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Seed traits in arable weed seed banks and their relationship to land-use changes

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Abstract

Recent studies have shown that relatively undisturbed plant communities, such as woodland and pasture, have generally low seed persistence, while seed longevity in frequently disturbed habitats, such as arable fields, is high. In addition, seed mass and shape were found to be closely linked to the living conditions of plants. The objective of the present study was to show how farming practice modifies these seed traits in the arable weed seed bank.

On 67.4 ha of arable land at the Scheyern Research Station in Germany, conventional arable use was converted to organic farming, to a reduced-tillage system and to set-aside. During the six subsequent years, seed bank data were collected at 283 sampling points to analyse the effects of (1) the farming systems (long-term effects), (2) individual crops (short-term effects) and (3) vegetation cover.

Set-aside arable land favoured a disk- or needle-like seed shape, greater mass and reduced seed longevity. Similarly, organic farming significantly increased seed mass and decreased longevity. Therefore, both types of land use reduced the selection for small and persistent seeds with a spherical shape. By contrast, an increasing persistence under reduced tillage suggested a higher selection pressure. The most consistent effect was that seed longevity increased with tillage frequency, independent from the farming system. Both high seed masses and a compact seed shape were frequently associated with a high crop cover.

The results prove that beyond the properties of living plants the arable farming practice also significantly impacts the seed traits in the soil seed bank.

Zusammenfassung

Aktuelle Untersuchungen belegen, dass Samen selten gestörter Pflanzenformationen wie Wälder und Wiesen eine niedrigere Persistenz aufweisen als solche aus häufig gestörten Ökosystemen (z.B. Ackerflächen). Zudem zeigten auch Form und Masse der Samen einen engen Bezug zu den jeweiligen Lebensbedingungen. Ziel der vorliegenden Untersuchung war es herauszufinden, inwieweit unterschiedliche Nutzungseinflüsse auch innerhalb ackerbaulich genutzter Ökosysteme diese Sameneigenschaften differenzieren.

Auf der Versuchsstation Scheyern in Süddeutschland wurden 67,4 ha konventionell bewirtschafteter Ackerflächen auf ökologischen Landbau und reduzierte Bodenbearbeitung umgestellt, ein kleinerer Teil wurde stillgelegt. Während den folgenden sechs Jahren wurde in diesen drei Systemen an 283 Messpunkten Samenbankproben entnommen und

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der Einfluss (1) der Bewirtschaftungsumstellung (Langzeiteffekte), (2) einzelner Kulturen (Kurzzeiteffekte) und (3) der Bestandesdeckung auf die Eigenschaften der im Boden lagernden Samen analysiert.

Die Stilllegung begünstigte Arten mit scheiben- oder nadelförmigen Samen, hoher Diasporenmasse und geringer Persistenz. Ebenso förderte auch der ökologische Anbau Sippen mit schweren und kurzlebigen Samen. Bei reduzierter Bodenbearbeitung kam es dagegen zur verstärkten Selektion von Arten mit persistenten Samen. Ein Effekt, der über alle Nutzungssysteme hinweg auftrat, war eine signifikante Zunahme langlebiger Diasporen mit Erhöhung der Bodenbearbeitungsfrequenz. Hohe Samengewichte und eine kompakte Form waren mit einer erhöhten Kulturpflanzendichte assoziiert.

Die Ergebnisse belegen, dass die Form der Ackerbewirtschaftung außer den Pflanzen im Bestand auch die Eigenschaften der Samen im Boden beeinflusst.

Keywords: Seed; Longevity; Mass; Shape; Set-aside; Organic farming; Reduced tillage; Crop

Introduction

Surveying the seed bank publications from northwest Europe, Thompson, Bakker, and Bekker (1997) collected information on the persistence of seeds and allocated every species record to the longevity classes ‘transient’ or ‘persistent’. Using this database, Thompson, Bakker, Bekker, and Hodgson (1998) derived a longevity index in which longevity is represented as the proportion of persistence records. Applying this index to plant communities, Bekker, Schaminée, Bakker, and Thompson (1998) and Thompson, Bakker et al. (1998) found great variation among the different vegetation types. Relatively undisturbed plant communities such as woodland and pasture had generally low seed persistence, whereas seed longevity in frequently disturbed habitats such as arable fields was high. This confirmed previous analyses by Cohen (1966), Venable and Brown (1988) and Rees (1993), who predicted generally lower seed persistence in more stable habitats. Thompson, Bakker et al. (1998) concluded that gradients of habitat disturbance are closely linked to changes in seed longevity. According to Thompson, Bekker, and Bakker (1998), a persistent seed bank is a basic requirement for success in arable habitats.

