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Composition of seed banks of roadsides, stream verges and agricultural fields in southern Norway

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The soil seed banks of three roadsides, one horsetrack, one stream verge and two agricultural fields were sampled in an agricultural landscape in southern Norway. Altogether 61 different vascular plant species germinated from soil samples from the five linear habitats, while only 16 species germinated from the agricultural fields. The low species number and low seed densities in the fields probably reflect modern weed management. Each linear habitat contained more or less specific subsets of plant species. The relative abundance of the different species exhibited an approximately log-normal distribution. Species composition in the seed banks of the linear habitats was compared with the aboveground vegetation. The seed bank had a higher frequency of annual species than the vegetation. Surveys restricted to the aboveground vegetation will tend to underestimate the number of species present by 15–30%.

Key words: Agricultural landscape, linear habitats, soil seed bank, species diversity

INTRODUCTION

In intensively managed agricultural areas the linear landscape elements (e.g. road verges, ditches, hedgerows) are among the few habitats left where a natural or a semi-natural vegetation subsists (Hansen & Jensen 1972, Pollard *et al.* 1974, Zanaboni & Lorenzini 1989, Bunce & Hallam 1993). The plant species diversity of these habitats constitutes a significant subset of the total biodiversity of such landscapes, and for this reason their management ought to be given careful consideration. In recent years linear landscape elements have also received attention as possible corridors of migration and re-establishment for populations locally extinct in other landscape elements such as groves (Verkaar 1988, 1990, Wilcox & Murphy 1989, Saunders & Hobbs 1991, Fritz & Merriam 1993, Smith & Hellmund 1993, Forman 1995). Some of the linear elements may also serve as refugia for species formerly associated with extensive semi-natural grasslands (pasture and meadows) that have been converted to crop fields or tree plantations (Ruthsatz & Haber 1981, Skånes 1990, Milberg & Persson 1994).

A number of studies have detailed aboveground plant species diversity of linear habitats in several countries (e.g. Bates 1935, 1937, Hansen & Jensen 1972, Svensson 1988). In contrast the soil seed bank of these habitats have received much less attention (Milberg & Persson 1994). The soil seed bank is however an important repository for the total plant species richness of a habitat. Quite often soil seed banks contain species or genotypes not found in the aboveground vegetation (e.g. Champness & Morris 1948, Levin 1990, Bennington *et al.* 1991, Del Castillo 1994). For the population dynamics and persistence of species, the soil seed bank plays a crucial role (Harper 1977). And for the rational management of diversity and abundance, knowledge of the seed bank is literally vital (Keddy *et al.* 1989).

As part of a project aimed to assess the plant biodiversity of Norwegian agricultural landscapes and develop guidelines for the maintenance of this diversity, the present study addresses the following questions: Which species are present in the soil seed bank of different linear habitats? What is their relative abundance? Do the seeds have an even distribution in the soil profile? How does the species richness of the seed bank compare with the aboveground vegetation? Does soil seed banks of linear habitats differ in species composition and density compared with adjacent agricultural fields?

MATERIALS AND METHODS

The study area

The study area is an agricultural landscape in the municipality of Frogn, Akershus county, in the eastern part of South Norway (59°4´N, 10°40´E), 60–90 m a.s.l. The bedrock consists of Precambrian gneisses, levelled by weathering and glacial erosion (Hageskov & Jorde 1980). At the end of the last ice age, the plain was covered by moraine deposits and also marine sediments (mainly clay) from a sea temporarily transgressing the area (Sørensen *et al.* 1990). Clearing for cultivation began in the Iron Age (Myckland 1967), and today the landscape is dominated by cereal fields, groves and farmyards. The linear landscape elements include hedges, roads, rivers, ditches and their verges. These elements constitute less than 1% of the study area. For the present study, we selected five different linear habitats and two adjacent fields. The aboveground vegetation in the linear habitats was investigated by Alvim (1995), and these data are used for comparison in the present paper.

Driveway verge

The verge runs E–W between a driveway and a cereal field, and connects to a farmyard in the eastern end and a gravel road in the west end. The verge is 50 m long; its width varies between 1 and 5 m and is on average 1.5 m. The verge is frequently cut, almost like a lawn. The most frequent species in the vegetation are *Plantago major, Taraxacum* sect. *Ruderalia, Dactylis glomerata, Trifolium repens* and *Elymus repens.*

Gravel road verge

The verge runs S–N along a gravelled road and a cereal field. The verge is 142 m long; its width varies between 0.5 and 1 m and is on average 0.9 m. The width differs slightly between years, depending on the ploughing of the field. The verge is cut at least once every year. The most frequent species in the vegetation are *Chamomilla suaveolens, Taraxacum* sect. *Ruderalia, Lamium purpureum, Sonchus asper* and *Matricaria perforata.*

Horsetrack

This track runs S–N, then E–W between two cereal fields, starting out from the intersection of the above-mentioned driveway and gravel road and ending in a field islet. The track is ca. 200 m long, its width varies between 2.8 and 4 m and is on average 3.2 m. The track is used for horse training and for driving to the fields. It is usually cut at least once a year. The most dominant species in the vegetation are *Festuca pratensis, Plantago major, Trifolium repens, Agrostis capillaris* and *Chamomilla suaveolens.*

Asphalt road verge

This verge runs SW–NE, between an asphalt road and a cereal field. The verge is 200 m long; its width varies between 1 and 1.4 m and is on average 1.3. The verge is cut by the local road authorities once or twice a year. The most frequent species in the vegetation are *Taraxacum* sect. *Ruderalia, Achillea millefolium, Polygonum aviculare, Poa pratensis* and *Artemisia vulgaris.*

