Arable weed seedbanks and their relation to soil properties

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Summary

Edaphic factors can affect arable weed seedbanks essentially, but they were seldom the focus of seedbank analyses. Thus, this study presents a detailed analysis on this relationship. Data were collected at both a regional scale with 140 arable fields in seven different areas of Bavaria, and at a farm scale in southern Bavaria including 299 sampling sites.

Results show that the soil-seedbank relationship highly depends on the scale of investigation. Thus, interactions with pH, N\(_2\) concentration, and C/N ratio predominantly emerged at the regional scale where a wider range of soil conditions occurred. Minor differences were observed for the K\(_{CAL}\) and P\(_{CAL}\) concentrations, which may have been levelled by long-term fertilisation. Relationship to available field capacity (= water holding capacity) was very close at both scales.

Soil conditions also can affect weed seed banks by indirect means. For example, in a sandy landscape soil conditions may necessitate the cultivation of rye or potatoes. In a loamy field, however, management will not be modified when sandy spots occur. Thus, soil conditions may indirectly increase natural differences in weed seedbanks at the landscape scale, but decrease them at the field scale. A clear separation between the effects of both the soil properties and the type of management is difficult.

Key words: C/N ratio, edaphic factors, field capacity, landscape, management, nitrogen, phosphorus, potassium, scale

Introduction

Investigations in different European countries have shown that weed seedbanks greatly vary among regions with different edaphic conditions. Wesolowski (1979) reported from southeastern Poland that in podzols and brown soils seedbanks ranged from 40,000 to 50,000 seeds m\(^{-2}\), while corresponding values for chernozem, black soil, and silt were only 10,000-20,000 seeds m\(^{-2}\). Jensen (1969) confirmed high seed numbers for sandy soils in Denmark. Comparing seven areas in Bavaria, which are characterised by different soil types, Albrecht & Bachthaler (1990) found that numbers of seeds in calcareous soils were mostly low. Mean levels were observed in soils with moderate acidic reaction and loamy to sandy textures. The highest seed densities occurred in fields with acidic sand and/or that were seasonally wet.

These results suggest that soil conditions significantly affect arable weed seed banks. The relationship between single soil variables and the characteristics of the seedbank, however, has not yet been investigated. Corresponding analyses exist for aboveground vegetation (Andreasen et al., 1991, Medlin et al., 2001, Dunker, 2002), but established weeds are governed mostly by
the present management practice. As seedbanks comprise the whole weed pool as shaped by long-term development, seedbank analyses may be more meaningful. Thus, the aim of this study was to analyse the relationship between soil properties and seed numbers, species composition, and the seed properties of persistence and weight. A factor potentially affecting these interactions is the scale of sampling. To examine its effects, studies were conducted at both a farm scale and landscape scale; the latter including areas with differing soil conditions.

**Study areas and methods**

*Study areas, soil sampling and seed bank analyses*

The two investigations described are designated A and B. Investigation A was conducted in 1986/87 on 140 arable fields in seven different areas in Bavaria. These areas distinctly varied in both natural site conditions and arable farming practices. Data of investigation B originate from one farm in southern Bavaria, 110 ha in size. Compared to the fields in investigation A, this farm was managed more homogeneously regarding rotation and tillage. Soil samples of investigation B were collected at 299 points in 1991. In both studies, soil cores were taken from the whole plough layer. Seedbanks were estimated using the seedling emergence method in which seeds were given 2 years to germinate. Methods and results of both investigations were published previously (Albrecht & Bachthaler, 1990, Albrecht & Pilgram, 1997).

Mean seed weights were calculated using values given by Cramer *et al.* (1991). Persistence was estimated employing the seedbank database for northwest Europe (Thompson *et al.*, 1997) and the 'longevity index' proposed by Thompson *et al.* (1998), in which the sum of persistent seeds is divided by the sum of all seeds found. It can take a value between 0 (all seeds transient) and 1 (all persistent).