Analysing the relationship between seed morphology and seed longevity, Thompson, Bakker et al. (1998), Bekker, Bakker et al. (1998) and Funes, Basconcelo, Díaz, and Cabido (1999) found persistence to be associated with low seed mass and a nearly spherical seed shape. The suspected explanation underlying this relationship is that small and compact seeds are more easily buried by rain, animals or gravity (Peart 1984). Persistence is advantageous when seeds are buried since it increases the probability of germination when favourable conditions recur. Consequently, small and round seeds tend to have a higher persistence. In contrast, high risk of predation and environmental conditions stimulating germination reduce the expected life span of large seeds at the soil surface (Hulme 1998).

The general hypothesis underlying the present study is that a corresponding relationship between seed persistence, mass and shape also exists within the arable weed communities. The Scheyern Research Station in southern Bavaria, Germany, offered ideal conditions for testing this hypothesis. On the entire farm, conventional arable use was converted to organic farming, reduced tillage or set-aside and thus allowed us to study over 6 years how farming systems, including the selection of crops, affected seed traits.

The analyses were carried out with seed bank data. The advantage of using seed bank instead of field data is that the weeds that emerge in the field are strongly determined by the actual cultivation practice. In contrast, seed banks represent a much larger part of the populations and reflect the long-term effects that site conditions and land use exert on the vegetation.

Materials and methods

Research area

After every tillage operation, 283 sampling points arranged in a $50 \times 50\,m^2$ grid over 67.4 ha of arable land were re-marked. Before the study began, this area had been cultivated equally with cereals for 2 years. Then it was separated into an integrated management system with reduced tillage (30.0 ha; 128 grid points), an organic farming area (31.2 ha, 132 points) and in set-aside land (6.2 ha, 23 points). The 4-yr crop rotation of the integrated system included potatoes, winter wheat, maize and winter wheat. Tillage intensity was reduced by replacing mouldboard ploughing with non-inversion tillage with a cultivator or a rotary tiller. To prevent erosion, surface run-off and nutrient-leaching soil was left covered with growing plants or plant residues as long as possible. This was realised by mulch tillage or by sowing catch crops under the preceding main crops (Fiener & Auerswald 2007). As this practice caused

Table 1. Characteristics of the farming systems including soil cover (± denotes standard deviation among field years with 20 fields and 6 years of observation).

System	Tillage operations (yr^{-1})	Herbicide applications (yr^{-1})	Mean annual cover (%)		Plant cover (%) at harvest	
			Plants	Litter	Crops	Weeds
Organic farming	4.0±3.1	0.0	44±25	5±5	59±27	20±20
Reduced tillage	2.8±1.8	2.4±1.0	44±16	18±14	61±19	7.6±10.6
Set-aside	0.0	0.0	83±18	30±27	n.e.	n.e.

Mean annual cover of plants includes crops, intercrops and weeds. n.e. = not estimated.

weed infestation problems by accumulating the seeds at the soil surface (Albrecht & Sprenger 2008), herbicide applications were split into several treatments with highly efficient compounds. On the organic farmland, a 7-yr rotation comprised grass–clover, potatoes, winter wheat, sunflowers, white lupine (replaced by a seed mixture recommended for rotational fallow from the 4th year), winter wheat and winter rye (Albrecht 2005). About 50% of the area was sown with under-crops each year (either legume-rich mixtures or the subsequent grass–clover main crop). Each element of the rotation occurring on approximately 4 ha in the organic and on 7 ha in the reduced-tillage system every year provided controlled experimental conditions on the farm scale. Set-aside fields remained undisturbed after abandonment (Albrecht 2003). The three systems differed considerably in crop, weed and plant residue cover, in tillage intensity and herbicide application (Table 1).

Data collection and analysis

Terminologies follow the international practice to refer to plant diaspores as seeds, even though many of them are in fact fruits. Nomenclature of species follows Wisskirchen and Haeupler (1998).

At all the 283 grid points, a $10 \times 10\,m^2$ quadrat was used for vegetation analyses.