Ditch verge

This ditch runs SE–NW between two cereal fields. The ditch is 150 m long; its width varies between 10 and 20 metres. The most frequent species of the vegetation are *Anthriscus sylvestris, Rubus idaeus, Cirsium arvense, Elymus repens* and *Urtica dioica.*

The fields

Two cereal fields adjacent to the linear habitats were sampled to see to what degree the species diversity and abundance of these seed banks coincide with those of the linear habitats. One of the fields borders the narrow roadverge, the other the horse track. Both fields were ploughed in the spring and cereals were sown. The fields are treated with herbicides during the growing season. The most common species besides the cereals are *Chamomilla suaveolens, Elymus repens, Filaginella uliginosa, Matricaria perforata,* *Persicaria maculosa, Poa annua, Polygonum aviculare* and *Viola arvensis.*

Seed bank study

The soil seed sampling was done on 21 and 22 June 1994. At this time of the year, most of the spring germination had ceased and it was still too early for seed release in most species. The seeds sampled thus mostly belonged to the persistent soil seed bank *sensu* Thompson and Grime (1979). A total of 235 samples were collected at one-metre intervals along transects running centrally in the linear elements. In the driveway verge, the gravel road verge, the asphalt road verge and the ditch 50 samples were collected. Along the horsetrack 35 samples were collected. In the two cereal fields a total of 54 samples were collected. Sampling transects in the fields were placed parallel to the gravel road verge (50-m transects) and the horsetrack (30-m transects) at distances 2, 4, and 6 m from the verge. In these transects samples were collected every five metres.

The soil samples were collected to a depth of 10 cm with a borer (Ø 3.4 cm). The top 5 cm and the bottom 5 cm were separated as sub-samples. Sub-samples were sieved through a mesh to remove stones and coarse plant fragments. The samples were then spread out in layers 0.5 cm deep in pots filled with sterile soil. The pots were kept in a greenhouse supplemented by extra light during the dark months of the year in a cycle of 18 h light/22°C and 6 h dark/16°C. The soil was kept moist by watering once a day.

The plants were mostly identified at the seedling stage, but some were replanted for identification at more mature stages. After 15 weeks the seedling emergence had ceased and the pots were transferred to cold (2–3°C) and dark storage for 19 weeks. The soil was watered well before the cold storage and kept moist during the storage period. The second germination period lasted 10 weeks. During this period, bryophytes grew abundantly with some pots being completely covered by bryophytes. To stimulate further germination the top layer was thoroughly stirred. The third germination period lasted 11 weeks.

Taxonomy and data on longevity

The nomenclature follows Lid and Lid (1994). Some of the species registered in the soil seed bank were identified only to species groups: *Chamomilla suaveolens* plus *Matricaria perforata, Galeopsis bifida* plus *G. tetrahit, Hypericum maculatum* plus *H. perforatum, Lamium hybridum* plus *L. purpureum* and *Sonchus asper* plus *S. arvense*. Some grasses died before identification could be made. These were pooled into a *Graminea* group. Each species group is counted as a single species in the quantitative data presented in the results.

Data on longevity (i.e. annual, biennial, perennial) are from Grime *et al.* (1988) and Lid and Lid (1994).

RESULTS

Species diversity and seed densities in the soil seed bank of different linear habitats

Altogether 61 species germinated from the soil samples (Table 1). The total number of species in

Table 1. Species and abundance in the soil seed bank of five linear habitats. *N* = number of soil samples.

	Driveway verge (*N* = 50)	Gravel road verge (*N* = 50)	Horse-track (*N* = 35)	Asphalt road verge (*N* = 50)	Ditch verge (*N* = 50)	Total
Achillea millefolium	1	11	–	3	–	15
Agrostis capillaris	3	2	56	5	1	67
Agrostis stolonifera	–	1	–	1	–	2
Alopecurus pratensis	–	–	–	–	1	1
Artemisia vulgaris	–	–	1	17	–	18
Betula pendula	122	15	8	2	5	152
Calluna vulgaris	–	–	–	1	1	2
Capsella bursa-pastoris	6	1	–	2	–	9
Carex sp.	–	1	–	–	1	2
Carduus crispus	–	–	–	6	–	6
Cerastium fontanum	–	–	14	47	–	6
Chamomilla suaveolens/Matricaria perforata	250	467	143	78	6	944
Chenopodium album	–	4	4	88	–	96
Chenopodium polyspermum	–	–	–	–	5	5
Cirsium arvense	–	–	–	–	2	2

(Continues …)

Table 1. Continued.

