Seed bank characteristics of Dutch plant communities

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SUMMARY

With the recent appearances of a new and well-documented classification of the Dutch plant communities (Schaminée et al. 1995a,b; 1996) and a database on the seed longevity of plant species of North West Europe (Thompson et al. 1997a) it was possible to investigate patterns of seed longevity in Dutch plant communities, considering the frequencies of plant species in various communities. This study revealed that arable weed communities have long-lived seeds compared to the transient seed bank of deciduous woodland; species-rich grassland communities tend to have a short-lived soil seed bank, intermediate between the latter two communities. Moreover, the present study showed that significant differences in community longevity exist between weed communities as well as between grassland communities. The approach based on soil seed bank spectra of plant communities gives support to existing phytosociological theories on different strategies of plant communities sensu Stortelder (1992) and Schaminée & Stortelder (1996). The information on seed longevity of communities is essential to the practice of nature conservation and nature development because it reveals the possible vulnerability of plant communities to extinction, including their soil seed banks, the necessity of their conservation and their possibilities for regeneration.

Key-words: arable weeds, grassland, phytosociology, seed longevity, woodland.

INTRODUCTION

Soil seed banks can be considered an important source of regeneration of plant species (Fenner 1992). Seeds that have developed in or dispersed into an area can either germinate immediately or can be incorporated into the seed bank for a certain period of time. The timespan that seeds can survive in the soil is then of interest, if possible

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Nomenclature follows Van der Meijden (1990) for plant species and Schaminée et al. (1995b, 1996) for syntaxa.

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for each individual plant species. Many studies on soil seed bank survival have shown that the longevity of single plant species is often difficult to determine accurately (Kivilaan & Bandurski 1981; Vyvey 1989a,b; Bernhardt & Poschlod 1993) or highly variable within single species due to, for example, variable edaphic conditions (Ibrahim *et al.* 1983; Murdoch & Ellis 1992), or variable genetic structure (Sawicka & Sadowska 1990). The application of condensed information on seed longevity either at the species level or at the level of communities would be very useful for the predictability of ecological processes and for the practice of nature conservation.

Basically, authorities in charge of nature conservation have the need for a tool to predict the possible re-establishment of plant communities with nature conservation interest. Especially when nature conservation has not succeeded in the establishment of target species the question of re-introduction arises (Prins *et al.* 1998, this issue). In The Netherlands the discussion on reintroduction of plant species focuses on the question of reachability and accessibility (Londo 1984; Londo & Van der Meijden 1991). Active reintroduction of species in general can be allowed when, with a certain level of certainty, one could know that diaspores of the to-be-introduced species are not available at the site in the soil seed bank and will not reach the site in the near future (Strykstra *et al.* 1998, this issue).

As this predictive tool does not so far exist, and the information on seed dispersal is scanty and scattered (Bakker *et al.* 1996), we considered it useful to make some generalizations on possible seed longevity of plant species on a community level.

The recent appearances of a new classification of Dutch plant communities, based on vegetation tables (Schaminée *et al.* 1995a,b; Schaminée *et al.* 1996) and a database of the seed longevity of plant species of North West Europe (Thompson *et al.* 1997a) provided the opportunity to investigate the potential for re-establishment of whole plant communities from the soil seed bank on the basis of the whole set of plant species belonging to the community. This link can also contribute to the discussion of vegetation strategies as proposed by Schaminée & Stortelder (1996), as we hypothesize that between syntaxa large differences exist in community longevity according to the differences in life history evolution of the communities.

METHODS

Seed longevity data

The data gathered in the database of Thompson *et al.* (1997a) include 275 sources on soil seed bank studies and contain information on 1189 species of North West Europe. Data on individual species in a publication were included if the source provided clear information on the species identity, seed densities and sampling methods. The longevity of seeds was classified using a decision scheme resolving the longevity into three different categories, transient (less than 1 year), short-term persistent (1–4 years) and long-term persistent (more than 4 years).

The information about a single species was hardly ever consistent; many species had been recorded in several categories of longevity. This is due mainly to the fact that for each species these data originate from different geographical regions, habitats and soil types. For comparative reasons, we summarized the different categories per species using a longevity index on a continuous scale from transient to persistent (Thompson *et al.* 1998). In short, this means that we calculated the proportion of persistent (shortterm and long-term persistent) records, i.e.:



Fig. 1. Distribution of the total number of species (n) in longevity index classes of the communities *Mesobromion* (n=70), *Caucalidion* (n=71) and the reference set of species (n=561). The presence of each species in each set is valued equally.

(short-term + long-term persistent records) (transient + short-term + long-term persistent records)

Hence, the index can vary between 0 and 1, where 0 means no persistent records and 1 stands for all persistent records. In the present paper the index was multiplied by 10 for technical reasons.