As seed banks in soil frequently show a clustered distribution, 20–30 small soil cores were taken from the whole plough layer using soil augers with a core diameter of 17 mm. The plough layer varied from 11 to 40 mm in thickness. The soil cores were pooled into one mixed sample of 1 kg fresh mass per point. To estimate the seed numbers potentially contributing to the subsequent vegetation, samples from fields of winter crops were collected after cultivation in late autumn and those of spring-sown crops in late winter before the cultivation started. First samples were taken in the winter before the change of management in 1992/1993 and ended 6 years later in winter 1998/1999, i.e. seven samples were taken per grid point. Seed numbers were analysed using the seedling emergence method in which seeds were given 2 years to germinate in a wire cage under open air conditions. Soil was filled in polystyrene seed trays and emerging seedlings were identified, recorded and removed. To stimulate germination, the samples were mixed thoroughly and watered regularly. The density of viable seeds was calculated by using the formula seed density (n/m^2) = soil bulk density (kg/m^3) × plough layer depth (m)/soil dry weight (kg) × number of germinated seedlings counted.

Persistence, mass and shape were used as seed attributes (see Appendix A). Seed persistence was calculated employing the longevity index by Thompson, Bakker et al. (1998). This calculation is based on the seed bank database for northwest Europe by Thompson et al. (1997) in which every published seed bank record for a species is allocated to one of three longevity types: type 1 (persistence <1 year), type 2 (persistence >1 but <5 years) and type 3 (persistence >4 years). The longevity index for individual species is then defined as

$$\text{Longevity index} = \frac{\sum(\text{type 2} + \text{type 3})}{\sum(\text{type 1} + \text{type 2} + \text{type 3})}$$

The corresponding values range from 0 (no type 2+3 records) to 1 (all records type 2+3). The longevity index for a soil sample was derived by weighting these species indices according to their proportion in the seed bank. Thereafter, the median of all samples was calculated.

The data on seed dimensions and seed masses in Appendix A were adopted from Cremer, Partzsch, Zimmermann, Schwär, and Goltz (1991), who measured ripe and air-dried seeds from different arable sites in Germany. Missing data were added from other references. The seed shape index was calculated according to Thompson, Band, and Hodgson (1993) as the variance of diaspore length, width and depth, after first transforming all values so that length is the unit. This variance has a minimum value of 0 in perfectly spherical diaspores and a maximum of about 0.3 in needle- or disc-shaped ones.

To characterise the farming systems in detail, all tillage operations and herbicide applications were recorded (Table 1). In the fields under arable use, plant (including crops and weeds) and residue cover was measured bi-weekly during the vegetation period, 4 weekly in autumn and spring, before and after each tillage treatment and shortly before harvest. Residue cover was measured along a pocket rule, while plant cover was determined from photographs taken from a height up to 4 m (in the case of full-grown maize) using picture analysis. In addition, weed and crop covers were estimated separately before harvest. In set-aside fields, cover was recorded only once a year in July.

Statistical analysis

The Kolmogorov–Smirnov test revealed that a major part of the data did not follow a normal distribution. In these cases, non-parametric methods (Sokal & Rohlf 1998) were used to analyse the data. Thus, significant differences between two independent data sets were tested using the Wilcoxon rank-sum test. Seed traits recorded at the same site in different years were compared using Friedman's method for randomised blocks. When this test revealed significant differences, paired comparisons were added using Wilcoxon signed-rank tests. Correlation was calculated with Spearman's coefficient of rank correlation if not stated otherwise. False discovery rates (FDRs) due to multiple testing were corrected according to Benjamini and Hochberg (1995). The analyses used SPSS 14.0 statistical package for Windows (Anonymous 2005).

Results

Seed traits and the plant cover

Under the initial conventional farming the medians and the 25th/75th percentiles for the 283 sampling points amounted to 0.28 (0.16/0.45) mg/seed for seed mass, 0.14 (0.12/0.16) for the seed shape index and 0.78 (0.74/0.82) for the seed longevity index. The distribution of the median seed mass, however, was strongly positively skewed and some sites achieved median values of even 3 mg/seed. The seed mass being negatively correlated to the seed shape index indicates that large seeds tend to have a more compact and spherical shape (Table 2). Seed longevity was correlated neither to the mass nor to the shape index. Crop cover showed a positive correlation to seed mass and a negative one to the shape index. Neither weed cover nor seed longevity was correlated to seed mass or total plant cover.