	Driveway verge (*N* = 50)	Gravel road verge (*N* = 50)	Horse-track (*N* = 35)	Asphalt road verge (*N* = 50)	Ditch verge (*N* = 50)	Total
Dactylis glomerata	1	–	–	–	–	1
Dechampsia cespitosa	–	–	–	1	–	1
Elymus repens	–	–	–	–	1	1
Epilobium watsonii	–	7	3	5	6	21
Erysimum cheiranthoides	–	–	–	2	–	2
Fallopia convolvulus	–	1	–	–	–	1
Festuca rubra	3	–	1	–	–	4
Filaginella uliginosa	8	95	502	29	11	645
Filipendula ulmaria	–	–	–	–	4	4
Galeopsis bifida/tetrahit	–	–	1	4	1	6
Geum rivale	1	–	–	–	–	1
*Graminea**	17	24	51	9	17	118
Hypericum maculatum/perforatum	1	46	11	–	–	58
Juncus bufonius	52	10	26	50	6	144
Lamium hybridum/purpureum	5	54	–	5	1	65
Lapsana communis	–	–	1	8	–	9
Leontodon autumnalis	2	11	–	–	–	13
Linaria vulgaris	–	6	4	1	–	11
Lotus corniculatus	–	2	–	–	–	2
Myosotis arvensis	–	22	–	5	–	27
Persicaria hydropiper	–	–	4	–	–	4
Persicaria maculosa	–	–	1	–	–	1
Phalaris arundinacea	–	–	–	–	18	18
Plantago major	99	20	25	64	–	208
Poa annua	70	9	2	5	–	86
Poa palustris	–	11	–	2	2	15
Poa pratensis	16	12	–	15	–	43
Polygonum aviculare	–	2	1	–	–	3
Ranunculus auricomus	–	–	–	–	1	1
Ranunculus repens	1	–	2	1	–	4
Rorippa palustris	–	1	–	27	–	28
Rubus idaeus	1	7	5	–	496	509
Sagina procumbens	1	–	–	–	–	1
Scirpus sylvaticus	–	–	–	–	2	2
Scrophularia nodosa	–	1	–	–	3	4
Senecio sylvaticus	1	–	–	–	–	1
Sonchus arvense/asper	5	4	–	6	–	15
Spergularia arvensis	–	–	1	–	–	1
Stellaria graminea	–	–	1	15	–	16
Stellaria media	3	1	11	8	–	23
Taraxacum sect. *Ruderalia*	4	26	7	343	3	383
Trifolium hybridum	1	1	1	5	10	18
Trifolium pratense	–	16	14	–	–	30
Trifolium repens	4	3	6	–	–	13
Urtica dioica	–	1	–	50	373	424
Veronica serpyllifolia	4	1	14	–	–	19
Viola arvensis	–	3	4	–	–	7
Number of species+	26	35	30	33	24	
Number of seedlings	682	899	925	910	977	

**Graminea* consists of grasses that died before identification could be made.
+*Graminea* is not included in the number of species.

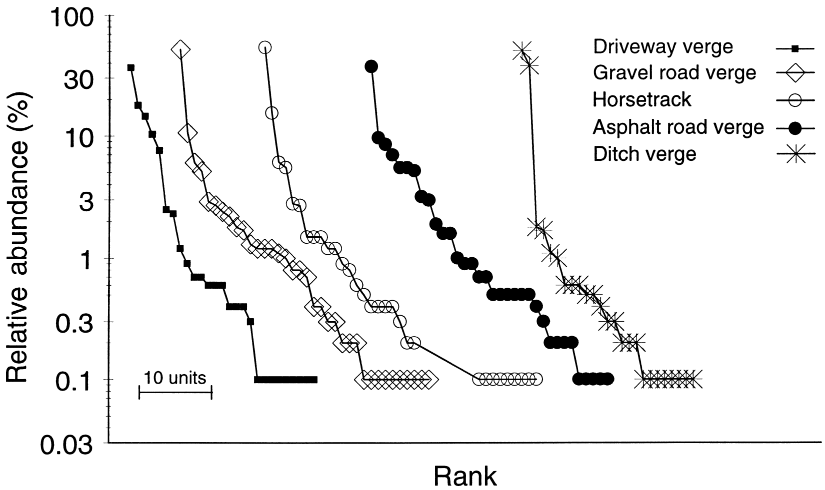


Fig. 1. Rank-abundance curves for five linear habitats. The proportion of seedlings for the most common species within one habitat is plotted first, then the next most common and so on.

a single habitat varied between 24 and 35. Only seven species were found in all habitats: *Agrostis capillaris, Betula pendula, Chamomilla suaveolens/Matricaria perforata, Filaginella uliginosa, Juncus bufonius, Taraxacum* sect. *Ruderalia* and *Trifolium hybridum*. Twenty species were found in a single element only: two in the gravel road verge, three in the horsetrack, three in the asphalt road verge, four in the driveway verge, and eight in the ditch verge. Thus almost half of the unique species were found in the ditch verge. The similarity of species composition between the habitats varied between 0.22 and 0.51 (Jaccards index) (Table 2) with the ditch verge consistently exhibiting lowest similarity to the four other elements.

A total of 4 393 seedlings germinated from the soil samples; 3 620 germinated in the first growing period, 511 in the second (after cold storage), and another 262 after stirring. All species found in the soil seed bank were represented in the first growing period.

The horsetrack had the highest density of seeds, 29 100 seeds/m^2, the ditch verge 21 500, the asphalt road verge 20 000, the gravel road verge 19 800, and the driveway verge 15 000. Seed densities per sample showed significant differences between different habitats (one-way ANOVA, $F = 5.82$, $df = 4$, $p < 0.001$), the horsetrack having significantly more seeds per sample than the other habitats (Duncan's multiple range test).

There were substantial differences in the relative abundance of the species in the soil seed bank (Table 1, Fig. 1). A few species contributed most of the seedlings, while most species were rather infrequent.

There was a positive correlation between soil volume (number of soil samples) and species richness (Fig. 2).

Species diversity in the cereal fields

The species richness of the cereal fields was lower than in any of the linear habitats. The field adjacent to the gravel road verge contained 14 species and the field adjacent to the horsetrack contained 12

Table 2. Similarity of the soil seed bank species composition in five linear habitats (Jaccards similarity index, $J = w/(A + B - w)$, where w is the number of species common in both samples, A is the number of species in sample one and B is the number of species in sample two).