The species in the seed bank database had to suit some criteria prior to the calculation of the index:

- the species should have at least five categorized records, or
- if a species has three or four unanimous categorized records it was included.

Applying these criteria, this resulted in a list of 561 species of the Dutch flora with a reliable seed bank characteristic. The distribution of the index was, although U-shaped, well balanced over the 561 species, as shown in Fig. 1. Only the 0-category and the 10-category were slightly over-represented, but this was to be expected according to the way the seed bank types have been assigned to the records in the database (see also Thompson*et al.* 1997a).

Phytosociological data

In The Netherlands the first three volumes of the national vegetation classification have been published recently (Schaminée *et al.* 1995a,b, 1996). At present the complete computerized database behind this classification comprises 170 000 vegetation relevés, but is still being expanded. Relevés from 1929 onwards have been included, although the majority of the relevés have been made in the last two decades. The relevés cover the country geographically and can be considered representative of its extant communities (Schaminée & Stortelder 1996).

The vegetation classification presented by Schaminée *et al.* (1995a) is based on the processing of large numbers of relevés for each syntaxon. Each syntaxon was described by a list of species frequencies of all species in the syntaxon, the vegetation table. Only species with a frequency of 10% or more were included in the final publication, except if the species is a character species of the syntaxon; these species can be included with



Fig. 2. Plant communities (classes and alliances) plotted according to their community strategies as proposed by Stortelder (1992). The vertices of the triangle form three different strategies, based on the concept that communities exist because of their social structure. At the top communities can found that avoid stress and disturbance by modifying their own environment ('transformers'). Communities that 'escape' unfavourable periods, mainly through high dispersability, form a separate strategy. 'Persistent' communities exhibit the strategy to survive under extreme environmental conditions. The communities printed in bold were investigated for their community longevity.

lower frequencies in a particular syntaxon. Obviously, these lists include vascular and non-vascular plants as well as mosses and ferns.

The data for deciduous woodland were not yet published at the time of analysis and, therefore, it is possible that small differences occur in the set of species of the *Carpinion betuli* used in the present analysis compared to the table that will appear in the final vegetation classification.

The equilateral triangle model for the classification of plant community strategies by Stortelder (1992) and further presented in Schaminée & Stortelder (1996) based on the theory behind Grime's model on plant functional types for individual species (Grime 1979) was used to select the different vegetation types for the present study (Fig. 2). The vertices of the triangle form three different strategies, based on the concept that communities exist because of their social structure. At the top, communities that avoid stress and disturbance by modifying their own environment are gathered in the strategy of 'transformation'. Communities that 'escape' unfavourable periods form a separate strategy from communities that exhibit the 'persistence' strategy and herewith survive under extreme environmental conditions.

In the present study we chose one or two communities from each vertex and two from the centre of the triangle, so that the whole range of community strategies was covered. We had difficulties choosing a community representing the 'persistence' strategy due to lack of seed bank data for the communities in this group.

Link between seed bank and vegetation data

The seed bank data do not include non-vascular plants, orchid species and ferns, therefore we eliminated those species from the vegetation classification lists. The vegetation classification was used at the level of alliances only. The frequency of a species in all relevés appointed to a syntaxon, the occurrence in the vegetation table was used as weighting factor of the seed bank characteristic, the longevity index. All frequency \times longevity index figures were presented as relative numbers from the sum of frequency \times longevity figures over all species in the syntaxon. If a species occurs, for instance, with 80% in the vegetation table and has a longevity index of 0.6, then it accounts for 48. Given, for instance, the total score of longevity \times frequency figures of the whole set of species being 480, this species makes up 10% of the community longevity, contributing to category 6.

The contribution of the character species, the core set of species defining the alliance, to the community longevity is estimated separately. The set of character species was defined as the total list of character species of the class, the order and the alliance of the syntaxon under study as distinguished by Schaminée *et al.* (1995a,b, 1996). Consequently, differential and accompanying species were excluded from this subset of species.

Missing species with no seed longevity index, due to lack of data, were excluded from the community calculation. In each of the figures the number of species with a longevity index is presented together with the total number of species that could have been included in the syntaxon.

The community longevity spectra were calculated with the program SPECTRUM, part of the software package TURBOVEG (Hennekens 1995).

Data analysis

All seed bank distributions of the selected syntaxa were compared with the reference distribution of the 561 species for which we could calculate a longevity index using a χ^2 test (rejection level P < 0.05). The actual numbers, not the percentages, of species in a certain class of longevity were used in this test. Prior to each test the distribution of the syntaxon was subtracted from the reference distribution to make sure that both distributions were independent.

To test whether the weighted distributions of the syntaxa differed significantly from each other we also used a χ^2 test. This test was performed on the distribution of the numbers of relevés in each index class, consisting of the occurrence of each single species in the vegetation table, summed up over all species in a certain index class.