Farming practice

Seed trait modifications following the change of management are shown in Fig. 1. The most obvious changes for all three traits occurred when the fields were set aside. In this case, the median longevity index fell from 0.73 to 0.60. This means that seeds from species able to produce persistent seeds decreased from 73% to 60%. When organic farming was introduced, longevity declined slightly but nonetheless significantly from 0.78 to 0.75. In contrast, reduced tillage significantly increased longevity from 0.77 to 0.80. In fact, under all management systems seed longevity was high. This indicates limited impact of the actual crop and particular importance of the previous cultivation.

Table 2. Spearman's correlation matrix among seed longevity, mass and shape in the weed seed bank and correlations with the covers of the established crops and weeds under the initial cultivation of spring barley.

	Longevity	Mass	Shape index
Correlations among seed traits			
Longevity	–	−0.055 n.s.	−0.015 n.s.
Mass	–	–	−0.295***
Correlations with vegetation cover			
Crop cover	−0.072 n.s.	0.315***	−0.166**
Weed cover	0.061 n.s.	0.064 n.s.	−0.011 n.s.

One and three asterisks denote $p<0.05$ and $p<0.001$, respectively; n.s. indicates $p>0.05$.

The median seed mass increased from 0.24 to 0.41 mg on fields set aside and from 0.27 to 0.37 mg after conversion to organic farming. The change from 0.34 to 0.38 mg during 6 years of reduced tillage was not significant despite a remarkable fluctuation during that time. In the seed shape index, long-term changes were observed only when fields were abandoned.

In the cultivated fields, most changes occurred shortly after the modification of management. Hence, the seed traits quickly adapted to the new living conditions and attained a new equilibrium within a few years. In the set-aside areas, however, seed traits changed a second time in the 6th year after abandonment. There, the modification of the seed characteristics seemed to occur in phases and equilibrium was not reached within the investigation period.

Individual crop species affected the seed traits predominantly in the organic management area (Table 3). In the organic potato fields, favourable germination conditions and frequent mechanical weed control obviously reduced species with short-lived seeds and thus extended overall seed persistence. Similarly, regular mulching in rotational set-aside prevented seed production and increased seed longevity. When winter cereals were cultivated after potatoes, plant development was less disturbed and longevity decreased again (results not shown). An influence of seed mass and shape on the longevity changes is unlikely since these traits showed no corresponding crop effects (Table 3) and correlations in