	Driveway verge	Gravel road verge	Horsetrack	Asphalt road verge
Gravel road verge	0.49	–	–	–
Horsetrack	0.40	0.44	–	–
Asphalt road verge	0.34	0.51	0.43	–
Ditch verge	0.22	0.31	0.23	0.30

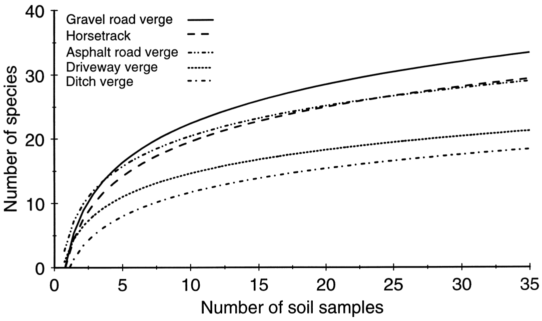


Fig. 2. Species-soil volume curves for five linear habitats. The curves are based on a random selection of 35 soil samples from each habitat. The 35 samples were added randomly 10 times and logarithmic regression lines obtained from the data according to the equation: $Y = a + b(\ln x)$. Gravel road verge: $R^2 = 0.94$, $a = 2.25$, $b = 8.75$, Horsetrack: $R^2 = 0.92$, $a = 1.67$, $b = 7.78$, Asphalt road verge: $R^2 = 0.94$, $a = 4.79$, $b = 6.80$, Driveway verge: $R^2 = 0.86$, $a = 2.56$, $b = 5.24$, Ditch verge: $R^2 = 0.84$, $a = -0.57$, $b = 5.33$.

species (Table 3). The fields did not contain any new species compared with the bordering linear habitats.

The fields also had lower seed densities than the linear habitats, varying between 9 700 to 12 300 seeds/m^2. We found no significant difference in seed density per sample in samples gathered two, four and six metres from the field edge (one-way ANOVA — field bordering the gravel road: $F = 1.26$, $df = 2$, $p = 0.30$, field bordering the horsetrack: $F = 2.28$, $df = 2$, $p = 0.13$).

Depth distribution of seeds

Due to small sample sizes and low occurrence frequencies it was not possible to obtain significant differences between the upper and lower part of the soil column when each linear habitat was treated separately. If however, the samples from all habitats are amalgated, it is seen that for 14 of the 22 species present in 5% or more of the soil samples, there was a significant difference between the number of seedlings emerging from the upper and lower five centimetres of the soil col-

Table 3. Species and abundance in the soil seed bank of two cereal fields. Each species group is counted as a single species in the quantitative data presented in the results. *N* = number of soil samples.

	Field bordering		Total
	the gravel road (*N* = 33)	the horsetrack (*N* = 21)	
Betula pendula	10	1	11
Calluna vulgaris	1	1	2
Chamomilla suaveolens/Matricaria perforata	171	32	203
Chenopodium album	–	2	2
Epilobium watsonii	7	–	7
Filaginella uliginosa	35	97	132
*Graminea**	2	1	3
Juncus bufonius	5	9	14
Lamium hybridum/purpureum	21	–	21
Lapsana communis	1	–	1
Myosotis arvensis	1	–	1
Poa annua	4	8	12
Poa palustris	1	–	1
Rubus idaeus	–	1	1
Spergularia arvensis	–	1	1
Stellaria media	2	11	13
Taraxacum sect. *Ruderalia*	–	1	1
Trifolium repens	1	–	1
Urtica dioica	1	–	1
Viola arvensis	–	2	2
Number of species$^+$	14	12	–
Number of seedlings	263	167	–

**Graminea* consists of grasses that died before identification could be made.
$^+$*Graminea* is not included in the number of species.

