_2$ solution) is 4.1–5.0 in pioneer stages or 4.5–4.7 in mid-successional stages (REMY & MENZEL 2004). On these sites the pioneer stages belong to the Spergulo morisonii-Corynephoretum typicum (C) and the mid-successional stages mainly belong to the Diantho deltoidis-Armerietum elongatae (D). Additionally there are stands of Spergulo morisonii-Corynephoretum cladonietosum/*Calluna vulgaris* stages (CC).

**Area 2.** Study site was the nature reserve "Ehemaliger August-Euler-Flugplatz von Darmstadt" (71 ha; 8°35′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 $CaCl_2$ 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 trachyphyllae (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-LANDEFELDT & SUKOPP 1965, OBERDORFER 1993). Area 1 is a historical grazing area (cattle), whereas in area 2 grazing has been established only since 1999 (sheep). For further information about the study areas see SCHWABE & KRATOCHWIL (2004) and STROH et al. (2005); for successional studies see SÜSS et al. (2004).

## 3 Methods

### 3.1 Seed bank sampling

Plots representative of the above-mentioned vegetation types were selected randomly (split-plots of area 2, see below) or judgemental (all plots of area 1 and plots K3/KA/A3 of area 2). Plot size was 25 $m^2$ or, in the case of split-plots, 2 × 24 $m^2$. Split-plots were established to investigate the influence of sheep grazing: one 24-$m^2$ plot had been subject to extensive sheep grazing (paddocks 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/KA), 2 (C/D) 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 distribute them evenly, a 1-$m^2$ 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 $m^2$. 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 phytomass 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 diaspores 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 diaspores) 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 diaspores of some species should be compensated by the long exposition 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 roofed at a height of 1.5–2 m by transparent plastic. Ventilation was sufficient to ensure exposition at ambient temperatures. Emerging seedlings were identified (Csapody 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 caryopses 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./*S. 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 m$^2$ 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 (Krolupper & Schwabe 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 (GREIG-SMITH 1964); this technique was adopted for seed bank studies (NUMATA et al. 1964, FORCELLA 1984, GROSS 1990). The number of species is displayed against the number of samples (or the sampled surface area). Adopting 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 species-area curves on the basis of a subsampling procedure. Thus, uneven curves 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: JACK1 = SO + r1(n − 1)/n (SO: the observed number of species, r1: 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 0, 1 and 2 of area 2 (n = 11 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 90 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-successional) and soil layer (1/2) and b) successional stage (pioneer/mid-successional), grazing (0/1) and soil layer (1/2). We regard it as extremely unlikely 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 inter-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 excluded from ordination. The same was done with *Poa bulbosa* 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 (diaspores viable for 1 yr to $< 5$ yr) and long-term persistent (diaspores viable for $\geq 5$ 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 estimated 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 0 differs significantly from layer 2 ($p = 0.0027$), but not from layer 1 ($p = 0.2951$; $n = 11$ per layer; area 2). The mean percentage decreases in the following order: layer 0 (83 %) > layer 1 (78 %) > layer 2 (72 %). This is due to the proportion of rare species: in the layers 0, 1 and 2 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 0 (0.038) < layer 1 (0.040) < 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 0 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 (as an exception, the position of CC is more discrete within data set 1 with close relation only to C, but not D; 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 Spergulo-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 3.1).

Analyses of **layer** 0 and **layer 2** composite samples are not displayed here; results are as follows: the segregation in layer 0 is as clear as in layer 1 (DCA, data set 2). Due to low diaspore densities and species numbers (C: 5, CC: 8, D: 10, K: 7, KA: 15, A: 17) and a mean percentage of 58 % (area 1) or 41 % (area 2) of species with occurrence in only one composite sample

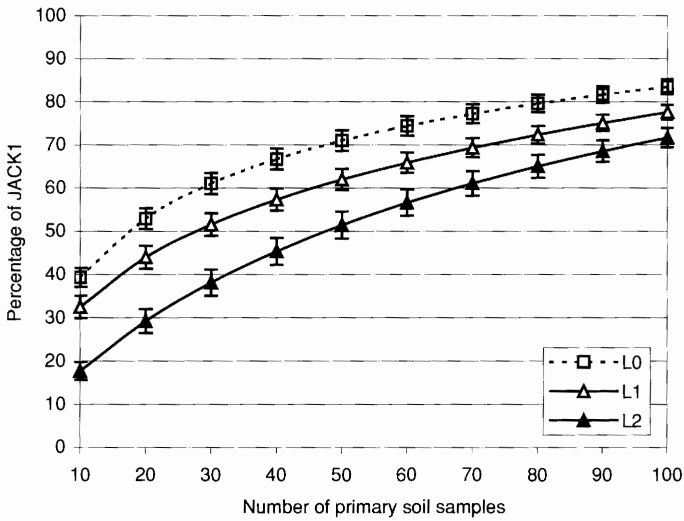


Fig. 1. Species-sample size curves: mean percentages (with standard errors) of the estimated total species number of seed bank plots of Koelerio-Corynephoretea inland sand vegetation depending on the number of primary soil samples for three soil layers: L0: 0–1 cm mineral soil + litter + complete phytomass of cryptogams and phanerogams (11 plots), L1: 1–6 cm (16 plots), L2: 11–16 cm (16 plots). JACK1: first-order jackknife estimator of species richness (see text).

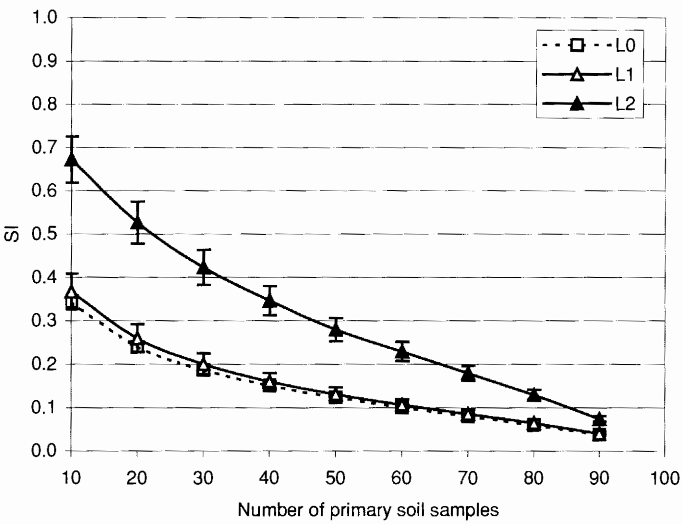


Fig. 2. Distance curves: mean SØRENSEN distances (SI) (with standard errors) of seed bank plots of Koelerio-Corynephoretea inland sand vegetation depending on the number of primary soil samples for three soil layers (for abbreviations and number of plots per layer see Fig. 1).

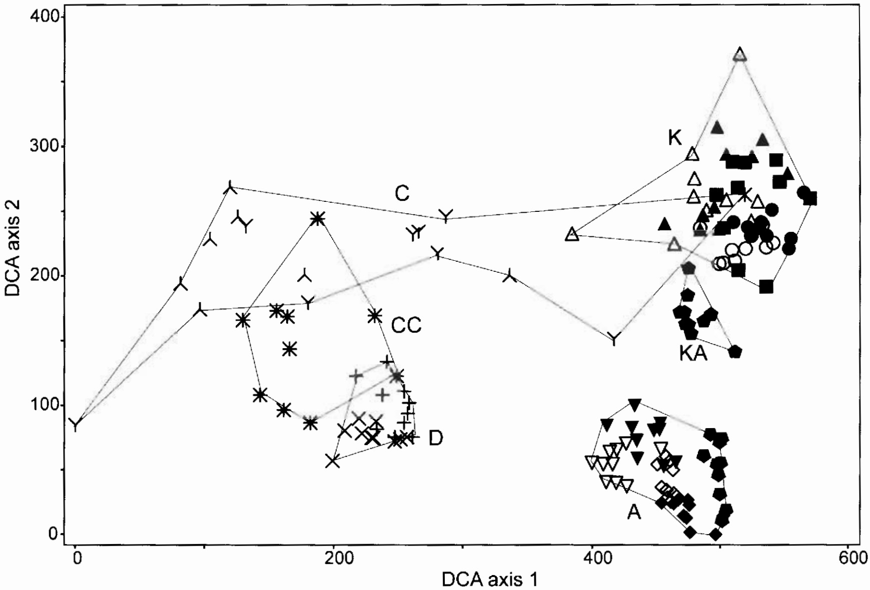


Fig. 3. Detrended correspondence analysis (DCA) of species composition in the composite seed bank samples (1–6 cm depth) based on log (x + 1) transformed diaspore numbers (158 composite samples, 92 species; two composite samples of C containing no seedlings were excluded). The DCA procedure was adjusted to: 26 segments, rescaling of axes, downweighting of rare species. The eigenvalues of axis 1, axis 2 and axis 3 are 0.624, 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 investigate grazing effects are indicated by symbols with the same shape (filled: grazed, empty: not grazed). Vegetation types: C: Spergulo-Corynephoretum typicum, CC: Spergulo-Corynephoretum cladonietosum/ *Calluna vulgaris* stage, D: Diantho-Armerietum, K: Koelerion glaucae, KA: Koelerion glaucae/Armerion elongatae, A: Armerio-Festucetum.