RESULTS

The distribution of the number of species in each class of longevity for two contrasting communities and the reference set with all 561 native Dutch species in the database that could be indexed is shown in Fig. 1. It is clear that both distributions of the syntaxa differ from each other and from the reference set. The seed longevity of all tested communities differs significantly from the reference set of species (Table 1). The *Littorellion* community could not be tested due to the high number of zero values in its distribution.

The syntaxon *Littorellion uniflorae* was defined by 114 relevés containing 39 vascular plant species, not being orchids and ferns (Fig. 3). From these 39 species the seed bank

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Table 1. The distribution of the number of species per class of longevity was pairwise tested against the distribution of all species in the database minus the species in the community involved, with a χ^2 test (d.f. = 10, critical value of $P < 0.05 = \chi^2 \ge 18.3$; $P < 0.01^{**}$, $P < 0.001^{***}$). The calculated χ^2 values and the level of significance are indicated

	Mesobromion	Junco- Molinion	Caucalidion	Fumario- Euphorbion	Carpinion
Reference	29.0**	83.0***	48.5***	54.1***	64.4***



Fig. 3. Seed bank spectrum of the *Littorellion* (total number of relevés n=114). Each longevity index of a species present in the community is weighted by the species occurrence (percentage of relevés) in the vegetation table. The longevity index was known from 13 of 39 taxa.

database missed information on 26 of them. Nine character species were assigned to this syntaxon, of which only one species was included in the seed bank database. This syntaxon is an example of a community that is poorly studied for its soil seed bank composition. Very few references have been incorporated in the seed bank database concerning this habitat type (Thompson *et al.* 1997a). This community consists of too few species to describe the pattern well; 55% of the frequency \times longevity figures in this community are accounted for by a single species (i.e. the only character species that could be included, *Juncus bulbosus*) filling one category (index 9) on its own. It seems that the community on average forms more persistent seeds than could be found in the reference set of species. However, in general we cannot give a distinct qualification to this community due to lack of data published.

The seed bank spectra of the arable weed communities showed a very clear pattern (Figs 4 and 5). The *Caucalidion* community represents a community of weed species in cereal crops on more or less calcareous soils, whereas the *Fumario-Euphorbion* community represents a community of weed species in root crops on relatively eutrophic soils. Both communities are well represented in the seed bank database with, respectively, 80% and 86% of the total number of species included and, respectively, 58% and 94% of the character species of these communities. These communities produce persistent seeds, although the *Caucalidion* community has more character species in the transient categories than the common *Fumario-Euphorbion* community. Both distributions, compared by the sum of the relevés in which each species occurred in the syntaxa, differ significantly (Table 2).



Fig. 4. Seed bank spectrum of the Caucalidion (n=91). In total 71 of 89 taxa could be indexed. See also Fig. 3.



Fig. 5. Seed bank spectrum of the Fumario-Euphorbion (n=130). The seed longevity of 62 of 72 taxa was known. See also Fig. 3.

Table 2. Each species with a certain class of longevity has a certain occurrence (number of relevés) in the vegetation table of a syntaxon. The distribution of the total number of relevés per class of longevity per syntaxon was pairwise tested against the distribution of the other communities with a χ^2 test (d.f. = 10, critical value of $P < 0.05 = \chi^2 \ge 18.3$; $P < 0.001^{***}$). The calculated χ^2 values for each pairwise comparison, the level of significance and the mean community longevity are indicated

	Junco- Molinion	Caucalidion	Fumario- Euphorbion	Carpinion	Mean community longevity
Mesobromion	695.3***	2521.2***	3324.9***	3173.7***	2.6
Junco-Molinion		3544.9***	4598.1***	5696.3***	2.9
Caucalidion			165.2***	5347.1***	6.4
Fumario-Euphorbion		94.		6884.6***	7.0
Carpinion					1.4

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Fig. 6. Seed bank spectrum of the Carpinion betuli (n=470). The index could be calculated for this community from 87 of 104 taxa. See also Fig. 3.



Fig. 7. Seed bank spectrum of the Junco-Molinion (n=268). The index of 95 of 117 taxa could be calculated for this community. See also Fig. 3.

The seed bank spectrum of deciduous woodland on limestone (*Carpinion betuli*) showed that more than 60% of this community forms transient seeds (Fig. 6). This is much more than the reference of the seed bank database. The number of species for which information on seed longevity was available amounted to 87 of 104 species in total; 44 character species of 54 could be indexed. This community can be assumed to build a transient seed bank.