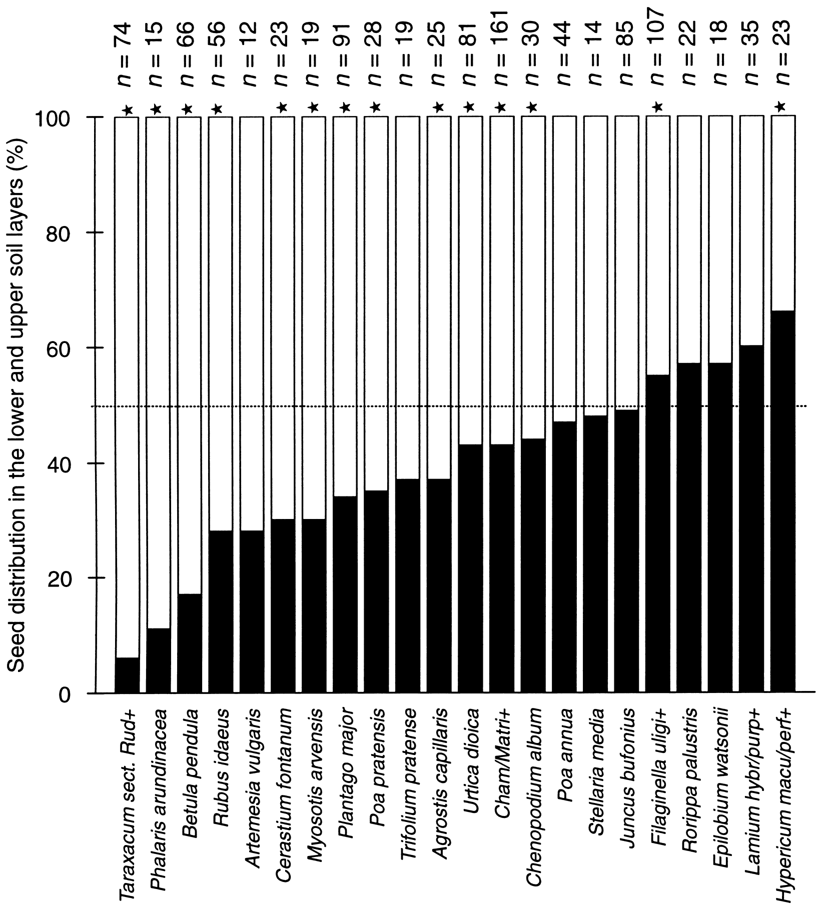


Fig. 3. The relative seed distribution (%) in the upper (❑) and lower (■) soil layer for species present in 5% or more of the soil samples of the linear habitats. Stars indicate significant differences between the soil layers (Logistic regression, $p < 0.05$), n = number of soil samples in which the species were present. + *Taraxacum* sect. *Rud = Taraxacum* sect. *Ruderalia, Cham/Matr = Chamomilla suaveolens/ Matricaria perforata, Filaginella uligi = Filaginella uliginosum, Lamium hybr/ purp = Lamium hybridum/ purpureum, Hypericum macu/perf = Hypericum maculatum/perforatum.*

umn (Fig. 3). Twelve of these had more seeds in the upper layer than the lower, while two species, *Filaginella uliginosa* and *Hypericum maculatum/ perforatum* had more seeds in the lower layer.

Soil seed bank of the linear habitats compared with the vegetation

The soil seed bank of the linear habitats and the fields examined contained 16 species not found in the aboveground vegetation (Fig. 4). Three of these, *Filaginella uliginosa, Betula pendula* and *Juncus bufonius*, were among the most frequent species in the soil seed bank. About half of the species (45) were found in both the soil seed bank and the vegetation, while 27 species were observed only in the vegetation. The latter group was dominated by the grasses *Festuca pratensis, Phleum pratensis* and *Poa trivialis* plus the umbellifer *Anthriscus sylvestris*. The two grasses *Elymus repens* and *Dactylis glomerata* were common in the vegetation and rare in the soil seed bank; a single seedling of each germinated from the soil samples.

The number of species found only in the soil seed bank differed between habitats, from 17 in the gravel road verge to eight in the horsetrack (Fig. 4). This represents 33% and 15% of the total above- and belowground species diversity of these habitats. The proportion of species found only in the seed bank is about one third in the gravel road verge, the asphalt road verge and the ditch verge, and about one seventh in the horsetrack and the driveway verge.

Short-lived species (annuals and biennials) dominated the soil seed bank, while perennials strongly dominated the species exclusive to the vegetation (Fig. 5). Perennials also dominated the group of species found both in the soil seed bank and the vegetation. Of the perennial species unique