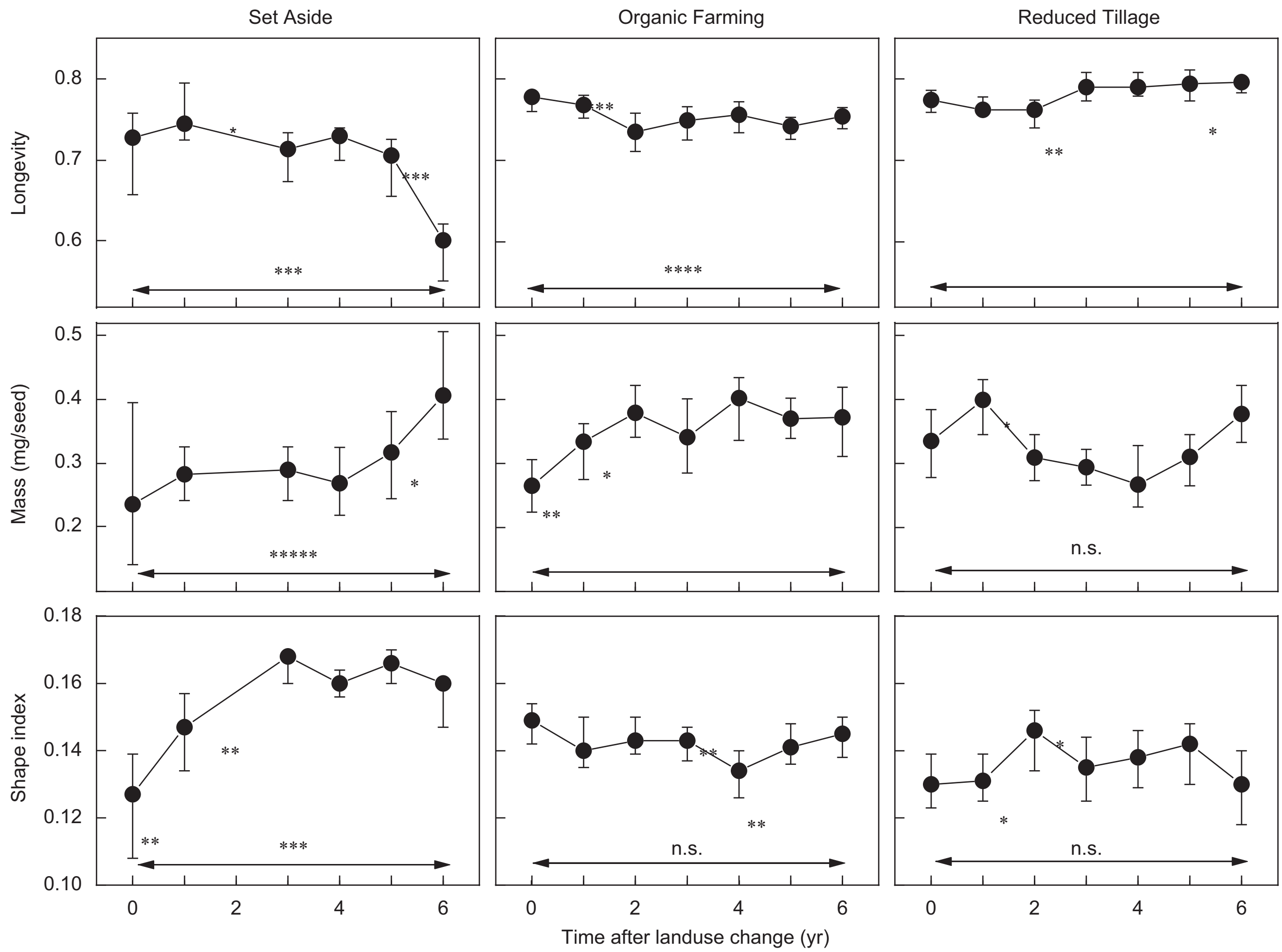

Fig. 1. Development of the longevity indices, mass and shape indices of seeds incorporated into the soil during 6 years following the change from conventional farming to set-aside, organic farming and reduced tillage (medians with 95% intervals of confidence). Only significant changes according to the Wilcoxon signed-rank test are indicated. False discovery rates due to multiple testing were corrected according to Benjamini and Hochberg (1995). Annual changes are quoted between data points, long-term changes above the horizontal arrow. One to three asterisks denote $p<0.05$, $p<0.01$ and $p<0.001$, respectively; n.s. indicates $p>0.05$.

the pre-phase were not significant (Table 2). Under reduced-tillage farming, the differences in the cultivation practices between individual crops had no such effects. The significant increase of seed longevity over the whole time period (Fig. 1) resulted from the farming system as a whole and not from individual crops (Table 3).

When the results from all individual crops at specific positions within the rotations and the set-aside fields were combined in one linear regression model (Fig. 2), longevity significantly increased with the number of tillage operations (Pearson's $r^2 = 0.638$). Remarkably, this model fitted for the set-aside land, the reduced-tillage crops and the organic crops together without a notable offset due to differing herbicide application intensities. The regression model indicates that each tillage operation reduces the longevity index by 0.005 and that longevity remains unchanged with four tillage operations per year. This frequency corresponded to the tillage intensity before the change of management and also to the average of both new farming systems (3.9).

Discussion

Seed traits in the arable weed seed bank

In previous investigations the means of longevity and other seed traits were calculated by averaging the indices of selected species that are characteristic for certain habitats (Bekker, Schaminée et al. 1998; Thompson, Bekker, et al. 1998). In contrast, the present study is based on weed seed bank data that include all detected species. Despite this difference, the results correspond well and the present study confirms that high persistence

Table 3. Median changes in seed traits per year by the cultivation of different crop species under organic management, reduced-tillage farming and set-aside.