Table 1a. Mean species numbers and diaspore densities per soil layer (diaspores $m^{-2}$) with standard errors (n = 2) of area 2 (split-plots). Soil layers: L0: 0–1 cm mineral soil + litter + complete phytomass of cryptogams and phanerogams, L1: 1–6 cm, L2: 11–16 cm. g: grazed, c: control.

| | | Number of species | | | Diaspores $m^{-2}$ | | |
|---|---|---|---|---|---|---|---|
| | | L0 | L1 | L2 | L0 | L1 | L2 |
| Koelerion glaucae | g | 27 ± 5 | 23 ± 6 | 11 ± 4 | 4355 ± 2539 | 3087 ± 124 | 308 ± 187 |
| | c | 28 ± 1 | 19 ± 3 | 6 ± 4 | 4793 ± 1819 | 1914 ± 190 | 124 ± 101 |
| Armerio- | g | 29 ± 6 | 34 ± 1 | 21 ± 1 | 3493 ± 1435 | 13061 ± 4369 | 1487 ± 29 |
| Festucetum | c | 27 ± 0 | 31 ± 4 | 17 ± 1 | 3556 ± 484 | 11612 ± 4061 | 1334 ± 233 |

Table 1b. Tests of fixed effects on soil seed bank data (species numbers, diaspore numbers) of the data set of 1a (excluding L0) 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.

| | Nd.f. | Dd.f. | Number of species | | Number of diaspores | |
|---|---|---|---|---|---|---|
| | | | F value | p | F value | p |
| Succession | 1 | 2 | 7.98 | 0.1058 | 15.31 | 0.0595 |
| Grazing | 1 | 6 | 9.66 | 0.0209 | 2.63 | 0.1560 |
| Soil layer | 1 | 6 | 102.04 | < 0.0001 | 69.39 | 0.0002 |
| Succession x grazing | 1 | 6 | 0.34 | 0.5813 | 1.47 | 0.2713 |
| Succession x soil layer | 1 | 6 | 0.04 | 0,8524 | 1.72 | 0.2375 |
| Grazing x soil layer | 1 | 6 | 0.04 | 0.8524 | 0.38 | 0.5603 |
| Succession x grazing x soil layer | 1 | 6 | 0.00 | 1.0000 | 0.38 | 0.5606 |

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 *Agrostis capillaris* is twofold lower in grazed plots (156 ± 40 diaspores $m^{-2}$, mean ± SE) than controls (357 ± 17) of layer 1 of A (layer 2: 23 ± 0 grazed/52 ± 35 control), but due to the low replicate number ($n = 2$) this tendency is not significant.

For **layer** 0, 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 aboveground relevés of the Ems 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 Koelerio-Corynephoretea (K-C) and (only in Table 3) Festuco-Brometea (F-B), as indicated behind the species names. Species that were detected in the seed banks (SB) of area 2 are designated (x) (cf. Table 3). The seedling of *Agrostis* sp. belongs with high probability to one of the two identified *Agrostis* species (*A. capillaris*, *A. vinealis*), but could not be definitely classified as a particular one; thus, *Agrostis* sp. was not counted as an individual taxon. Vegetation types: C: Spergulo-Corynephoretum typicum, CC: Spergulo-Corynephoretum cladonietosum/*Calluna vulgaris* stage, D: Diantho-Armerietum. Red List status (RL): G: Germany (according to Korneck et al. 1996)/L: Lower Saxony (according to Garve 2004), 3: vulnerable, NT: near threatened (in the lowland), *: least concern. juv: juvenile.

| RL G/L | SB area 2 | Stratum | Seed bank 1-6 cm | | | | | Seed bank 11-16 cm | | | | | Aboveground vegetation | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Vegetation type | C | | CC | D | | C | | CC | D | | C | | CC | D | |
| | | Plot code | C1-1 | C2-1 | CC-1 | D1-1 | D2-1 | C1-2 | C2-2 | CC-2 | D1-2 | D2-2 | C1-v | C2-v | CC-v | D1-v | D2-v |
| | | Plot size (m²) | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 21 | 25 | 25 |
| | | Number of diaspores/stratum | 98 | 139 | 524 | 308 | 430 | 27 | 8 | 67 | 69 | 12 | - | - | - | - | - |
| | | Number of species/stratum | 12 | 12 | 23 | 16 | 19 | 6 | 4 | 8 | 12 | 7 | 44 | 20 | 33 | 32 | 32 |
| | | Number of phanerogam species/stratum | 12 | 12 | 23 | 16 | 19 | 6 | 4 | 8 | 12 | 7 | 36 | 16 | 15 | 28 | 26 |
| | | Number of cryptogam species | - | - | - | - | - | - | - | - | - | - | 8 | 4 | 18 | 4 | 6 |
| | | Total plant cover (%) | - | - | - | - | - | - | - | - | - | - | 40 | 45 | 75 | 95 | 97 |
| | | Cover of grasses + herbs (%) | - | - | - | - | - | - | - | - | - | - | 35 | 30 | 55 | 70 | 75 |
| | | Cover of cryptogams (%) | - | - | - | - | - | - | - | - | - | - | 7 | 25 | 30 | 50 | 30 |
| | | Cover of bare ground (%) | - | - | - | - | - | - | - | - | - | - | 60 | 55 | 25 | 5 | 3 |
| | | **Present in the soil seed bank and in the aboveground vegetation** | | | | | | | | | | | | | | | |
| | x | Rumex acetosella s.l. (K-C) | 5 | 6 | 179 | 49 | 164 | . | . | 1 | 7 | 2 | 2m | 1 | 2m | 2m | 2m |
| | x | Corynephorus canescens (K-C) | 13 | 52 | 101 | . | 3 | 3 | 4 | 6 | . | . | 2b | 2b | 2m | . | . |
| | | Aira praecox (K-C) | 7 | 3 | 17 | 15 | . | . | . | 5 | 1 | . | 2m | 1 | 2m | . | . |
| | | Carex arenaria (K-C) | 2 | 56 | 110 | 1 | . | 18 | . | 8 | . | . | 2m | 2m | 2m | . | . |
| | x | Agrostis capillaris | . | 1 | 5 | 81 | 83 | . | . | . | 8 | 3 | 1 | 1 | + | 2b | 2a |
| | | Poa pratensis s.str. | 2 | . | 1 | 14 | 1 | . | . | . | 1 | . | 2m | . | . | 2m | 2m |
| | x | Sedum acre (K-C) | 1 | 6 | 1 | . | . | . | 1 | . | . | . | 2m | + | . | + | . |
| | | Trifolium dubium | . | . | . | 43 | 48 | . | . | . | 4 | 1 | 1 | . | . | 1 | 2m |
| | | Veronica serpyllifolia | . | . | . | 11 | 6 | . | . | . | 1 | 1 | r | . | . | . | 1 |
| | x | Cerastium semidecandrum (K-C) | 22 | 2 | . | . | . | 2 | . | . | . | . | 2m | 1 | 1 | 1 | + |
| | x | Erophila verna (K-C) | 17 | 9 | . | . | 17 | . | . | . | . | . | 2m | 1 | . | 1 | 1 |
| | | Spergula morisonii (K-C) | . | 1 | 6 | . | . | . | 2 | . | . | . | 1 | + | 2m | . | . |
| | | Festuca rubra s.l. | . | . | 5 | . | . | . | . | 2 | 12 | . | 2m | . | . | 3 | 3 |
| | x | Agrostis vinealis (K-C) | . | . | . | 16 | 15 | . | . | . | 6 | . | 2m | 2m | 2a | 2a | 3 |
| | | Teesdalia nudicaulis (K-C) | 25 | 1 | . | . | . | . | . | . | . | . | 1 | 2m | 2m | . | . |
| */3 | | Dianthus deltoides (K-C) | . | . | . | 3 | 7 | . | . | . | . | . | . | . | . | 2m | 2m |
| | x | Cerastium arvense | . | . | . | 2 | 2 | . | . | . | . | . | . | . | . | 2m | 1 |
| | x | Cerastium holosteoides | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | 1 |
| | | Stellaria graminea | . | . | . | . | 4 | . | 1 | . | . | . | . | . | + | + | 1 |
| | x | Arabidopsis thaliana | . | 1 | . | . | . | . | . | . | . | . | 2m | 1 | . | . | . |
| | | Calluna vulgaris | . | . | 33 | . | . | . | . | . | . | . | . | . | 1 | . | . |
| | | Luzula campestris | . | . | 3 | . | . | . | . | . | . | . | 1 | . | 2m | . | . |
| | | Alopecurus pratensis | . | . | 1 | . | . | . | . | . | . | . | . | . | . | 1 | 1 |
| | | Cytisus scoparius | . | . | 1 | . | . | . | . | . | . | . | 1(juv) | . | . | . | . |
| | | Tanacetum vulgare | . | . | . | 1 | . | . | . | . | . | . | . | . | . | 1 | . |
| | | **Only present in the soil seed bank** | | | | | | | | | | | | | | | |
| | | Juncus bufonius | 1 | . | 6 | 3 | 1 | 1 | . | . | 17 | 3 | . | . | . | . | . |
| | x | Conyza canadensis | 2 | 1 | 1 | . | . | 2 | . | . | . | . | . | . | . | . | . |
| | | Salix cf. cinerea | 1 | . | . | 1 | 1 | . | . | . | . | 1 | . | . | . | . | . |
| | | Juncus effusus | . | . | 5 | . | 3 | . | . | 1 | 8 | . | . | . | . | . | . |
| | x | Polygonum aviculare agg. | . | . | . | 45 | 70 | . | . | . | 2 | . | . | . | . | . | . |

