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The significance of the seed bank as a potential for the reestablishment of arable-land vegetation in a marginal cultivated landscape

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As part of the German Research Foundation (DFG) project "Land Use Concepts for Marginal Regions", since 1997 we have made analyses of the seed bank of 22 cultivated allotments, as well as of 15 meadow/pasture and 16 fallow allotments on former arable land of the Lahn-Dill Highlands, a marginal cultivated landscape in Hesse, Germany. One aim of this study is to determine according to which dynamic laws the seed bank of arable-land weeds is depleted after cultivation is abandoned.

Depending on the intensity of the arable land use, the seed banks of rankers and cambisols that are presently still cultivated contain up to 1 004 800 seeds of arable-land species capable of germination m^{-3}. Soils that were last cultivated less than ten years ago have much lower seed densities, while the seed bank of arable-land species is largely exhausted after only ca 20 yr. This points to an exponential depletion of the seed bank of arable-land species and their abundance over time. On the basis of the present results, < 20 yr remain in the Lahn-Dill Highlands for the reestablishment of characteristic arable-land vegetation from the seed bank.

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The vegetation of cultivated landscapes essentially reflects the current land use, in addition to the characteristic features of the natural region. However, the respective plant species that are present (including those in the seed bank) also give an indication of the specific land-use history of a cultivated landscape. Ultimately, the vegetation of future land-use systems can only develop on the basis of this species inventory, assuming that no new species are introduced in the course of the land use. Hence, the seed bank is of major importance as a developmental potential for future vegetation types (Bakker et al. 1996).

Since around 1950, cultivation in central Europe's marginal cultivated landscapes has increasingly been abandoned in favour of meadow/pasture use. Hence, the arable-land weed species that are associated with cultivation are lost from these landscapes: they very quickly disappear from the establishing vegetation of the subsequent land use, and their seed reserve is more or less rapidly depleted. If arable-land species are to be retained as a developmental potential for future land uses, it must be borne in mind that the seed reserve will only be available for a limited time after cultivation has been abandoned (Parker et al. 1997).

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The aim of the present study is to analyze the dynamics of the seed bank of (formerly) cultivated areas using the example of the Lahn-Dill Highlands, a marginal landscape in central Germany. The results will be used for the development of future land-use systems for this landscape (Frede and Bach 1999) as part of the interdisciplinary German Research Foundation (DFG) project "Land Use Concepts for Marginal Regions".

Materials and methods

Study area

The Lahn-Dill Highlands (Hesse) is a region in Germany's central highlands (altitude 200–600 m a.s.l.) with conditions that are relatively unfavourable for cultivation (Frede and Bach 1999). These conditions are: 1) climatic (mean annual temperature 5–8°C, annual precipitation 700–1200 mm); 2) edaphic (acidic shallow rankers to moderately shallow cambisols over Devonian clay slates, gravel slates, and greywackes, predominating on slopes of over 20°); and 3) agricultural and structural (extremely small rural structures, many secondary occupations). The traditional rotation of arable and grassland farming, as described by Kohl (1978) has been largely abandoned. This applies especially the formerly frequent cultivation of potatoes. Nowadays meadow/pasture is predominant.

The (former) arable land weed community of grain fields that is typical of the landscape is the Aphano-Matricarietum chamomillae R. Tx. 37, in the sub-associations "scleranthetosum" und "thlaspietosum". The communities Spergulo-Chrysanthemetum segetum R. Tx. 37 and Thlaspio-Fumarietum officinalis Görs 66 are associated with the cultivation of row crops (Nowak and Wedra 1988, Waldhardt et al. 1999a, b).

Methods

Since September 1997, we have analyzed the seed bank of 22 cultivated allotments, as well as of 15 meadow/pasture and 16 fallow allotments on former arable land. In order to record the variability of the seed bank over small areas, and in order to avoid soil surface contamination from seeds of more recent origin (cf. Bakker et al. 1996), we have taken 25 auger samples on 5 × 5 m subplots, from a soil depth of 5–10 cm, and combined these to obtain a mixed sample with a total volume of ca 1 litre. Sampling was generally repeated four times on each allotment, three allotments were sampled three times. The samples were spread into germination trays (28 × 18 × 2.5 cm), and exposed under field conditions until the end of October 1999. The samples were covered with gauze to prevent contamination by incoming seeds. When germination declined, the samples were dried for two weeks in a greenhouse, the soil material was crumbled, mixed, watered and exposed again.

This paper deals with results concerning the weed species only. Their seed bank is essential to reestablish arable land vegetation in an area where crop farming has largely vanished from the actual range of land use, assuming that recolonisation of newly established fields from the surroundings cannot be expected. A classified evaluation of the relative frequencies of the arable-land weeds (in the narrowest sense) and their seed densities (phytosociological classification according to Hüppe and Hofmeister 1990) has been made for 1) allotments that are still cultivated today, as well as for allotments in which cultivation was abandoned 2) 1–8, 3) 9–18, 4) 19–33, 5) 34–44, or 6) > 44 yr prior to sampling. The age of the seed banks was determined by interpretation of aerial photographs (scale: 1:12 000) from the above periods (Fuhr-Bossdorf et al. 1999).