Crop	TO	HA	MPC	No. of seeds in soil			Longevity		Mass		Shape index	
	(yr^{-1})	(yr^{-1})	(%)	*n*	(%)	Sign.	Median	Sign.	Median	Sign.	Median	Sign.
Organic farming												
Potatoes	8.6	0	23	111	−7	n.s.	0.034	***	0.045	n.s.	−0.003	n.s.
Winter cereals	3.5	0	57	324	33	***	−0.022	***	0.011	n.s.	0.000	n.s.
Spring cereals	3.0	0	45	28	53	***	−0.001	n.s.	0.198	n.s.	−0.018	*
Sunflowers	4.7	0	38	95	33	**	−0.014	n.s.	0.084	n.s.	−0.003	n.s.
Lupins	7.5	0	32	52	31	n.s.	0.007	n.s.	−0.008	n.s.	0.007	n.s.
Grass–clover	0.3	0	95	98	−39	***	−0.019	n.s.	0.049	n.s.	−0.010	n.s.
Rotational set-aside, sown	3.4	0	58	71	−8	n.s.	0.008	*	−0.063	n.s.	0.003	n.s.
Reduced-tillage farming												
Potatoes	4.7	3.0	32	169	−22	***	−0.008	n.s.	−0.018	n.s.	−0.004	n.s.
Winter cereals	2.9	2.2	56	342	8	n.s.	0.000	n.s.	0.006	n.s.	−0.005	n.s.
Maize	1.3	2.4	64	208	−16	*	−0.006	n.s.	0.022	n.s.	0.005	n.s.
Set-aside	0	0	83	124	11	n. s.	−0.025	***	0.029	*	0.001	n.s.

Significance was calculated using the Wilcoxon signed-rank test. One to three asterisks denote $p<0.05$, $p<0.01$ and $p<0.001$, respectively; n.s. indicates $p>0.05$. False discovery rates due to multiple testing were corrected according to Benjamini and Hochberg (1995). TO = tillage operations; HA = herbicide applications; MPC = mean plant cover.

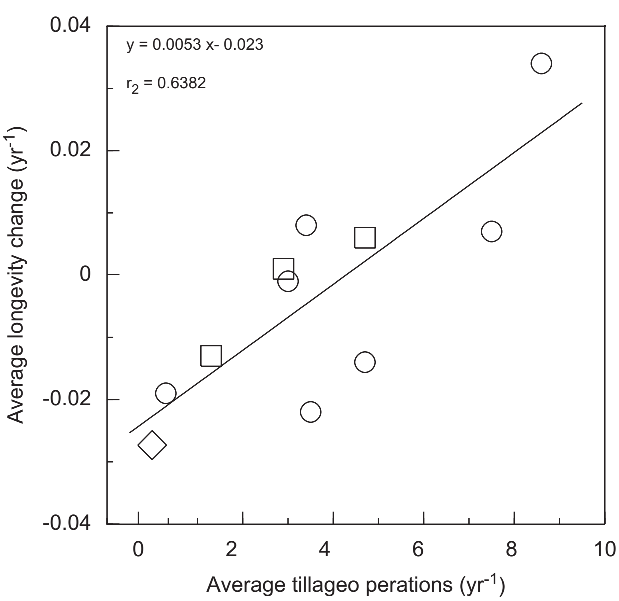

Fig. 2. Average annual change in seed longevity by individual crops depending on average number of tillage operations (squares: reduced-tillage crops; circles: organic crops; diamond: set-aside; for individual crops see Appendix A).

is essential to survive in regularly disturbed habitats (Hodgson & Grime 1990).

Median seed masses below 0.5 mg indicate that arable land use particularly favours small-seeded species, which at a given level of resource availability produce more seedlings (Turnbull, Rees, & Crawley 1999). This is an advantage for the arable weeds because many small seeds have a better chance to escape the effects of frequent disturbance than a few large ones. The positively skewed distribution of the median seed mass, which also caused the large error bars in Fig. 1 and the poor statistical separation in Tables 2 and 3, however, gives evidence that some arable fields also provide favourable living conditions for large-seeded weeds. High seed masses were consistently associated with a dense plant cover. Thus, a significant positive correlation between crop cover and seed mass during the initial, homogeneously managed cereal years (Table 2) indicates a selection for competitive and large-seeded weeds at fertile sites with a dense crop canopy. Enforced competition also rapidly increased the seed mass in the set-aside areas (Fig. 1).