Cryptogams present in the aboveground vegetation: **C1-v:** Brachythecium albicans 2m, Ceratodon purpureus 2m, Cladonia furcata +, Dicranum scoparium 1, Polytrichum juniperinum 2m, P. piliferum 2m, Rhytidiadelphus squarrosus 1, Scleropodium purum +; **C2-v:** Campylopus introflexus 2b, Ceratodon purpureus 2m, Cladonia pyxidata agg. 1, Polytrichum piliferum 2m; **CC-v:** Campylopus introflexus 2m, Ceratodon purpureus 2b, Cetraria aculeata +, Cladonia arbuscula 2m, C. ciliata 2m, C. coccifera 1, C. furcata 1, C. macilenta ssp. floerkeana 2m, C. portentosa 1, C. pyxidata agg. 1, C. subulata +, C. uncialis 2m, Dicranum scoparium 2m, Hypnum cupressiforme s.l. 2m, Pleurozium schreberi 2m, Polytrichum juniperinum 1, P. piliferum 2a, Rhytidiadelphus squarrosus 2m; **D1-v:** Brachythecium albicans 2a, Ceratodon purpureus 2m, Rhytidiadelphus squarrosus 3, Scleropodium purum 2m; **D2-v:** Brachythecium albicans 2m, B. rutabulum 1, Ceratodon purpureus 2m, Polytrichum juniperinum 1, Rhytidiadelphus squarrosus 3, Scleropodium purum 2m.

Table 2. (cont.)

| | Stratum | Seed bank 1-6 cm | | | | | Seed bank 11-16 cm | | | | | Aboveground vegetation | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Vegetation type | C | | CC | D | | C | | CC | D | | C | | CC | D | |
| */NT | Sedum sexangulare (K-C) | . | . | 41 | . | . | . | . | 43 | . | . | . | . | . | . | . |
| | Juncus articulatus | . | . | 2 | . | . | . | . | . | 1 | . | . | . | . | . | . |
| | Poa trivialis | . | . | 2 | . | . | . | . | . | . | 1 | . | . | . | . | . |
| | Urtica dioica | . | . | 1 | . | 1 | . | . | . | . | . | . | . | . | . | . |
| x | Herniaria glabra (K-C) | . | . | . | 22 | 1 | . | . | . | . | . | . | . | . | . | . |
| | Holcus lanatus | . | . | . | . | . | 1 | . | 1 | . | . | . | . | . | . | . |
| | Plantago major ssp. intermedia | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| x | Poa annua | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| | Sagina apetala (K-C) | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| x | Chenopodium album agg. | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . |
| | Further taxa | | | | | | | | | | | | | | | |
| | Agrostis sp. (capillaris/vinealis) | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . |
| | **Only present in the aboveground vegetation** | | | | | | | | | | | | | | | |
| x | Veronica arvensis | . | . | . | . | . | . | . | . | . | . | 2m | + | 2m | 1 | + |
| */NT | Leontodon saxatilis | . | . | . | . | . | . | . | . | . | . | 1 | + | . | 1 | 1 |
| | Hypochaeris radicata | . | . | . | . | . | . | . | . | . | . | + | 1 | . | 2a | 1 |
| | Festuca filiformis (K-C) | . | . | . | . | . | . | . | . | . | . | 2a | . | 3 | 2m | . |
| | Anthoxanthum aristatum (K-C) | . | . | . | . | . | . | . | . | . | . | 2m | . | . | 2m | 2m |
| | Stellaria media | . | . | . | . | . | . | . | . | . | . | 1 | . | + | . | . |
| x | Achillea millefolium | . | . | . | . | . | . | . | . | . | . | . | . | . | 2a | 2a |
| | Bromus hordeaceus | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 2m |
| */NT | Galium verum agg. (K-C) | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 2m |
| | Linaria vulgaris | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 2m |
| | Anthoxanthum odoratum | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | + |
| */NT | Ranunculus bulbosus (K-C) | . | . | . | . | . | . | . | . | . | . | . | . | . | + | + |
| | Taraxacum sect. Ruderalia | . | . | . | . | . | . | . | . | . | . | . | . | . | + | 1 |
| x | Arenaria serpyllifolia agg. (K-C) | . | . | . | . | . | . | . | . | . | . | 2m | . | . | . | . |
| | Claytonia perfoliata | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| x | Erodium cicutarium (K-C) | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| (x) | Scleranthus annuus agg. (K-C) | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| x | Trifolium campestre (K-C) | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . |
| | Cerastium glomeratum | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . |
| | Elymus repens | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . |
| | Geranium pusillum | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . |
| x | Ornithopus perpusillus (K-C) | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . |
| x | Trifolium arvense (K-C) | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . |
| x | Crepis capillaris | . | . | . | . | . | . | . | . | . | . | r | . | . | . | . |
| x | Potentilla argentea agg. (K-C) | . | . | . | . | . | . | . | . | . | . | r | . | . | . | . |
| | Filago minima (K-C) | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . |
| x | Plantago lanceolata | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | . |
| | Lolium perenne | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . |
| x | Trifolium repens | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + |

species numbers and diaspore 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; six species additionally in layer 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., *Carex arenaria*, *Corynephorus canescens*, *Agrostis capillaris* and *Polygonum aviculare* agg.; in area 2: *Potentilla argentea* agg., *Rumex acetosella* s.l., *Vicia lathyroides*, *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 diaspore densities in each vegetation type are shown in Table 4a. Data analyses by mixed linear models revealed that

Table 3. The data from the soil seed bank analysis (number of seedlings) and the aboveground 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 (SB) of area 1 are designated (x) (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. verna*), but could not be definitely classified as a particular one; thus, *Veronica* sp. was not counted as an individual taxon.