**Soil variables**

To relate the seedbank data to edaphic variables the following physical and chemical soil characteristics were recorded: field capacity (derived from the percentage of different grain size fractions), pH measured in CaCl₂, potassium (K) and phosphorus (P) extracted by the CAL method (VDLUFA, 1991), the total concentration of elemental nitrogen N and the C/N ratio.

**Statistical Analysis**

Variables were visualised by box-plots showing minima, median values, 25% and 75% quartiles, maxima and outliers. To demonstrate differences in variation between investigation A and B, quotients of the quartiles were calculated as follows: (75% quartile in A / 25% quartile in A) / (75% quartile in B / 25% quartile in B). For example, the equation for the N concentration is: (0.250 / 0.113) / (0.170 / 0.130) = 1.69, indicating that in A the range is 69% wider than in B. Differences between median values were tested with the Mann and Whitney U test.

The first step to compare the seedbank data to the different soil characteristics was to calculate a correlation matrix. The results revealed strong co-linearity among the independent variables. To avoid resulting numerical distortions and over-fitting in multiple linear regression models, soil variables were aggregated into uncorrelated synthetic factors by performing a principal component analysis (PCA) on the standardised matrix of soil variables (Bühl & Zöfel 2000). PCA axes were interpreted by comparing the loadings of original variables. Relationships between seed number, weight and persistence and the soil factors were examined by calculating Spearman correlation coefficients.

To analyse the relationships of species composition in the soil seed bank to environmental variables, a Canonical Correspondence Analysis (CCA) was performed (Jongman *et al.*, 1987).
To avoid distortion of the CCA results by rare species, only taxa found in at least five samples were included in the analyses.

**Results**

**Soil and seed bank characteristics**

Soil characteristics greatly varied in both data sets (Fig. 1). In study A this variation was more pronounced than in investigation B, especially for the pH, N, concentration and C/N ratio. For these variables, the ratio between quartiles from A and B was > 1.3. In addition, the median values significantly differed. Corresponding ratios for the K and P concentrations and for field capacity (AFC), however, were < 1.3. Moreover, the median P concentrations in A and B did not differ significantly. For field capacity, the median values significantly differed, but the ranges in both data sets were nearly identical.

Great differences between A and B were observed for the seedbank variables 'total number of seeds' and 'mean seed weight' but not for 'seed longevity' (Fig. 2). The median value of 8,870 seeds m⁻² in investigation A was significantly higher than the 4,950 seeds m⁻² in investigation B. Seed weights were 0.49 and 0.22 mg/seed, in A and B respectively. Ratios between the 75% and 25% quartiles in A and B were 5.3 and 4.7 for the total number of seeds and 2.4 and 3.1 for the seed weights. These values indicate great variation within the data sets. Scarcely any variation between both investigations was detected in the longevity indices, however. There, the medians for A and B were 0.77 and 0.79, respectively, and also the quartiles were narrow and nearly identical (Fig. 2).

*Fig. 1. Box plots for soil characteristics measured in investigations A and B. Samples without seeds and extreme values were excluded.*
Due to some exceptionally high values, distribution curves of several variables were positively skewed. As log-transformation did not lead to different conclusions, statistical analyses with the original data are presented here.

**Fig. 2.** Box plots for seed characteristics measured in investigation A and B. Samples without seeds and extreme values were excluded.

**Relationship between soil characteristics and the total number of seeds**

In the PCA of investigation A (Table 1) two factors were extracted, which explained 48% and 23% of the total variance, respectively. High positive loadings for pH, field capacity, and K, and a negative loading for C/N ratio indicate that these variables essentially contribute to the 1st factor. They all stand for high resource availability and characterise loamy, highly fertile soils with a fast microbial turnover of the organic matter. The 2nd factor is related to a high P and N. Thus, it may represent soils with high nutrient input, most of it presumably as organic material.

High seed numbers being characteristic for soils with a low fertility is suggested by the negative correlation to the 1st factor. A significant correlation of this factor to seed weight indicates that loamy, highly fertile soils favour weeds that produce big seeds.