The only significant relationship among the seed traits themselves was the negative correlation between seed mass and the seed shape index. This was mainly due to *Matricaria recutita*, which was the most frequent weed species in the research area and which occurred in samples from 92% of the grid points. It produces elongated seeds (seed shape index: 0.157) with a low mass (0.07 mg/seed). We suppose that these seed characteristics of *M. recutita* also contributed to the crop cover being positively correlated to seed mass but negatively to seed shape index.

Seed longevity was not correlated with the other seed traits. This is in contrast to near natural ecosystems, where Thompson, Bakker et al. (1998), Bekker, Bakker et al. (1998) and Funes et al. (1999) found persistence to be clearly related to low seed mass and a nearly spherical seed shape. These authors argued that small and compact seeds would be more easily incorporated into the soil, where persistence would be advantageous to survive until favourable conditions for germination recur. Our results substantiate the assumption of Thompson, Bakker et al. (1998) that no such link between ease of burial and seed morphology exists in arable fields since tillage mixes seeds into the soil independent of size and shape.

Relationship to the farming system

Set-aside fields

In general, seed longevity increases from relatively undisturbed communities such as woodland and pasture to frequently disturbed ecosystems such as arable fields (Thompson, Bakker et al. 1998; Bekker, Bakker et al. 1998). In the set-aside area, the median longevity followed this gradient and decreased when mechanical disturbance was ceased. The concomitant increase of seed mass from 0.27 to 0.37 mg/seed indicates an increased need to produce large seeds because they bring forth more competitive plants (Turnbull et al. 1999), which have a better chance to establish in stands with 95% plant cover and a 50% litter cover in the 6th year after abandonment (Albrecht 2003).

The significant increase of the seed shape index may also be related to plant cover. Thus, the lack of crop competition during the first phase after abandonment favoured species with flattened or needle-shaped seeds like *Taraxacum officinale* (Fig. 1), which can rapidly colonize open field areas by wind dispersal. Thereafter, taller and more competitive herbs like *Cirsium arvense*, *Urtica dioica*, *Elymus repens* and *Arrhenaterum elatius* became dominant (Albrecht, Toetz, & Mattheis 1998; Albrecht 2003). The significant decline in longevity and the increase in seed size during the 6th year of abandonment were mainly due to the loss of annual weeds. Since most of annual weed seeds loose viability within a few years (Schweizer & Zimdahl 1984; Barralis, Chadoeuf, & Longchamp 1988), they hardly had a chance to survive after the plant canopy had attained complete cover in the 4th year of succession.

Organic farming

During organic farming, seed longevity and seed mass developed less expressed but similarly to set-aside areas. As plant cover was maintained over the whole year for soil protection purposes (Auerswald, Albrecht, Kainz, & Pfadenhauer 2000), weeds were constantly competing with crops or intercrops. Consequently, seed masses increased as in the abandoned areas. However, as the phytomass was regularly harvested or buried by ploughing, plant cover never attained the densities observed in undisturbed set-aside sites. Therefore, selection for a high seed mass in the organic management area was less pronounced.

In contrast to set-aside, organic farming did not change the seed shape significantly. Tillage operations normally enable seedlings to establish close to their parental origin. On set-aside land, space is usually occupied by the perennial parents. Consequently, the need to develop disk- or needle-shaped seeds, which would have facilitated wind dispersal to new potential habitats, may have been reduced under organic farming.

Seed longevity was significantly affected by the cultivation of different crops. Over-wintering cereals reduced seed longevity while spring-sown potatoes, in particular, increased it. This increase within potato fields is likely an effect of the frequent ridging operations, which reduce the chance of reproduction by destroying the established weeds and thus favour species with dormant seeds. Conversely, longer undisturbed periods in over-wintering cereals benefit species with a transient seed bank. Bekker, Bakker, Ozinga, and Thompson (2003) even suggested that this low seed longevity associated with an intensified weed control is a major reason for the severe decline of winter annual weeds during the last decades.

Reduced tillage

Reduced tillage affects weed populations predominantly by accumulating the seeds at the soil surface (Swanton, Clements, & Derksen 1993), where they face a greater risk of loss through germination, predation or accelerated ageing (Ghersa & Martínez-Ghersa 2000). Since germination and ageing affect short-lived seeds more than persistent ones, longevity increased when tillage was reduced.