| RL G/H | SB area 1 | Stratum | Layer 0 0-1 cm | | | | | | | | | | | Seed bank 1-6 cm | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Vegetation type | K | | | | | KA | A | | | | | K | | | | | KA |
| | | Plot code | K1-0 | K1'-0 | K2-0 | K2'-0 | K3-0 | KA-0 | A1-0 | A1'-0 | A2-0 | A2'-0 | A3-0 | K1-1 | K1'-1 | K2-1 | K2'-1 | K3-1 | KA-1 |
| | | Plot size (m²) | 24 | 24 | 24 | 24 | 25 | 25 | 24 | 24 | 24 | 24 | 25 | 24 | 24 | 24 | 24 | 25 | 25 |
| | | Treatment | g | c | g | c | g | g | g | c | g | c | g | g | c | g | c | g | g |
| | | Number of diaspores/stratum | 1196 | 1147 | 315 | 516 | 335 | 902 | 357 | 533 | 855 | 701 | 999 | 557 | 299 | 514 | 365 | 155 | 911 |
| | | Number of species/stratum | 31 | 28 | 22 | 27 | 20 | 31 | 23 | 27 | 34 | 27 | 22 | 29 | 21 | 17 | 16 | 17 | 31 |
| | | Number of phanerogam species/stratum | 31 | 28 | 22 | 27 | 20 | 31 | 23 | 27 | 34 | 27 | 22 | 29 | 21 | 17 | 16 | 17 | 31 |
| | | Number of cryptogam species | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | Total plant cover (%) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | Cover of grasses + herbs (%) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | Cover of cryptogams (%) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | Cover of bare ground (%) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | | **Present in the soil seed bank and in the aboveground vegetation** | | | | | | | | | | | | | | | | | |
| | | Arenaria serpyllifolia agg. (K-C) | 6 | 13 | 31 | 35 | 21 | 55 | 22 | 7 | 56 | 13 | 100 | 6 | 10 | 44 | 61 | 16 | 72 |
| | x | Rumex acetosella s.l. (K-C) | 20 | 11 | . | 1 | 2 | 11 | 87 | 68 | 17 | 27 | 16 | 26 | 25 | 1 | 6 | . | 77 |
| | | Verbascum phlomoides | 14 | 5 | 3 | 9 | . | 246 | . | 1 | 3 | 16 | 14 | 32 | 2 | . | 1 | 1 | 277 |
| | x | Cerastium semidecandrum (K-C) | 22 | 24 | 8 | 8 | 20 | 17 | 32 | 41 | 44 | 11 | 23 | 4 | 5 | 16 | 9 | 15 | 24 |
| 3/3 | | Medicago minima (K-C) | 14 | 3 | 14 | 8 | 3 | 196 | . | 1 | 16 | 1 | 167 | 1 | . | 3 | . | 1 | 6 |
| | x | Conyza canadensis | 570 | 721 | 10 | 11 | 30 | 4 | 6 | 3 | 1 | 10 | 10 | 182 | 56 | . | 1 | 15 | 6 |
| | x | Chenopodium album agg. | 13 | . | 8 | 2 | . | 2 | . | 1 | . | 5 | . | 3 | 3 | 3 | 4 | . | 22 |
| | | Veronica arvensis | 4 | 9 | 8 | 3 | . | 16 | 69 | 99 | 37 | 68 | 63 | 5 | 6 | . | . | . | 8 |
| | | Poa angustifolia | 13 | 14 | 9 | 2 | . | 46 | 12 | . | 10 | 19 | 3 | 4 | 2 | . | 3 | . | 1 |
| | x | Sedum acre (K-C) | 9 | 20 | 45 | 134 | 17 | 11 | . | . | 1 | . | 8 | 45 | 24 | 138 | 104 | 31 | 147 |
| | | Saxifraga tridactylites (K-C) | 76 | 43 | 26 | 57 | 48 | 106 | . | . | 5 | . | 8 | 87 | 28 | 237 | 137 | 43 | 61 |
| | | Potentilla argentea agg. (K-C) | 2 | . | . | 2 | . | 1 | 15 | 190 | 366 | 244 | 245 | 2 | . | . | . | . | 4 |
| | | Erodium cicutarium (K-C) | 3 | 2 | 2 | 4 | . | 5 | . | 4 | 2 | . | . | 5 | 5 | 9 | 18 | . | 69 |
| */2 | | Vicia lathyroides (K-C) | 1 | 2 | . | . | . | 18 | 3 | 20 | 82 | 76 | 128 | . | . | . | . | . | 17 |
| | | Carex hirta | 21 | 56 | 100 | 52 | . | . | 4 | 1 | . | . | . | 95 | 97 | 44 | 7 | . | 1 |
| | | Trifolium campestre (K-C) | 1 | . | . | . | . | 18 | 18 | 18 | 68 | 40 | 108 | . | . | . | . | . | 8 |
| | | Myosotis ramosissima + stricta (K-C) | . | . | . | 2 | . | . | 28 | 31 | 26 | 13 | 19 | 1 | . | . | . | 3 | . |
| | | Geranium molle | . | . | . | . | . | 15 | 1 | 1 | 19 | 19 | 52 | . | . | . | . | . | 16 |
| | | Vulpia myuros (K-C) | 52 | 31 | 9 | 11 | 51 | 4 | 2 | . | 1 | . | . | 3 | 7 | 2 | 4 | 4 | . |
| | | Trifolium arvense (K-C) | 4 | . | . | . | . | . | 9 | 2 | 9 | 3 | . | 2 | . | . | . | . | . |
| | | Veronica verna (K-C) | 7 | 8 | . | 5 | 11 | 1 | 7 | 1 | . | 1 | . | 3 | . | . | . | 1 | . |
| 3/2 | | Silene conica (K-C) | 6 | 5 | . | . | 1 | 4 | 1 | . | 5 | 7 | . | 8 | 4 | . | . | 3 | 2 |
| | | Crepis capillaris | . | . | . | 1 | . | 21 | . | 1 | 1 | 2 | 2 | 1 | . | 2 | . | . | 2 |
| | | Setaria viridis | 153 | 71 | 12 | 10 | . | 13 | . | . | . | . | . | 15 | 5 | 2 | . | . | 3 |
| | | Psyllium arenarium | 24 | 2 | 7 | 9 | 7 | 20 | . | . | . | . | . | 3 | 1 | 4 | 3 | . | 1 |
| | x | Agrostis capillaris | . | . | . | . | . | 1 | 26 | 17 | 11 | 27 | . | . | . | . | . | . | . |
| | | Koeleria macrantha (F-B) | . | . | . | 3 | . | 3 | 1 | 2 | 1 | 13 | 3 | . | . | . | . | . | 2 |
| | | Oenothera biennis s.l. | 103 | 30 | 1 | 120 | . | . | . | . | . | . | 2 | 2 | 1 | . | 1 | 1 | . |
| | | Salsola kali ssp. tragus | 29 | 7 | 4 | 5 | 60 | 3 | . | . | . | . | . | 3 | . | . | . | 8 | 10 |
| 3/2 | | Silene otites (F-B) | 12 | 40 | . | . | . | 32 | 1 | . | 7 | 12 | . | . | 7 | . | . | . | 2 |
| | x | Erophila verna (K-C) | . | 1 | . | . | 15 | 3 | . | . | . | . | . | . | . | 1 | 1 | 1 | 30 |
| */3 | x | Corynephorus canescens (K-C) | . | 6 | 2 | 10 | . | . | . | . | . | . | . | 6 | 2 | 2 | 4 | . | . |
| | | Petrorhagia prolifera (K-C) | . | 2 | . | . | . | 3 | . | 1 | 12 | 17 | . | . | . | . | . | . | 2 |
| 3/2 | | Armeria maritima ssp. elongata (K-C) | . | . | . | . | . | 2 | 2 | 3 | 3 | 8 | 6 | . | . | . | . | . | . |
| | | Ornithopus perpusillus (K-C) | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| */3 | | Veronica praecox (K-C) | 4 | 6 | . | . | 6 | . | 1 | . | . | . | . | . | . | . | . | 7 | . |
| 2/2 | | Phleum arenarium (K-C) | 1 | 4 | . | . | 6 | . | . | . | . | . | . | 2 | . | . | . | 1 | . |
| | | Echium vulgare (K-C) | . | . | 10 | 6 | . | . | . | . | . | . | . | . | . | . | . | . | 10 |
| | x | Agrostis vinealis (K-C) | . | . | . | . | . | . | 3 | 3 | . | . | . | . | . | . | . | . | . |
| | x | Cerastium arvense | . | . | . | . | . | . | . | 5 | 2 | 2 | . | . | . | . | . | . | . |
| | | Achillea millefolium | . | . | . | . | . | . | . | . | 1 | 32 | . | . | . | . | . | . | . |
| | | Euphorbia cyparissias (F-B) | 1 | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | 2 | 1 |
| | | Plantago lanceolata | . | . | . | . | . | 13 | . | . | 9 | . | 1 | . | . | . | . | . | . |
| | | Thymus pulegioides s.l. | . | . | . | . | . | . | 1 | 5 | . | . | . | . | . | . | . | . | . |
| | | Hypericum perforatum | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Scleranthus annuus agg./perennis (K-C) | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . | . |
| | | Carduus nutans | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . |
| | | Bromus tectorum | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2 |
| | | Senecio vernalis | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Ononis repens (F-B) | . | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . |
| | x | Cerastium holosteoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 3/2 | | Helichrysum arenarium (K-C) | . | . | . | . | 4 | . | . | . | . | . | . | . | . | . | . | . | . |