The two factors extracted in study B (Table 2) explain a lower percentage of total variance than those in investigation A. The 1st factor is determined by K, P, and pH, thereby indicating input of fertilizers, including lime. The 2nd factor explains a similar percentage of variance and characterises the availability of N and water. The seed numbers increased with the C/N ratio and decreased with the AFC. This agrees with study A. The negative correlation of the 2nd factor to the seed weight, however, seems to be inconsistent to investigation A. It may be caused by a co-linearity of variables with diverging effects. In both study A and B, seed weights show an indifferent or positive relation to variables representing a high nutrient supply but a neutral or negative relationship to AFC. Thus, species producing big seeds seem to prefer nutrient rich soils but avoid soils with a high AFC (Fig. 3).

Longevity of seeds was not correlated with soil properties in either study.

**Relationship between soil characteristics and the species composition**

For both investigations, the CCA ordination of the weed seed bank composition with environmental data (Fig. 4) was highly significant ($P = 0.0005$; Monte Carlo permutation test). Axes 1 and 2, accounted for only 13.7% (A) and 6.6% (B) of the cumulative variation in the species data, which implies that important variables were not included in the present analysis. One missing variable is management, which may be the most important environmental factor for arable weed seedbanks (Albrecht & Pilgram, 1997).
Table 1. Component matrix of a PCA of co-variables and Spearman correlation between co-variables and seed bank characteristics for investigation A (samples collected in 1986/87 from 140 fields in seven regions in Bavaria)

<table>
<thead>
<tr>
<th>Co-variable factors</th>
<th>CoF1</th>
<th>CoF2</th>
<th>Spearman correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed number</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed weight</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed longevity</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>3.163</td>
<td>1.468</td>
<td>0.461*** 0.195* 0.141 n.s.</td>
</tr>
<tr>
<td>Variance explained %</td>
<td>45.2</td>
<td>21.0</td>
<td>-0.732*** 0.487*** -0.051 n.s.</td>
</tr>
<tr>
<td>Cumulative variance %</td>
<td>45.2</td>
<td>66.2</td>
<td>0.118 n.s. 0.021 n.s. 0.021 n.s.</td>
</tr>
<tr>
<td>C/N ratio</td>
<td>-0.885</td>
<td>0.053</td>
<td>-0.425*** 0.117 n.s. -0.051 n.s.</td>
</tr>
<tr>
<td>pH level</td>
<td>0.849</td>
<td>0.265</td>
<td>0.118 n.s. 0.021 n.s. 0.021 n.s.</td>
</tr>
<tr>
<td>Available field capacity</td>
<td>0.800</td>
<td>-0.027</td>
<td>-0.423*** 0.393*** -0.010 n.s.</td>
</tr>
<tr>
<td>K concentration</td>
<td>0.603</td>
<td>0.327</td>
<td>-0.312*** 0.129 n.s. -0.038 n.s.</td>
</tr>
<tr>
<td>N&lt;sub&gt;4&lt;/sub&gt; concetration</td>
<td>0.373</td>
<td>0.760</td>
<td></td>
</tr>
<tr>
<td>P concentration</td>
<td>-0.146</td>
<td>0.907</td>
<td></td>
</tr>
<tr>
<td>Total number of seeds</td>
<td>-0.588***</td>
<td>-0.019 n.s.</td>
<td></td>
</tr>
<tr>
<td>Seed weight</td>
<td>0.337***</td>
<td>0.202*</td>
<td></td>
</tr>
<tr>
<td>Seed longevity</td>
<td>0.054 n.s.</td>
<td>0.087 n.s.</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Component matrix of a PCA of co-variables and Spearman correlation between co-variables and seed bank characteristics for investigation B (samples collected in 1991 from 299 points in a 110 ha area in southern Bavaria)