Results

Seedlings from a total of 152 plant species germinated in the 209 germination trays. In addition to 59 meadow/pasture species and 32 ruderal species, 38 arable-land weeds (in the narrowest sense) made up the predominant phytosociological species groups.

On average, there were 8.0 arable land species with 137 900 m^{-3} seeds, preserved in the soils of allotments that are still cultivated today (Fig. 1). The ranges of weed species counts (0–22) and seed densities (0–1 004 000) are conspicuously wide. After abandonment of cultivation, the seed bank of arable-land species is rapidly depleted: after ca 10 yr, there are on average only 6.5 arable land species left, with 28 800 seeds that are still capable of germination, and after ca 20 yr only 1.5 species with 4300 seeds. This points to an exponential depletion over time of the seed bank of arable-land species and their abundance.

Base indicators and predominantly summer-annual species (including *Thlaspi arvense* (L.) and *Euphorbia helioscopia* (L.)) and the low-nutrient and low-moisture indicator *Papaver argemone* (L.), which occur in the seed bank of present-day arable land, although with comparatively low frequencies, are almost completely lacking in the seed banks of former arable land (Table 1). In contrast, numerous, predominantly winter-annual species that are widespread in Germany (including *Matricaria chamomilla* Auct., *Stellaria media* (L.) Vill., and *Capsella bursa-pastoris* (L.) Med.) could be found with high frequencies in the first 20 yr following land-use change. Only a few, similarly widespread arable-land species, e.g. *Chenopodium album* (L.), *Viola arvensis* Murray and *Aphanes arvensis* (L.), as well as Vicia species that are typical of Aphano-Matricarietum scleranthetosum (*V. hirsuta* (L.) S.F. Gray, *V. tetrasperma* (L.) Schreber, *V. angustifolia* (L.)) and also *Scleranthus annuus* (L.), are also present in the seed bank of the older meadow/pasture and fallow-field allotments. *Spergula ar-*

Table 1. Floristic variables, together with percentage constancies and maximal seed counts, of arable land species* in seed banks of different ages.

Years since last in cultivation	0		1–8		9–18		19–33		34–44		> 44	
(n)	88		8		12		53		24		24	
	Median	Min. Max.	Median	Min. Max.	Median	Min. Max.	Median	Min. Max.	Median	Min. Max.	Median	Min. Max.
Species counts/allotment												
– Total	14.0	2 28	14.0	8 21	6.5	4 14	5.0	1 15	7.5	3 22	7.0	2 11
– of the arable-land species*	8.0	0 22	6.5	3 7	1.5	0 6	1.0	0 5	1.0	0 4	0.0	0 4
Seed counts × 100 m^{-3}												
– Total	2017	26 11 865	582	188 1900	511	129 1741	203	15 3935	429	89 5373	379	52 1409
– of the arable-land species*	1379	0 10 048	288	94 444	43	0 390	12	0 194	14	0 108	0	0 147
	Const. (%)	Max.**	Const. (%)	Max.**	Const. (%)	Max.**	Const. (%)	Max.**	Const. (%)	Max.**	Const. (%)	Max.**
Lamium purpureum	24	2330	.	.	.	.	.	.	.	.	.	.
Lamium amplexicaule	19	990	.	.	.	.	2	70	.	.	.	.
Thlaspi arvense	18	1370	.	.	.	.	.	.	.	.	.	.
Aethusa cynapium	15	1290	.	.	.	.	.	.	.	.	.	.
Fumaria officinalis	9	5250	.	.	.	.	2	60	.	.	.	.
Sonchus asper	7	170	.	.	.	.	.	.	.	.	.	.
Sinapis arvensis	6	2690	.	.	.	.	.	.	.	.	.	.
Euphorbia helioscopia	6	990	.	.	.	.	.	.	.	.	.	.
Papaver argemone	18	5380	.	.	.	.	.	.	.	.	.	.
Matricaria chamomilla	53	6400	75	990	.	.	4	130	.	.	4	80
Apera spica-venti	48	18 920	13	70	.	.	2	270	.	.	.	.
Veronica arvensis	44	1840	38	310	.	.	4	100	.	.	8	110
Stellaria media	39	8670	50	80	.	.	2	220	.	.	.	.
Papaver dubium	24	2580	13	70	.	.	.	.	.	.	.	.
Anthemis arvensis	22	21 990	38	220	.	.	2	100	.	.	.	.
Centaurea cyanus	11	890	25	70	.	.	.	.	.	.	.	.
Polygonum persicaria	7	930	13	80	.	.	.	.	.	.	.	.
Tripleurospermum inod.	67	13 020	50	310	17	200	2	60	.	.	4	70
Capsella bursa-pastoris	38	5630	38	540	17	70	.	.	4	70	.	.
Fallopia convolvulus	40	890	13	80	8	80	2	80	.	.	4	150
Chenopodium album	56	44 110	75	690	42	300	19	300	25	190	13	150
Viola arvensis	72	6640	100	990	42	1580	15	160	13	310	8	400
Vicia hirsuta	47	4650	13	190	17	210	19	490	4	60	13	420
Aphanes arvensis	43	9960	25	220	.	.	15	270	17	470	17	230
Vicia tetrasperma	27	1260	.	.	.	.	6	240	8	130	4	110
Scleranthus annuus	25	11 350	13	80	50	630	.	.	4	60	8	130
Vicia angustifolia	9	360	13	250	.	.	9	240	4	250	4	90
Anagallis arvensis	7	130	.	.	.	.	.	.	13	130	.	.
Spergula arvensis	2	130	.	.	25	190	.	.	.	.	.	.