Vegetation types: K: Koelerion glaucae, KA: Koelerion glaucae/Armerion elongatae, A: Armerio-Festucetum. g: grazed, c: control. Red List status (RL) (according to KORNECK et al. 1996): G: Germany/H: Hesse, 2: endangered, 3: vulnerable, *: least concern. For further abbreviations see Table 2.

| | | | | | Seed bank 11-16 cm | | | | | | | | | | | Aboveground vegetation | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | | | | | K | | | | | KA | A | | | | | K | | | | | KA | A | | | | |
| A1-1 | A1'-1 | A2-1 | A2'-1 | A3-1 | K1-2 | K1'-2 | K2-2 | K2'-2 | K3-2 | KA-2 | A1-2 | A1'-2 | A2-2 | A2'-2 | A3-2 | K1-v | K1'-v | K2-v | K2'-v | K3-v | KA-v | A1-v | A1'-v | A2-v | A2'-v | A3-v |
| 24 | 24 | 24 | 24 | 25 | 24 | 24 | 24 | 24 | 25 | 25 | 24 | 24 | 24 | 24 | 25 | 24 | 24 | 24 | 24 | 25 | 25 | 24 | 24 | 24 | 24 | 25 |
| g | c | g | c | g | g | c | g | c | g | g | g | c | g | c | g | g | c | g | c | g | g | g | c | g | c | g |
| 1508 | 1310 | 3024 | 2719 | 2078 | 86 | 39 | 21 | 4 | 8 | 102 | 253 | 191 | 263 | 272 | 84 | - | - | - | - | - | - | - | - | - | - | - |
| 34 | 27 | 33 | 34 | 28 | 14 | 9 | 7 | 2 | 6 | 15 | 21 | 18 | 20 | 16 | 14 | 50 | 47 | 34 | 38 | 33 | 39 | 43 | 38 | 41 | 31 | 27 |
| 34 | 27 | 33 | 34 | 28 | 14 | 9 | 7 | 2 | 6 | 15 | 21 | 18 | 20 | 16 | 14 | 43 | 41 | 31 | 34 | 27 | 34 | 41 | 36 | 38 | 29 | 25 |
| - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 7 | 6 | 3 | 4 | 6 | 5 | 2 | 2 | 3 | 2 | 2 |
| - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 98 | 100 | 95 | 98 | 60 | 98 | 99 | 98 | 100 | 100 | 100 |
| - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 50 | 47 | 35 | 55 | 35 | 90 | 95 | 80 | 100 | 100 | 100 |
| - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 85 | >90 | 60 | 40 | 40 | 40 | 60 | 60 | 61 | 71 | 20 |
| - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 | <1 | 5 | 2 | 40 | 0 | 1 | 2 | 0 | 0 | 0 |
| 56 | 27 | 51 | 78 | 98 | 3 | 2 | 3 | 3 | . | 5 | 3 | 1 | 3 | 4 | 3 | 2m | 2m | 2m | 2m | 2m | 2m | 2m | 1 | 2m | 1 | + |
| 592 | 409 | 113 | 462 | 57 | 7 | 3 | . | . | . | 22 | 145 | 96 | 145 | 144 | 17 | 2m | 2m | . | . | . | 2m | 2m | 2m | 2m | 2m | 2m |
| 8 | 1 | 4 | 77 | 35 | 4 | . | 2 | . | 1 | 25 | 3 | 2 | 6 | 3 | 3 | 1 | 1 | + | r | . | 1 | + | . | + | r | . |
| 84 | 58 | 49 | 40 | 16 | . | . | . | . | . | 2 | 3 | 5 | 1 | . | . | 2m | 2m | 2m | 1 | 2m | 2m | 1 | + | 2m | r | 2m |
| 7 | . | 3 | 14 | 9 | . | 2 | 1 | . | . | 1 | 2 | 3 | 1 | 6 | 1 | 2m | 2m | 2m | 2m | 2m | 2m | . | . | + | . | 1 |
| 2 | 2 | 2 | 5 | 5 | 6 | 8 | . | . | 1 | . | . | . | 1 | . | . | 2m | 2m | + | + | 1 | + | r | . | . | . | . |
| 13 | 13 | 3 | 19 | 1 | 8 | 10 | . | . | . | 12 | 20 | 19 | 14 | 24 | 1 | 1 | . | . | . | . | . | . | . | . | . | . |
| 154 | 50 | 94 | 159 | 123 | . | . | . | . | . | . | 6 | 5 | 1 | 2 | 1 | 2m | 2m | 2m | 1 | . | 1 | 2m | + | 2m | 2m | 2m |
| 90 | 1 | 116 | 140 | 29 | 2 | . | . | . | . | . | . | . | 2 | 2 | 1 | 2m | . | 1 | 2m | . | 2b | 2m | 2m | 2b | 2b | 2b |
| 8 | 4 | 1 | 3 | 50 | 3 | 4 | . | . | . | 3 | . | . | . | . | . | 2m | 2m | 2m | 2b | 1 | 2m | 2m | 1 | 2m | . | 1 |
| . | . | 5 | . | 58 | . | 1 | 3 | . | . | 8 | . | . | 1 | . | 9 | 2m | 2m | 2m | 2m | 2m | 2m | . | . | . | . | . |
| 62 | 538 | 1953 | 1114 | 1210 | . | . | . | . | . | 2 | 5 | 7 | 45 | 13 | 30 | . | + | r | r | . | . | 1 | 2m | 2m | 2m | 2m |
| 73 | 20 | 28 | 32 | 7 | . | . | . | . | . | . | 2 | 1 | 1 | . | . | 2m | 2m | 2m | 2m | + | 1 | + | + | . | . | . |
| 36 | 15 | 278 | 155 | 174 | . | . | . | . | . | 1 | 13 | 12 | 14 | 23 | 6 | 2m | 2m | . | . | . | r | . | . | . | . | 1 |
| 30 | 2 | . | . | 5 | 2 | 4 | . | . | . | . | 2 | 2 | . | . | . | 2a | 2b | 1 | 2a | . | 1 | 2m | 2m | . | . | + |
| 125 | 30 | 100 | 136 | 54 | 1 | . | . | . | . | . | 5 | 5 | 1 | 13 | . | 2m | 2m | . | . | . | 2a | 1 | 1 | 1 | 1 | 2m |
| 27 | 17 | 53 | 49 | 38 | . | . | . | . | . | . | 4 | 7 | 4 | 3 | 6 | 1 | + | 1 | 1 | 2m | + | + | + | + | 1 | . |
| 7 | 3 | 68 | 72 | 76 | . | . | . | . | . | . | 1 | 5 | 8 | 3 | . | + | + | + | . | . | 1 | 1 | 1 | 2m | + | 1 |
| . | . | . | . | . | . | 2 | . | . | 2 | . | . | . | . | . | . | 2a | 2m | 2m | 1 | 2a | 2m | 2m | + | 2m | . | . |
| 10 | 8 | 4 | 5 | . | 1 | . | . | . | . | . | 1 | 2 | 5 | 3 | . | 2m | r | . | . | r | r | 1 | + | 2m | . | . |
| 7 | . | . | 6 | 1 | . | . | . | . | . | . | 1 | . | . | . | . | 2m | 2m | 2m | 1 | 2m | . | . | . | . | r | . |
| 1 | . | 1 | 3 | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 2m | 2m | 2m | 2m | 1 | 1 | . | . | . | . |
| 1 | 1 | 2 | 1 | . | . | . | . | . | . | . | 1 | . | . | . | . | + | . | . | . | . | 2m | . | r | 1 | + | 1 |
| . | . | . | . | . | 42 | . | 6 | . | . | 1 | 12 | . | . | . | . | 2m | 1 | 2m | . | . | . | . | . | . | . | . |
| . | . | . | . | . | 4 | . | 5 | . | . | . | . | . | . | . | . | 2m | 1 | 1 | 2m | 1 | . | . | . | . | . | . |
| 34 | 59 | 20 | 65 | . | . | . | . | . | . | . | 4 | 3 | 4 | 15 | . | . | . | . | . | . | . | 2b | 2b | 2b | 2b | 1 |
| 3 | 3 | 4 | 2 | 9 | . | . | . | . | . | . | . | . | . | . | . | 1 | 1 | 2b | 2m | . | 3 | 2a | 2b | 3 | 3 | 3 |
| . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | 1 | + | . | r | + | . | . | . | . | . | . |
| . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | 1 | r | + | + | 2b | . | . | . | . | . | . |
| . | . | 6 | 3 | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 2m | + | r | + | . | . | . | + | 1 | + |
| 1 | . | . | . | . | . | . | . | . | . | 14 | . | . | . | . | . | r | r | + | . | + | . | . | . | . | . | . |
| . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2b | 2a | 2m | 2a | 2a | . | . | . | . | . | . |
| . | . | . | 8 | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 1 | 1 | + | . | + | . | . | r | + | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2a | 2m | 2m | 2m | 2m | 2m |
| 1 | 2 | 1 | 1 | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | r | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 2m | . | r | 2m | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 2m | . | . | 2m | . | . | . | . | . | . |
| . | . | . | . | 2 | . | . | 1 | . | . | . | . | . | . | . | . | + | 1 | 1 | 1 | . | 1 | . | . | . | . | . |
| 8 | 19 | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2b | 2b | + | . | . |
| 2 | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2a | 2a | 2m | 2b | 3 |
| . | 2 | 1 | 26 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 1 | 2m | 2m | 2a |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 2m | . | . | + | . | . | . | . | . | . |
| . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | r | . | 1 | 1 | 1 |
| 3 | 3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2a | 2a | . | . | . |
| . | . | 2 | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | r | . | . | . | . | . |
| 21 | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | + | . | . | . |
| . | . | 4 | 3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | 2m | + | + |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 2m | 2m | 1 | 2m | 2m | + | + | 1 | . | . |
| 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 1 | . | . | 1 | . | . | . | . | . | . |
| . | . | . | . | 3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | 2m | 1 | . | . | . | . | 2b |
| . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 1 | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 1 | 1 | 2m | 2m | + | + | + | . | . | . |