<table>
<thead>
<tr>
<th>Co-variable factors</th>
<th>CoF1</th>
<th>CoF2</th>
<th>Spearman correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed number</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed weight</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Seed longevity</td>
</tr>
<tr>
<td>Eigenvalues</td>
<td>1.768</td>
<td>1.494</td>
<td>-0.017 n.s. 0.092 n.s. 0.024 n.s.</td>
</tr>
<tr>
<td>Variance explained %</td>
<td>29.5</td>
<td>24.9</td>
<td>-0.067 n.s. 0.106 n.s. -0.001 n.s.</td>
</tr>
<tr>
<td>Cumulative variance %</td>
<td>29.5</td>
<td>54.4</td>
<td>-0.026 n.s. 0.031 n.s. 0.071 n.s.</td>
</tr>
<tr>
<td>K concentration</td>
<td>0.794</td>
<td>-0.129</td>
<td>-0.105 n.s. -0.099 n.s. 0.033 n.s.</td>
</tr>
<tr>
<td>P concentration</td>
<td>0.768</td>
<td>-0.020</td>
<td></td>
</tr>
<tr>
<td>pH level</td>
<td>0.710</td>
<td>0.158</td>
<td></td>
</tr>
<tr>
<td>N&lt;sub&gt;4&lt;/sub&gt; concetration</td>
<td>-0.149</td>
<td>0.732</td>
<td></td>
</tr>
<tr>
<td>C/N ratio</td>
<td>-0.146</td>
<td>-0.823</td>
<td>0.261*** 0.073 n.s. -0.083 n.s.</td>
</tr>
<tr>
<td>Available field capacity</td>
<td>0.017</td>
<td>0.490</td>
<td>-0.133* -0.181** 0.045 n.s.</td>
</tr>
<tr>
<td>Total number of seeds</td>
<td>-0.068 n.s.</td>
<td>-0.210***</td>
<td></td>
</tr>
<tr>
<td>Seed weight</td>
<td>0.072 n.s.</td>
<td>-0.176**</td>
<td></td>
</tr>
<tr>
<td>Seed longevity</td>
<td>0.040 n.s.</td>
<td>0.097 n.s.</td>
<td></td>
</tr>
</tbody>
</table>

In the joint plot for investigation A (Fig. 4A), five environmental variables exhibit a strong relationship to the species composition by exceeding the cut off value of \( r^2 = 0.15 \). Small angles between the pH, P, and N<sub>4</sub> vectors suggest a high correlation among these variables indicating the nutrient status of the soils. Most species in investigation A seemed to prefer the nutrient-rich soils. Particularly indicative of high N were *Galium aparine*, *Tripleurospermum inodorum* and

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Elymus repens. In contrast, Juncus bufonius, Spergularia rubra and Rumex acetosella seemed to prefer sites with a wide C/N ratio. Sites with a high AFC were preferred by Gnaphalium uliginosum and Chenopodium album. Erophila verna, Arabidopsis thaliana, Viola arvensis, and Persicaria maculata, however, were common on dry substrates.

![Graph showing the relationship between weed seed weight and available field capacity](image)

**Fig. 3.** Relationship between the weed seed weight (median with quartiles) and the available field capacity in soils of investigation B ($r = -0.181^{**}$)

The ordination diagram in Fig. 4B shows that the available field capacity was the only variable in investigation B not eliminated by the cut off value. Species frequently found at sites with high AFC-values were Sonchus asper, Poa annua, Veronica persica and, in contrast to investigation A, Arabidopsis thaliana, Viola arvensis, Anthemis arvensis, and Fallopia convolvulus prevailed at sites with low AFC. The majority of species, however, comprising Chenopodium album, C. polyspernum and Poa annua, were not associated with the AFC vector. This indicates that other environmental factors may have influenced their occurrence in study B.