also occasionally present: *Alopecurus myosuroides, Atriplex patula, Cerastium glomeratum, Chenopodium polyspermum, Kickxia elatine, Raphanus raphanistrum, Sonchus arvensis, Veronica agrestis, Veronica persica.*
* Phytosociological classification according to Hüppe and Hofmeister (1990).
** seed count m^{-3}.

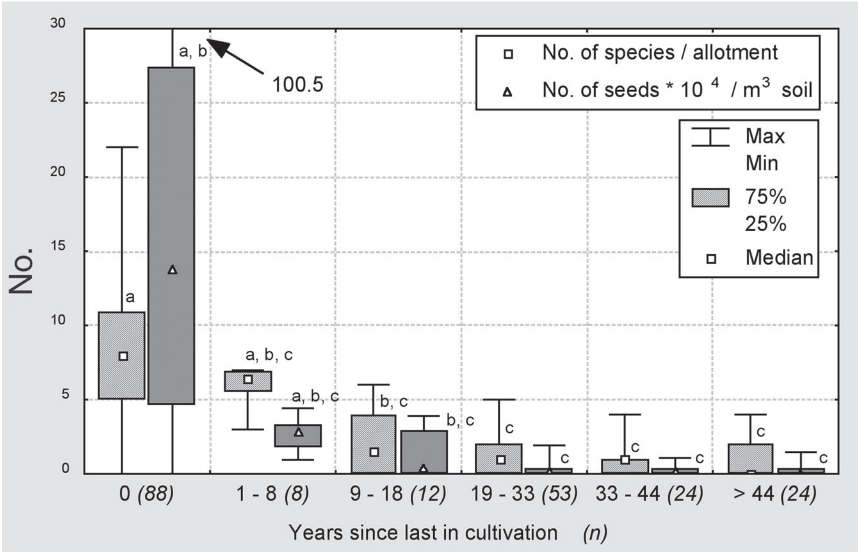

Fig. 1. Depletion of the seed bank of arable-land species following land-use change (soil sampling depth: 5–10 cm). a–c: values not sharing the same letter are significantly different at the 95% probability level (Tukey-HSD-Test).

vensis (L.), a characteristic species of Spergulo-Chrysanthemetum segetum, could only be found once in the seed bank of the present-day grain fields, but germinated from several samples from the 9 to 18 yr-old seed banks. We were unable to find any other characteristic plant species of this plant community (*Chrysanthemum segetum* (L.), *Stachys arvensis* (L.) and others), one that was once common, but is now rare in this region.

Discussion

The presence of plant species in seed banks is essentially influenced by 1) seed densities, 2) the spatial distribution of seeds, and 3) species-specific depletion rates (Otte 1992, Bekker et al. 1998). Species with low seed densities, clumped seed distributions, and short-lived seeds (*Lamium purpureum* (L.), *L. amplexicaule* (L.), and *Papaver argemone*, amongst others) were therefore absent from the older seed banks that we have studied, although it may be assumed that they were present in the former arable-land vegetation.

However, the seed banks of present-day arable land, and of former arable land abandoned only in the last 20 yr, reflect the different types of management used during cultivation: 1) The wide ranges of species counts and abundance of arable-land species in the seed bank of present-day arable land can be explained in terms of different management intensities (Cavers and Benoit 1989). 2) The presence of base indicators in the seed bank of the present-day arable land is favoured by the currently widespread practice of lime application and by a generally improved nutrient supply in the soils. These factors promote arable-land species with high nutrient requirements (cf. Otte 1990). 3) The comparatively low frequencies of these predominantly summer-annual species, which develop more rarely and are less abundant in grain fields than in row-crop fields, are also an indication of the paucity of row-crop cultivation in the region today. The presence of *Spergula arvensis* in older seed banks, and the absence of this species in the seed bank of present-day arable land, may be explained in an analogous manner. Its seeds, which according to Ødum (1965, 1974) and Thompson et al. (1997) are long-lived, may be considered a relic of the formerly frequent cultivation of potato, a typical row-crop species.

However, most of the seeds of the arable-land species in the aggregate-rich, shallow to moderately shallow soils of the Lahn-Dill Highlands are exhausted within the first 20 yr after cultivation is abandoned. The seed bank, which since Brenchley (1918) has been known to reflect the land-use history of a site, can be used for the reestablishment of arable-land vegetation only during this brief period. In order to retain the species diversity of the landscape, this will need to be considered in the land-use concepts for the Lahn-Dill Highlands.

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