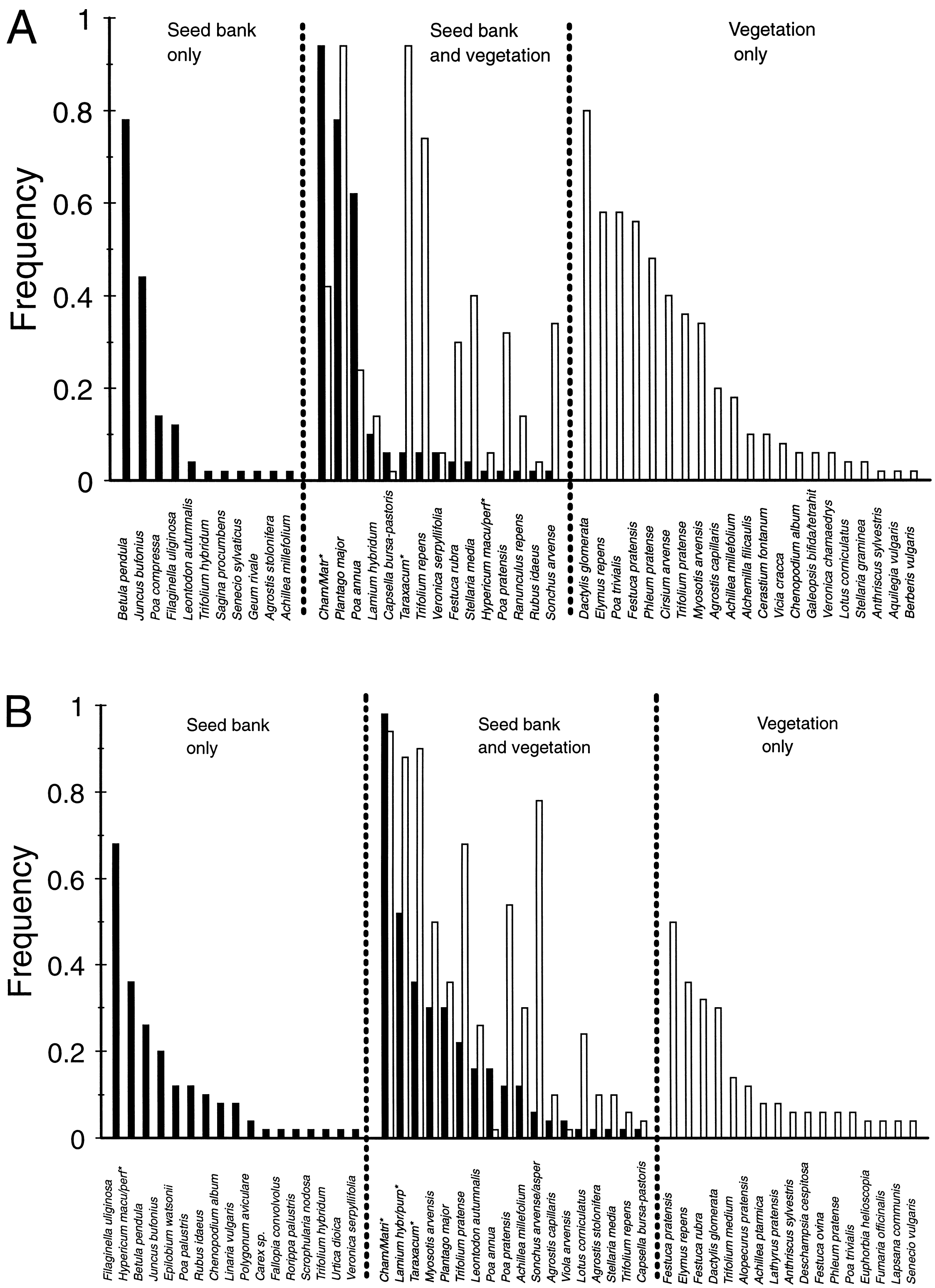
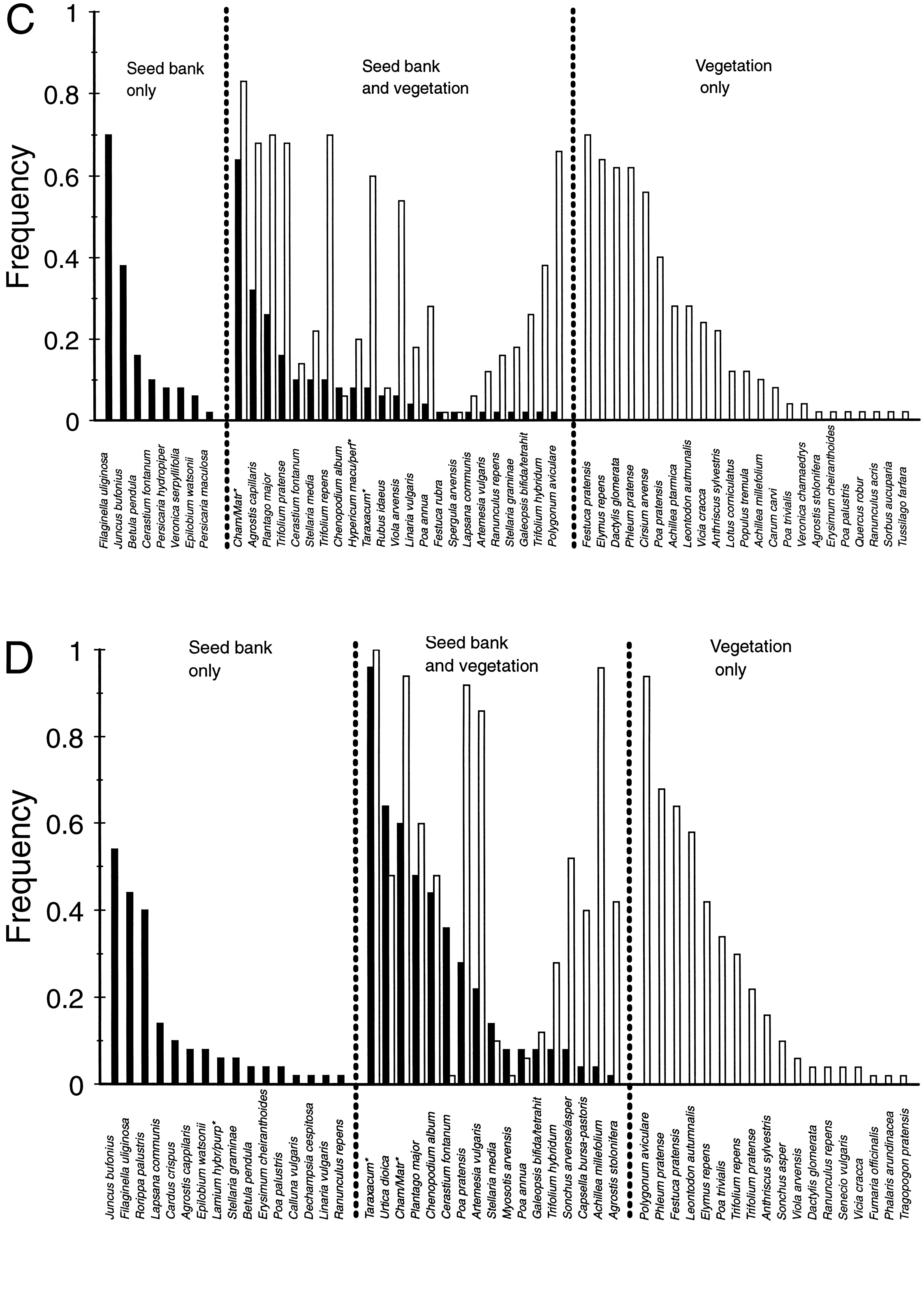


Fig. 4. (Continues …)