**Discussion**

*The influence of scale on soil properties and seedbank characteristics*

The present investigation clearly shows that the relation between soil characteristics and the weed seedbank highly depends on the investigation scale. Thus, a major reason for the great variation of the pH values in investigation A is that the samples were collected in both calcareous and siliceous landscapes. In contrast, samples for investigation B come from only one area with moderately acidic soils. Similarly, the higher variation in the N concentrations and in the C/N ratios of A can be explained by a wider range of site conditions. Consequently, correlations between soil properties and seedbank characteristics were highly significant when landscapes with different soil conditions were regarded. Within landscapes, these influences may still be recognisable but they are less pronounced.

Not all soil characteristics differed greatly between the two investigation scales. Thus, minor differences were observed for the K and P concentrations. Apart from the natural site
conditions, these results may reflect the influences of land use. More precisely, they reflect the effects of preceding fertilisation practices. That is, farmers in both investigation areas had similarly applied K and P for decades to avoid deficiencies in crop nutrition. This practice may have levelled natural differences in soil properties.

Another soil variable that scarcely differed between the two scales was the AFC. Nevertheless, it was related closely to soil seedbank data in both investigations. On the one hand, this may be due to the essential influences that water exerts on plant growth. On the other hand, the AFC hardly can be changed by cultivation practice.

In general, soil conditions can affect arable weed seed banks directly and indirectly. Direct effects occur, for example, when waterlogged pores hinder the entrance of oxygen into soil. This prevents germination and leads to an accumulation of seeds. Indirect effects occur when soil conditions influence the management practice and this, in turn, affects the seed banks. That may occur, for instance, when sandy soils necessitate the cultivation of soil-specific crops like rye and potatoes. In this case, natural variation in site-seedbank interactions may even be increased by the cultivation practice. On the scale of a field with loam soil, however, management is not altered because of some sandy spots occur within the field. In this latter case, arable farming reduces natural variation in seedbanks due to soil properties. Therefore, to separate the effects of soil conditions and management practice clearly, and to ascribe seedbank characteristics to only one of the two factors, is scarcely possible.

**Relationship of soil characteristics to the total number of seeds and the species composition**

Both the numbers of seeds and the species composition were linked closely to field capacity. As AFC data were derived from the percentages of grain size fractions, the negative correlation to the total number of seeds corresponds to Cavers & Benoit (1989) and Sjursen (2001), who noted a higher richness of seedbanks in coarse soils. The AFC also affects single species by influencing population dynamics and selecting site-specific weed communities. In the present study, seeds of *Poa annua* and *Veronica persica* predominantly occurred in substrates with a high AFC, while *Viola arvensis* seemed to prefer drier sites. This agrees with results of aboveground records by Andreasen et al. (1991), who found that those species were related to the clay percentage (which determines water holding capacity). The correlation with soil texture found for *Aspera spic-a-venti*, *Myosotis arvensis*, *Polygonum aviculare*, *Galium aparine*, and *Stellaria media* by Andreasen et al. (1991) and Dunker (2002), however, was not confirmed. In the present study, these species seemed to depend more on nutrient levels or on type of management. The occurrence of *Chenopodium album*, being closely linked to AFC in study A but not in B, also suggests that management could have affected this relationship. In general, the cultivation of row crops (beet, potato, maize) is more common in regions with high than low AFC. For the arable fields of Bavaria this correlation is highly significant ($r^2 = 0.18$ for $n = 12749$; Auerwald, unpublished). In contrast to region A where crop rotations markedly varied among sites, rotations were nearly identical in the area of study B. *Chenopodium album* may react more to the interactions between management and AFC than to the AFC on its own.

A second variable highly accounting for the variation in seedbanks was the C/N ratio. In both studies, it was significantly correlated to the total number of seeds. A wide C/N ratio always indicates a restricted microbial turnover of organic matter. In woodland this is frequently caused by acidity or a low nutrient availability. Both hardly occur on arable land. There, microbial activity can be reduced by a lack of oxygen at very wet sites or by a lack of water in sandy substrates. In the present study, the latter is more likely. Obviously, a limited turnover of organic matter may also conserve seeds.