Table 3. (cont.)

| RL G/H | SB area 1 | Stratum | Layer 0 0-1 cm | | | | | | | | | | | Seed bank 1-6 cm | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Vegetation type | K | | | | | KA | A | | | | | K | | | | | KA |
| | | Plot code | K1-0 | K1'-0 | K2-0 | K2'-0 | K3-0 | KA-0 | A1-0 | A1'-0 | A2-0 | A2'-0 | A3-0 | K1-1 | K1'-1 | K2-1 | K2'-1 | K3-1 | KA-1 |
| | | **Only present in the soil seed bank** | | | | | | | | | | | | | | | | | |
| | x | Polygonum aviculare agg. | . | . | . | . | . | . | . | 3 | . | . | . | 2 | . | . | . | . | 4 |
| | | Betula pendula | 1 | . | 1 | 1 | 1 | . | . | 1 | . | . | . | 1 | . | 2 | . | . | . |
| | | Sisymbrium altissimum | 1 | . | . | . | . | . | . | . | 3 | . | . | . | . | . | . | . | . |
| | | Salix cf. viminalis | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| | x | Herniaria glabra (K-C) | . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . |
| | | Cardamine hirsuta | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Medicago lupulina (F-B) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | x | Arabidopsis thaliana | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Epilobium tetragonum s.l. | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Holosteum umbellatum (K-C) | . | . | . | . | 24 | 3 | . | . | . | . | . | . | . | . | . | . | . |
| | | Silene latifolia ssp. alba | . | . | . | . | . | . | . | . | 17 | . | . | . | . | . | . | . | . |
| | | Fragaria x ananassa | . | . | . | . | . | . | . | . | . | . | 2 | . | 1 | . | . | . | . |
| | | Amaranthus cf. albus | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . |
| | | Trifolium repens | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Digitaria sanguinalis | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Buddleja cf. davidii | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| | | Populus sp. | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . |
| | | Diplotaxis tenuifolia | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . |
| | | Eragrostis minor | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 5 |
| | | Epilobium hirsutum | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Epilobium parviflorum | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Salix caprea | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Urtica urens | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Oxalis cf. stricta | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | x | Poa annua | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Jasione montana (K-C) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Solanum nigrum | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Further taxa | | | | | | | | | | | | | | | | | |
| | | Further Dicotyledoneae | 6 | 3 | 1 | 2 | 2 | 7 | 2 | 2 | 9 | 7 | 13 | 5 | 5 | 2 | 1 | 1 | 10 |
| | | Unidentified | 1 | 2 | . | . | . | . | . | . | . | 2 | 2 | 1 | 2 | . | . | . | . |
| | | Further Poaceae | . | . | 1 | . | 2 | . | 1 | 1 | 5 | 1 | . | . | . | . | . | . | . |
| | | Further Monocotyledoneae | . | 3 | 1 | 2 | . | . | . | . | . | . | 1 | 1 | . | 1 | . | . | . |
| | | Veronica sp. (arvensis/praecox/verna) | . | 1 | . | . | 1 | 2 | 2 | . | . | . | . | . | . | . | . | 1 | 9 |
| | | Further Fabaceae | . | . | . | . | . | . | 1 | . | 1 | 1 | . | . | . | . | . | . | . |
| | | Further Caryophyllaceae | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . |
| | | **Only present in the aboveground vegetation** | | | | | | | | | | | | | | | | | |
| | | Festuca ovina agg. (F-B) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Asparagus officinalis | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Centaurea stoebe (F-B) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Medicago falcata + x varia (F-B) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 2/2 | | Koeleria glauca (K-C) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Elymus repens | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Bromus hordeaceus | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Hieracium pilosella (K-C) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Berteroa incana | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Hypochaeris radicata | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 3/2 | | Stipa capillata (F-B) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Elymus campestris | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 3/3 | | Carex praecox | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Silene vulgaris s.l. (F-B) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Vicia angustifolia (F-B) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Galium verum agg. (K-C) | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Erigeron annuus | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | Cynoglossum officinale | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |

Cryptogams present in the aboveground vegetation: **K1-v:** Brachythecium albicans 2m, Cetraria aculeata +, Cladonia pyxidata r, C. rangiformis/C. furcata 2a, Hypnum cupressiforme var. lacunosum 3, Peltigera rufescens 2m, Tortula ruraliformis 3; **K1'-v:** Cetraria aculeata 2m, Cladonia pyxidata 2m, C. rangiformis/C. furcata 3, Hypnum cupressiforme var. lacunosum 5, Peltigera rufescens 2m, Tortula ruraliformis 2a; **K2-v:** Brachythecium albicans 2m, Hypnum cupressiforme var. lacunosum 2m, Tortula ruraliformis 4; **K2'-v:** Cladonia rangiformis/C. furcata 2m, Hypnum cupressiforme var. lacunosum 2b, Peltigera rufescens r, Tortula ruraliformis 2b; **K3-v:** Brachythecium albicans 2m, Cetraria aculeata 1, Cladonia rangiformis/C. furcata 1, Hypnum cupressiforme var. lacunosum 2b, Peltigera rufescens +, Tortula ruraliformis 3.

| Seed bank 11-16 cm | | | | | | | | | | | | | | | | Aboveground vegetation | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | | | | | K | | | | | KA | A | | | | | K | | | | | KA | A | | | | |
| A1-1 | A1'-1 | A2-1 | A2'-1 | A3-1 | K1-2 | K1'-2 | K2-2 | K2'-2 | K3-2 | KA-2 | A1-2 | A1'-2 | A2-2 | A2'-2 | A3-2 | K1-v | K1'-v | K2-v | K2'-v | K3-v | KA-v | A1-v | A1'-v | A2-v | A2'-v | A3-v |
| 11 | 6 | . | 4 | . | . | . | . | . | . | 2 | 14 | 14 | . | 5 | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | 2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . |
| 2 | . | . | . | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | 1 | . | . | . | . | . | . | 1 | . | . | 3 | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | 1 | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 2 | . | . | . | 1 | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | 26 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 2 | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
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| . | . | . | **1** | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
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| . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
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| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . |
| 9 | 11 | 24 | 25 | 8 | 1 | 2 | . | . | . | 2 | 1 | 1 | 2 | 6 | 3 | . | . | . | . | . | . | . | . | . | . | . |
| 1 | . | . | 5 | 4 | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| 2 | 2 | 1 | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . |
| . | **1** | . | 1 | . | . | 1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| 12 | . | . | . | . | . | . | . | . | . | . | 4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
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| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 1 | 2m | + | . | 2m | 2m | 2m | 2b | 2b | 3 |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | . | . | . | 1 | + | + | + | + | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | r | r | . | r | + | + | + | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | r | . | 2a | 1 | 2a | 2a | . | + |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | **1** | 2m | 2m | 1 | 2b | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 1 | . | . | r | 2m | . | . | + |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | **1** | 2m | **+** | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 2m | 2a | 2m | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | r | r | . | + | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | r | + | r | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 1 | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2m | 2m | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | 1 | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | r | 1 | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1 | + | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | r | 2m | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . | . | . | . | . | . |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | + | . | . | . | . | . |

Cryptogams (cont.): **A3-v:** Brachythecium albicans 2m, Hypnum cupressiforme var. lacunosum 2b; **KA-v:** Brachythecium albicans 2m, Cladonia rangiformis/C. furcata 2m, Hypnum cupressiforme var. lacunosum 3, Tortula ruraliformis 2a, further Acrocarpi 2m; **A1-v:** Cladonia rangiformis/C. furcata 2m, Hypnum cupressiforme var. lacunosum 4; **A1'-v:** Cladonia rangiformis/C. furcata 2m, Hypnum cupressiforme var. lacunosum 5; **A2-v:** Cladonia rangiformis/C. furcata **1**, Hypnum cupressiforme var. lacunosum 4; Plagiomnium rostratum 2m; **A2'-v:** Cladonia rangiformis/C. furcata 1, Hypnum cupressiforme var. lacunosum 4.
Poa bulbosa (K-C) present in the aboveground vegetation: **K1-v:** 1; **K1'-v:** 2m; **K2'-v:** + (P. bulbosa was excluded from the seed bank analysis; see text).

Table 4a. Mean species numbers and diaspore densities per soil layer (diaspores $m^{-2}$) with standard errors of the soil seed banks of areas 1 and 2. Values of grazed and not grazed plots of Koelerion glaucae and Armerio-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 phytomass of cryptogams and phanerogams, L1: 1–6 cm, L2: 11–16 cm. –: no data.

| | n | Number of species | | | Diaspores $m^{-2}$ | | |
|---|---|---|---|---|---|---|---|
| | | L0 | L1 | L2 | L0 | L1 | L2 |
| Vegetation types on acidic sand | | | | | | | |
| Spergulo-Corynephoretum typicum | 2 | – | 12 ± 0 | 5 ± 1 | – | 683 ± 118 | 101 ± 55 |
| S.-C. cladonietosum/ *Calluna vulgaris* stage | 1 | – | 23 | 8 | – | 3020 | 386 |
| Diantho-Armerietum | 2 | – | 18 ± 2 | 10 ± 3 | – | 2127 ± 352 | 233 ± 164 |
| Vegetation types on primarily calcareous sand | | | | | | | |
| Koelerion glaucae | 3 | 25 ± 3 | 20 ± 3 | 7 ± 2 | 3693 ± 1536 | 1965 ± 536 | 159 ± 101 |
| Koelerion glaucae/ Armerion elongatae | 1 | 31 | 31 | 15 | 5199 | 5251 | 588 |
| Armerio-Festucetum | 3 | 26 ± 2 | 31 ± 2 | 17 ± 2 | 4269 ± 928 | 12217 ± 2436 | 1102 ± 318 |

Table 4b. Tests of fixed effects on soil seed bank data (species numbers, diaspore numbers) of the data set of 4a 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.

| | Nd.f. | Dd.f. | Number of species | | Number of diaspores | |
|---|---|---|---|---|---|---|
| | | | F value | p | F value | p |
| Area | 1 | 6 | 17.07 | **0.0061** | 11.02 | **0.0160** |
| Succession | 1 | 6 | 17.44 | **0.0058** | 17.53 | **0.0058** |
| Soil layer | 1 | 6 | 124.90 | **< 0.0001** | 61.84 | **0.0002** |
| Area x succession | 1 | 6 | 2.20 | 0.1889 | 2.66 | 0.1543 |
| Area x soil layer | 1 | 6 | 8.59 | **0.0262** | 0.29 | 0.6071 |
| Succession x soil layer | 1 | 6 | 0.41 | 0.5451 | 0.01 | 0.9236 |
| Area x succession x soil layer | 1 | 6 | 0.01 | 0.9300 | 0.41 | 0.5464 |

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 2 are richer in species and diaspores than the soil seed banks of area 1. 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).

**b) 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 or 1.9 (C/D, layer 1 or layer 2) and 1.6 or 2.3 (K/A, layer 1 or layer 2). Again, diaspore densities show the same interrelation 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 diaspore density of the pioneer vegetation on base-rich soils (K) was approximately as high as the diaspore density of the mid-successional vegetation on acidic soils (D). Layer 1 of Armerio-Festucetum showed the highest diaspore densities (on average 12,217 diaspores $m^{-2}$) and species numbers (on average 31 species). *Potentilla argentea* agg., *Rumex acetosella* s.l. and the endangered therophyte *Vicia lathyroides* constitute 68 % of the diaspore pool in both layers 1 and 2 of Armerio-Festucetum.

**c) Soil depth.** All seed banks show a clear decrease of species richness and diaspore 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 diaspore reservoir of layer 0 was richer in species than that of layer 1 by the factor 1.3; in case of Armerio-Festucetum it 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 Garve 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 (*Dianthus 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 sexangulare*, 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 (Stroh & Kratochwil 2004).

In area 2, seven Red List species (according to Korneck et al. 1996) were found both in the seed banks 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 0: *Armeria maritima* ssp. *elongata* and *Helichrysum arenarium*.

Three Red List species (*Sedum sexangulare, Vicia lathyroides, Medicago minima*) were found in layer 1 and layer 2 and fulfil 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 A; mean ± SE) and *Sedum sexangulare* (236 diaspores $m^{-2}$ in layer 1 of CC), the mean diaspore 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 sand vegetation types in (a) the Ems 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 KORNECK et al. 1996) and Lower Saxony (5a; GARVE 2004) or Hesse (5b; KORNECK et al. 1996): 2: endangered, 3: vulnerable, NT: near threatened (in the lowland), *: least concern. Vegetation types: C: Spergulo-Corynephoretum typicum, CC: Spergulo-Corynephoretum cladonietosum/*Calluna vulgaris* stage, D: Diantho-Armerietum, K: Koelerion glaucae, KA: Koelerion glaucae/Armerion elongatae, A: Armerio-Festucetum; soil layers: L1: 1–6 cm, L2: 11–16 cm; lr: last record (time span [months] between the date of the soil sample exposition and the last seedling emergence record; see text).

| (a) | C (n = 2) | | CC (n = 1) | | D (n = 2) | | Pres. (%) | | lr |
|---|---|---|---|---|---|---|---|---|---|
| | L1 | L2 | L1 | L2 | L1 | L2 | L1 | L2 | |
| *Sedum sexangulare* (*/NT) | . | . | 236 | 248 | . | . | 20 | 20 | 3 |
| *Dianthus deltoides* (*/3) | . | . | . | . | 29 ± 12 | . | 40 | 0 | 25 |

| (b) | K (n = 3) | | KA (n = 1) | | A (n = 3) | | Pres. (%) | | lr |
|---|---|---|---|---|---|---|---|---|---|
| | L1 | L2 | L1 | L2 | L1 | L2 | L1 | L2 | |
| *Medicago minima* (3/3) | 6 ± 2 | 3 ± 2 | 35 | 6 | 40 ± 10 | 13 ± 4 | 100 | 86 | 25 |
| *Vicia lathyroides* (*/2) | . | . | 98 | 6 | 799 ± 334 | 71 ± 21 | 57 | 57 | 25 |
| *Silene conica* (3/2) | 17 ± 10 | . | 12 | . | 5 ± 3 | . | 71 | 0 | 19 |
| *Silene otites* (3/2) | 7 ± 7 | . | 12 | . | 9 ± 9 | . | 43 | 0 | 25 |
| *Corynephorus canescens* (*/3) | 13 ± 7 | . | . | . | 1 ± 1 | . | 43 | 0 | 25 |
| *Phleum arenarium* (2/2) | 4 ± 2 | . | . | . | . | . | 29 | 0 | 19 |
| *Veronica praecox* (*/3) | 13 ± 13 | . | . | . | . | . | 14 | 0 | 19 |