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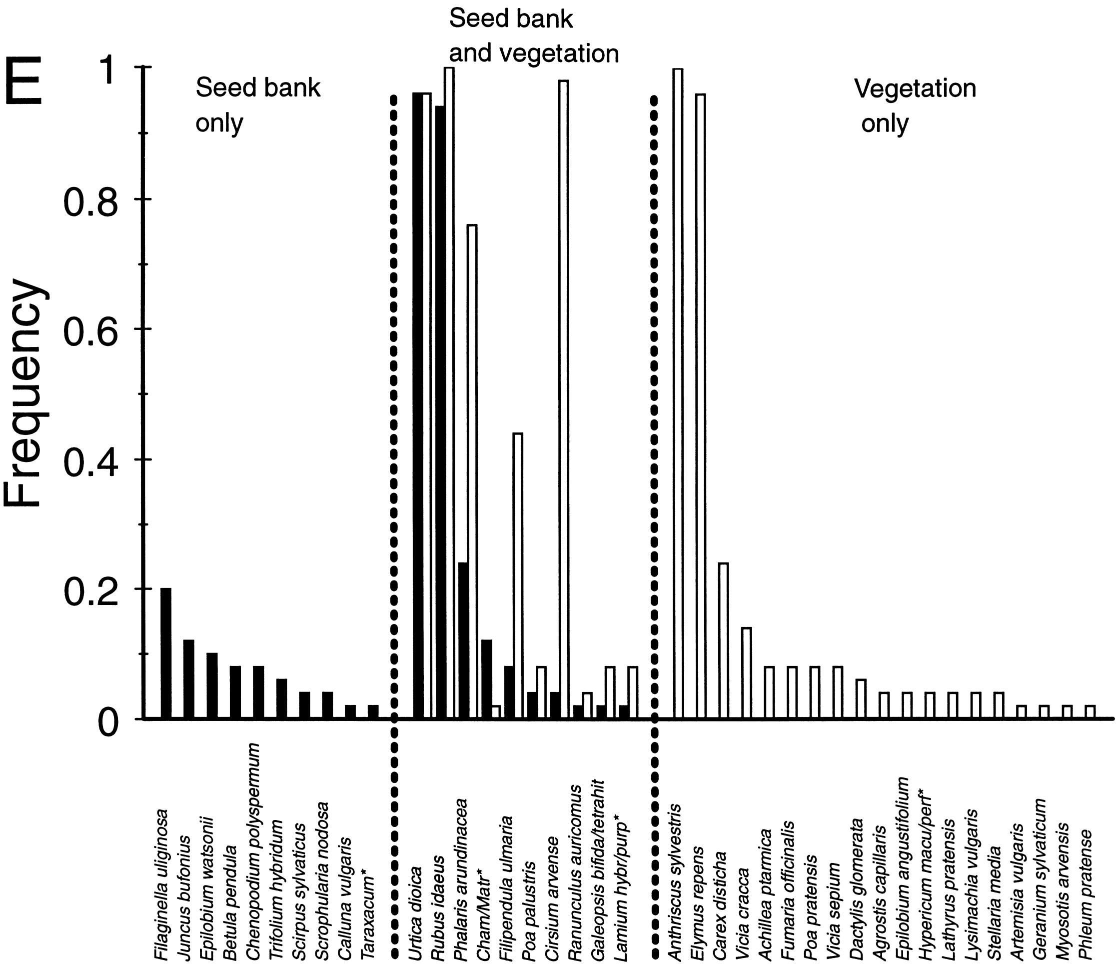

Fig. 4. The frequency of species present in the soil seed bank (■) and the vegetation (❑) of the linear habitats. a) The driveway verge, b) The gravel road verge, c) The horsetrack, d) The asphalt road verge and e) The ditch verge. **Cham/Matr = Chamomilla suaveolens/Matricaria perforata, Hypericum macu/perf = Hypericum maculatum/perforatum, Lamium hybr/purp = Lamium hybridum/purpureum, Taraxacum = Taraxacum* sect. *Ruderalia.*

to the soil seed bank one or two have the ability to grow vegetatively, *Scirpus sylvaticus* and to a lesser degree *Epilobium watsonii*; the others are dependent on seeds for reproduction. Thus 80% of the perennials unique to the soil seed bank depend on seeds for reproduction. In contrast, approximately 30% of the species found in the vegetation depend on seeds for reproduction.

DISCUSSION

This study clearly demonstrates that the soil seed banks of different linear habitats are important repositories of vascular plant diversity in an agricultural landscape. Surveys restricted to the aboveground vegetation will underestimate the number of species present in these habitats by 13–33%. For a variety of reasons germination methods may also underestimate the number of species present in the soil seed bank (Kropác 1966, Roberts 1981, Baskin & Baskin 1989, Gross 1990, Brown 1992). Thus the real proportion of species residing in the soil seed bank is likely to exceed the detected values.

The differences in species composition between the linear habitats show that they sample the plant species diversity of the landscape in more or less habitat-specific subsets. The low similarity of the ditch verge with all the road/track habitats presumably reflects the difference in abiotic environmental factors and disturbance regimes between these two habitat types. Different habitats have different dominant species, but the vast majority of seeds in the different soil seed banks come from only a few species: *Chamomilla suaveolens/ Matricaria perforata, Filaginella uliginosa, Rubus idaeus, Urtica dioica, Taraxacum* sect. *Ruderalia, Plantago major* and *Betula pendula* (75% of the total amount of seedlings found). With the exception of *Taraxacum* sect. *Ruderalia*, all these species have a persistent soil seed bank (Grime *et al.* 1988). *Taraxacum* sect. *Ruderalia* flower and fruit early in the season, and the seedlings of this species registered in our study probably derive from seeds produced the year of sampling. These abundance distributions from linear landscape elements are not dissimilar to those previously described from a number of natural communities (Williams 1964), and also the seed banks of arable fields. In Robert and Stokes' (1965) study of the soil seed banks of fields in England the seven most common species accounted for 78% of the seedlings. Also in Jensen's (1969) survey of 57 fields in Denmark the seven most common species accounted for 78% of the seeds.