Seed accumulation significantly increased the number of seedlings and enforced weed competition, thus necessitating split herbicide applications with highly efficient compounds (Albrecht & Sprenger 2008). This practice significantly promoted *Veronica persica*, *Stellaria media*, *Poa annua*, *Poa trivialis* and *Epilobium ciliatum*. Due to their broad amplitude of germination temperatures these species still established after the application of herbicides and also profited from omitting the tillage operations after harvest. Each of these species has an above average longevity index.

General effects across different farming systems

In summary, the effects of the different systems and crops followed some general relations (Fig. 3). Seed

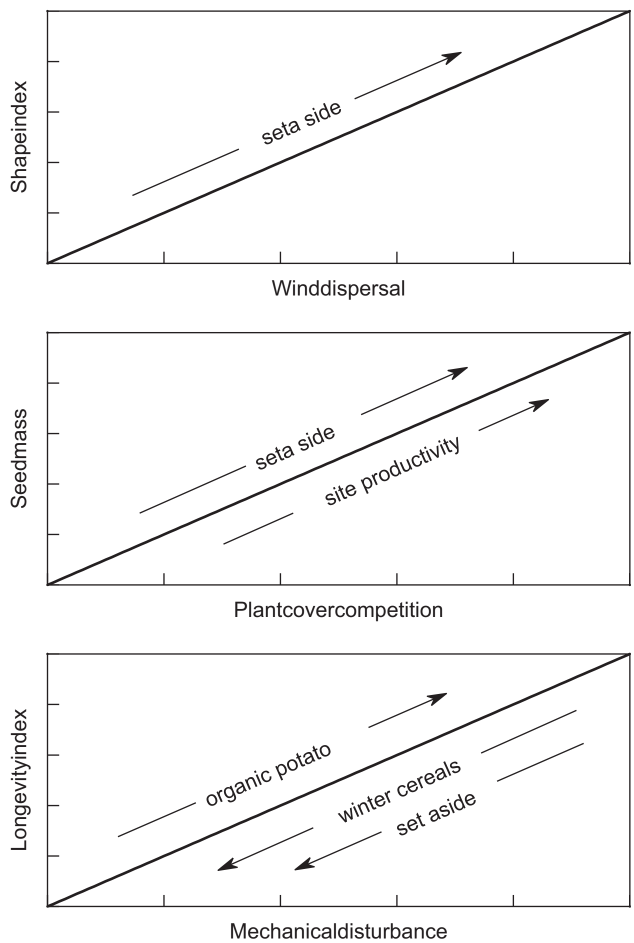

Fig. 3. Conceptual model of major influences on traits of weed seeds under arable use.

longevity was correlated with tillage frequency. As these practices damage short-lived seeds more than persistent ones, mean longevity increased especially under organic potatoes, which received the most frequent tillage. In contrast, it decreased under set-aside and, to a smaller extent, under organic winter cereals. Seed mass was related to plant competition. Hence, it increased during undisturbed set-aside and – under regular cultivation – at fertile sites with a dense crop canopy. Seed shape was mainly modified on set-aside land, where wind-dispersed species with typically aspherical seeds rapidly colonized the open areas during the early phase of abandonment.

Factors indirectly affecting the seed traits in arable weeds

Our results indicate a strong relationship between the land use practice and the seed traits in the weed seed bank, which can – to a large degree – be explained by the direct effects of arable farming. However, management may also exert an indirect influence on the seed traits. Such effects occur when farming practices affect species from different phylogenetic groups unequally. For example, since Gramineae (*Apera spica-venti*, *Holcus lanatus*) and Asteraceae (*Anthemis arvensis*, *Galinsoga ciliata*, *Sonchus asper*) mainly produce aspherical seeds, whereas most species of other plant families have more compact diaspores (*S. media*, *Anagallis arvensis*, *Chenopodium album*, *Viola arvensis*; see Appendix A; Hodgson & Mackey 1986; Peat & Fitter 1994), different sensitivities of these groups to frequently applied herbicides may exert a strong indirect influence on the mean seed shape.

Conclusions

Seed bank traits clearly adapt to different types of arable farming. Seed longevity is favoured by frequent tillage, while seed mass is favoured by plant competition. Seed shape is modified where wind dispersal becomes important for seed distribution like on set-aside land. However, compared to the variation among ecosystems, these differences were small and could only be proven with a large experimental effort by repeated sampling on 283 plots during six subsequent years.

Appendix A. Supplementary material

The online version of this article contains additional supplementary data at doi:10.1016/j.baae.2009.02.002.

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