The pH level being closely related to the soil seedbank in investigation A, but not in B, may be due to the high variation in soil buffer systems and pH levels among the seven areas included in investigation A. Wilson (1990) and Hofmeister & Garve (1998) documented clear differences between weed communities on high-pH calcareous soils, and those on low-pH silicate substrates. In the present study *Anagallis arvensis*, *Lamium amplexicaule*, *Myosotis*
arvensis, Plantago intermedia, and Veronica persica predominantly grew on soils with high pH. Andreasen et al. (1991) and Dunker (2000) also observed positive correlations with alkaline soils for these species. No such relations were observed in investigation B, whose moderately acidic soils were limed and thereby homogenised. In general, these results suggest that pH still has a great influence on soil seedbanks when areas with varying soil conditions and buffer systems are compared. Within homogeneously managed landscapes, however, such differences hardly occur.

In the PCA analysis of investigation A, the P and N concentrations mainly contributed to the 2nd factor, which is presumed to represent the input of organic matter into the soil. Hence, non-significant correlations suggest that this factor scarcely affects seedbank densities. The relation to species composition, however, was easier to perceive. There, the observation of Dunker (2000) was confirmed that Galium aparine and Stellaria media prefer high N concentrations in soils. In general, the present results suggest that the P and N affected more the species composition than the number of seeds. That no such relation was observed in investigation B may be due to the lower variation of N in study B, but it also could indicate that scale-dependent effects on management play a role. Finally, the effects of the K concentration on weed seedbanks seemed to be less important. This result agrees with conclusions drawn from investigations in the aboveground weed flora by Andreasen et al. (1991) and Dunker (2002).

Relationship of soil characteristics to seed weight and seed longevity

Correlation of seed weights to variables indicating a good nutrient supply may be due to competition. Hence, big seeds have a better chance to develop tall and healthy plants able to survive and reproduce even under a dense crop canopy on nutrient rich soils. The results on the relation between seed weight and field capacity were inconsistent. In investigation B seeds in soils with low AFC values (= sandy soils) were significantly heavier than those in soils with a fine texture. One reason for this could be that limited water supplies occurring at the surface of sandy soils favours large seeds. Such seeds produce vigorous seedlings, the roots of which may quickly penetrate the subsurface layers and thereby decrease drought stress. Another reason may be the negative relationship between seed size and seed persistence (Thompson et al., 1993). Thus, seeds in soils with a fine texture are frequently enclosed in aggregates (Reuss et al., 2001). There, they are exposed to a high moisture and low oxygen supply during most of the year (Pareja & Staniforth, 1985; Renault & Stengel, 1994). Such conditions are not conducive to seed germination and encourage the maintenance of seed dormancy (Murdoch & Ellis, 1992) or induce secondary dormancy (Qi & Upadhyaya, 1993). Conversely, in drier sandy soils fluctuation in soil moisture during the year causes hydration-dehydration cycles, which result in increased germination of weed seeds (Cavers & Benoit, 1989). In this way, soils with a high AFC may select for species with small and persistent seeds. In the present analysis, however, no such correlation was found. In addition, the results of investigation A do not confirm those of investigation B. There, small seeded species like Juncus bufonius, Erphila verna, Arabidopsis thaliana, and Spergularia rubra frequently occurred in the seedbanks of soils with low AFC. This then became a significant correlation. Juncus bufonius also occurs at high frequency in seedbanks of sandy fields in Denmark (Jensen, 1969). Most of the 35,960 seeds m⁻² found there belonged to this taxon. These results indicate the relationship between seedbank characteristics and field capacity to be very complex and to depend largely on individual properties of the dominant species.

In contrast to seed weights, seed longevity indices showed barely any variation in the present study. Thus, seed longevity may be a characteristic that is highly constant under the environmental conditions in arable fields.
Fig. 4. CCA ordination of the seedbank composition with environmental variables. Eigenvalues of axes 1 and 2 are 0.563 and 0.276 in investigation A, and 0.174 and 0.136 in investigation B. Variables below a cut off value of r² = 0.15 were not included.
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