The species-rich grassland communities are represented by the seed bank spectrum of the Junco-Molinion (wet oligo-mesothrophic meadows; Fig. 7), and the spectrum of the Mesobromion, a chalk grassland community (Fig. 8). Both communities have a skewed distribution to the transient side of seed longevity. The Junco-Molinion has the best fit of the number of species involved (88%) against an also-high fit of 80% of the species in the chalk grassland community. Concerning the character species in the meadow community, we could take into account 22 species of 26; their seed longevity indices vary between 0 and 6. Ten of 11 character species of the Mesobromion could be indexed, varying between the longevity classes 0 and 3. This implies that the majority



Fig. 8. Seed bank spectrum of the *Mesobromion* (n=138); 70 of 88 taxa of this community could be indexed See also Fig. 3.

of the species of chalk grasslands produces transient seeds that are, on average, shorterlived than the seeds of a *Junco-Molinion* community (Table 2).

Both grassland communities differ significantly from the reference set if we consider only the presence of the species in the syntaxa (Table 1). If we take into account the actual number of relevés in which the species occur, and then compare the distribution in the classes of longevity for each community (Table 2), it is clear that not only both communities differ significantly from each other but also from all other communities.

DISCUSSION

The present study revealed that the combination of single species data on seed longevity into a community level resulted in large significant differences not only between distinct but also between closely related communities, even though we did not have data for the complete species lists of every community. Although we would like to include data on the longevity of all individual species in discussions on vegetation management, the results of the present study already reveal applicable differences in community longevity for the practice of nature management. Based upon mean community longevity in Table 2 we can rank the tested communities according to their decreasing community longevity of the seed bank as follows:

Fumario-Euphorbion>Caucalidion>>Junco-Molinion>Mesobromion>>Carpinion.

To underpin the value of this ranking for the practice of nature conservation we will discuss each of the communities presented in this study separately.

The arable weed communities, not surprisingly, form persistent seed banks. Many authors have found the same result for individual species in soil seed bank studies on arable fields (Roberts 1981; Vyvey 1989a,b; Fenner 1992). Previously, however, the difference between the two communities was never clear. The present study made clear why the *Caucalidion* contains so many Red List species in contrast to the *Fumario-Euphorbion*. Projects on the restoration of the rare *Caucalidion* have shown that many of the species did not have a long-term persistent seed bank and needed to be re-introduced into the fields deliberately (Otte 1990; Smeding 1993; Schneider *et al.* 1994).

The woodland community could be seen as climax vegetation on its substrate. The © 1998 Royal Botanical Society of The Netherlands, Acta Bot. Neerl. 47, 15-26

highly transient seed production is therefore in accordance with Harper (1977) and Fenner (1987), who already suggested that late successional, shade-tolerant species tend to form large and short-lived seeds. This community is not subjected to a high frequency of biomass removal or soil disturbance compared to the arable weed communities. Also in this respect many authors have stated that woodland species are less likely to form long-term persistent seed banks than to form persistent seedling banks (Fenner 1987; Houle 1991).

The grassland communities take an intermediate position in comparison with the aforementioned communities. They are subject to a regular removal of biomass as they are usually cut once a year or grazed. Only a fraction of the grassland species form a long-term persistent seed bank. This is in agreement with many studies on the restoration or conservation of grassland communities (Thompson & Grime 1979; Willems 1988; Hutchings & Booth 1996; Bekker 1997). The difference in community longevity between the two communities might reflect the difference in the number of *Carex* and *Juncus* species belonging to each of the communities, respectively 14 in the *Junco-Molinion* and two in the *Mesobromion*. Both genera usually have persistent seeds (Thompson *et al.* 1997a).

The Littorellion community could not be qualified properly with the present approach, but it showed a tendency towards the production of long-lived seeds. This is in agreement with the findings of Roelofs *et al.* (1996). They found that Littorellion-like communities were easy to restore from the soil seed bank, even after the character species had disappeared for many years from the vegetation. Given the present dataset on seed longevity it was the best represented community of the group of 'persistent' vegetation types (Fig. 2). More published data are needed on seed longevity of species contributing to the permanent pioneer communities.

The seed bank characteristics can be seen as an illustration of differences in vegetation strategies between the plant communities mentioned in this study. The 'transformation' communities, woodland in the present study, invest more in growth (clonal growth included) than in reproduction. The 'persistent' communities, in general, rely on survival and therefore invest marginally in reproduction but if they do, only a fraction of them produces long-lived seeds. The 'escape' communities, i.e. arable weed alliances, rely on maximal reproduction and therefore produce many seeds of which the majority are long-lived.

If data on the longevity of more species, especially on species of the 'persistent' communities, become available, more contrasts between closely related communities can be shown, providing more insight into the possibilities of regeneration of these communities. Based on the present study we can conclude that communities with a short-lived seed bank need to be preserved with high priority. If nature development in newly created areas aims at communities with short seed bank longevity, care must be exercised in the prediction of feasibility within a certain timespan. Extra measures to help complete plant communities to establish must be considered.

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