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 conica*, *S. otites*, *Veronica praecox*) were transient (THOMPSON et al. 1997). In types 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 the 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 $1^1/_2$ 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 (20 %) only in vegetation and 15 (22 %) or 23 (25 %) only in seed banks (Tables 2 and 3). The proportion of target species (Koelerio-Corynephoretea, Festuco-Brometea) among species which occurred exclusively in the seed bank was low (20 % 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 succession gradient and the specific characters of seed banks and vegetation due to species occurring only in one of the two types. While the samples of KA occupy intermediate positions between K 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 communties. 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

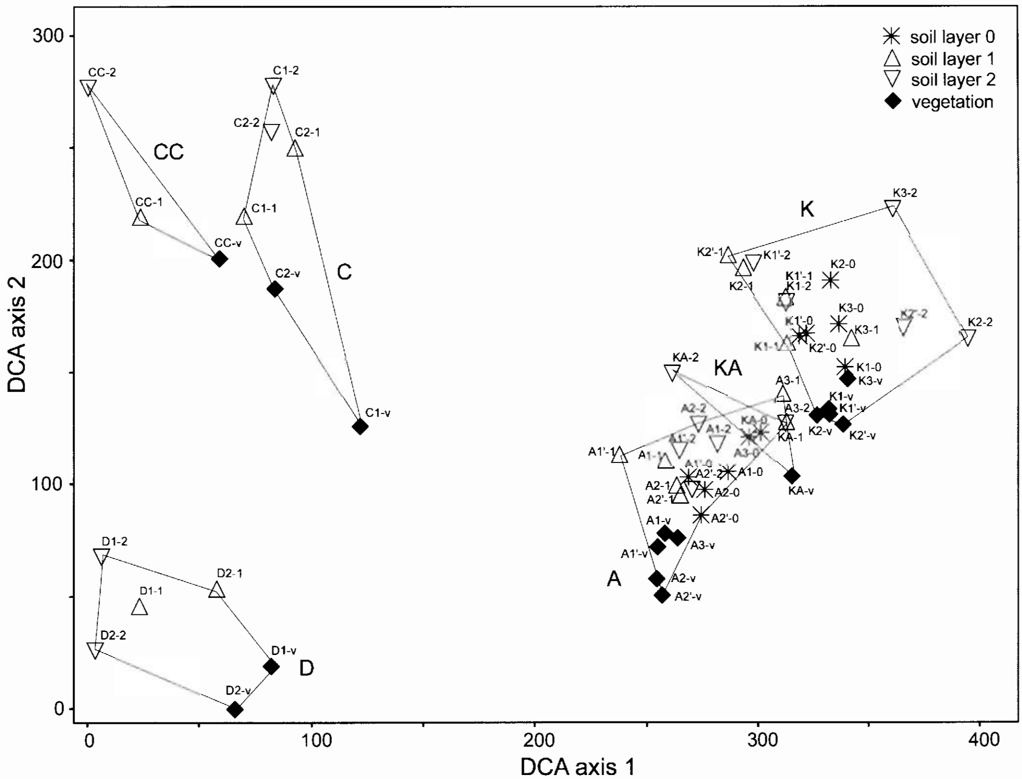


Fig. 4. Detrended correspondence analysis (DCA) of species composition of soil seed bank data and aboveground-vegetation data (presence-absence data, 135 species, 59 plots). The DCA procedure was adjusted to: 26 segments, rescaling of axes, downweighting of rare species. The eigenvalues of axis 1, axis 2 and axis 3 are 0.530, 0.242 and 0.146, respectively. Plot codes include vegetation-type abbreviations (see Fig. 3), replicate number (if $n > 1$) and type of stratum (0/1/2: number of soil layer, v: vegetation); plots indicated with ' were not grazed (all other plots were grazed). Soil layer 0: 0–1 cm mineral soil + litter + complete phytomass of cryptogams and phanerogams, soil layer 1: 1–6 cm, soil layer 2: 11–16 cm.

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 100 primary samples have been established as a sufficient number for seed bank analysis in various ecosystems by Champness (1949), Forcella (1984), Benoit et al. (1989), Gross (1990), Ter 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 MEISSNER & 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 1988). 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 JUTILA (1998) 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 infructescenses 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. LEVASSOR 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 (BEGON et al. 1996). There are some indications that the associated seed banks behave the same. KROLUPPER & SCHWABE (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 (1059 ± 320, 49 ± 27 diaspores $m^{-2}$) for soil seed banks of Spergulo-Corynephoretum typicum in the northern upper Rhine area similar to that observed during the present study in the Ems area (Table 4a) (sample exposition time was a little bit shorter in the case of KROLUPPER & SCHWABE 1998: 14 months, but > 80 % of the total species number and the total diaspore number were already detected in data sets 1 and 2 after 14 months in the present study, so the results are roughly comparable). KUNZMANN (2000) found that soil seed banks of inland sand vegetation on base-rich soils in north-eastern Germany were richer in species, but poorer in diaspores than seed banks of acidic soils.

The observed decrease of diaspore density corresponding to the soil depth is a generally observed phenomenon. The above-mentioned phenomenon of seed bank enrichment in the course of succession is reflected by the fact that the seed density and species diversity were maximal in layer 0 compared with layers 1 and 2 in the case of pioneer stages (Koelerion glaucae), but not in the mid-succesional stages (Armerio-Festucetum), where they were maximal in layer 1.

## 5.4 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 sexangulare* 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 & BEKKER 2004).

In previous investigations six 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, KRATOCHWIL et al. 2002; area 2: *Alyssum montanum* ssp. *gmelinii*, *Poa badensis* and *Teesdalia nudicaulis* in 1–6 cm depth, *Euphorbia seguieriana* and *Mibora minima* in 1–6 cm and 11–16 cm depth, KROLUPPER & SCHWABE 1998).

## 5.5 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-successional 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 hordeaceus* (areas 1 and 2), as well as the occurrence of some pioneer species in the seed banks but not the vegetation of later successional stages, such as *Aira praecox* (area 1), *Saxifraga tridacylites* (area 2) and *Corynephorus 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 pioneer species in the seed banks of later successional stages was more an exception than the rule, and their diaspore densities were mostly low. A decrease of seed banks of early successional species in the course of succession has also been shown by BEKKER et al. (2000) for hayfields in the Netherlands, MATUS et al. (2003) for sandy steppe-meadows in Hungary and BOSSUYT & HERMY (2004) for dune slacks in Belgium.

In contrast, some annual pioneer species with a broader successional amplitude showed an accumulation of diaspores in the soil during early to mid succession (e.g. *Arenaria serpyllifolia* agg., *Cerastium semidecandrum* and *Medicago minima* in area 2). These subordinate herbs are well-adapted to colonise gaps in grass-dominated communities, e.g. livestock trails of sheep (SCHWABE 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 diaspore production because the diaspores survive in the soil, but these diaspores are not able to buffer 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, aeolian 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 diaspore persistence in soil enables these species to colonise gaps efficiently or other mechanisms (e.g. high annual diaspore production, effective diaspore dispersal) are more important, or whether it is the combination of many processes, seems to be a worthwhile issue for future research.

**Acknowledgements.** Parts of the study were supported by the "German Ministry of Research and Technology" (BMBF, No. 01LN0003) and by a PhD grant for C. Eichberg from the "Evangelisches Studienwerk e.V. Villigst". The studies have been made possible by cooperation with the "Regierungspräsidium Darmstadt", the "Landkreis Emsland" (Meppen) and the "Bezirksregierung Weser-Ems" (Oldenburg). We thank S. Binhold, J. Ostendorp, M. Stroh and B. Wierspecker for assistance and A. Tschuschke for technical support. We are grateful to two referees for their most valuable comments. The improvement of the English text by Dr. A. Thorson (Oxford) is much appreciated.

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Addresses of the authors:

Dr. Carsten Eichberg, Dr. Christian Storm and Prof. Dr. Angelika Schwabe, Darmstadt University of Technology, Department of Biology/Vegetation Ecology, Schnittspahnstr. 4, 64287 Darmstadt, Germany. E-mail: schwabe@bio.tu-darmstadt.de

Prof. Dr. Anselm Kratochwil, University of Osnabrück, Department of Ecology, Barbarastr. 11, 49069 Osnabrück, Germany. E-mail: kratochwil@biologie.uni-osnabrueck.de