The density of seeds found in the linear elements are relatively large compared with many other habitats (Leck *et al.* 1989). Large soil seed banks are usually found in regularly disturbed habitats such as wetlands exposed to floods, heaths exposed to fire, and arable soils (Chippindale & Milton 1934, Kropác 1966, Jensen 1969, Grime 1979, van der Valk & Davis 1979, Roberts 1981, Cavers & Benoit 1989, Thompson 1992). Somewhat in contrast to this, the arable soils investigated in the present study had lower seed densities than the different verges. This is probably due to modern agricultural practice where reduced crop rotation, widespread use of fertilisers and herbicides, irrigation, drainage, and improved seed cleaning methods accelerate the trend towards fewer weed species (Roberts & Nielson 1982, Caver & Benoit 1989, Wilson & Aebischer 1995).

The vertical distribution of the seeds of different species may in part be explained by their shape and size, and in part by the time since deposition (van der Valk & Davis 1979, Kiirikki 1993,

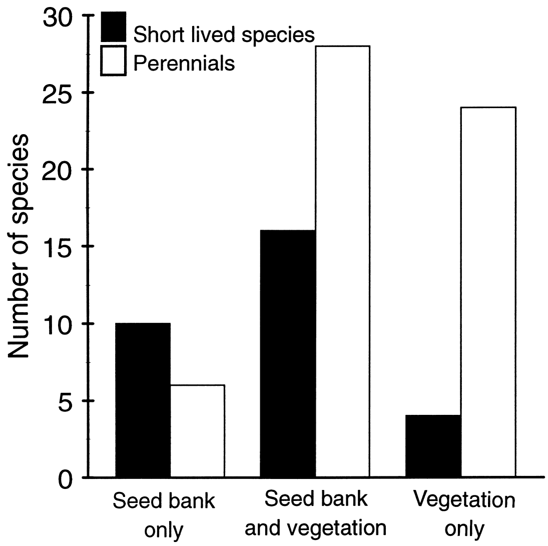

Fig. 5. The distribution of short-lived species (annuals and biennials) and perennials among species found only in the soil seed bank, in the soil seed bank and the vegetation, and in the vegetation only in five linear habitats (data on longevity are gathered from Grime *et al.* 1988 and Lid & Lid 1994).

Thompson *et al.* 1993, Milberg 1995). The two species which are more abundant in the lower layer, *Filaginella uliginosa* and *Hypericum maculatum/perforatum*, both produce small seeds. The species most frequent in the top layer, *Taraxacum* sect. *Ruderalia, Phalaris arundinacea* and *Betula pendula* have seeds of a size and shape that make burial in the soil difficult. In addition *Taraxacum* sect. *Ruderalia* dispersed diaspores during the sampling period, and thus its vertical seed distribution can be explained by the time of seed dispersal in relation to time of soil sampling. The vertical distribution of seeds in the soil core does not seem to reflect long time changes in the vegetation history of the habitat, i.e. with the lowermost species belonging to an earlier vegetation type or associated with former farming practises. Many of the one time pasture and meadow species of interest in plant conservation do not build persistent soil seed banks and are accordingly lost from the landscape soon after the pastures or meadows have been subjected to different management or use (Doneland & Thompson 1980, Bakker 1989, Gugerli 1994, Milberg 1995).

A striking feature of the linear habitats in the agricultural landscape is the dissimilarity between the species composition in the soil seed bank and the vegetation. This dissimilarity may suggest that the soil seed bank here in part acts as a sink and dead end for propagules released from plant populations in other landscape elements, e.g. the fields and groves. *Filaginella uliginosa* is common in the field and *Betula pendula* is common in the groves but they are absent from the aboveground vegetation of the linear habitats. A number of the species common to both the soil seed bank and the aboveground vegetation are annual and ruderals with a persistent seed bank, and for these the soil seed bank probably plays an important part in their population dynamics, e.g. *Chamomilla suaveolens/Matricaria perforata* and *Plantago major*. In contrast, quite a number of species have a low frequency in the soil seed bank, and for these the soil seed bank probably plays a minor role in their population dynamics. Note however that some of these 'rare' species have a ruderal-opportunistic life strategy and may emerge when small disturbance patches are created in the linear habitats, e.g. *Viola arvensis, Capsella bursa-pastoris*. The aboveground vegetation in our localities has a high frequency of perennial species, especially the grasses *Agrostis capillaris, Dactylis glomerata, Elymus repens, Poa pratensis, Festuca pratensis* and *Phleum pratensis*. Many perennial grasses reproduce vegetatively and have no persistent soil seed bank. Only *Agrostis capillaris* and *Poa pratensis* had a certain amount of seeds in the soil seed bank. The mixture of annuals and perennials in the aboveground verge communities probably reflects the intermediate disturbance regime of these habitats.

With regard to the function of linear habitats as possible corridors of plant migration, the soil seed bank would seem to play an important role for species without vegetative reproduction or easily dispersed propagules. Many of the more common agricultural weeds, however, are more likely to move through the fields than the grassy edges. For some easily dispersed species, the linear elements may indeed also function as sinks for propagules, a 'fence' of vegetation stopping the flow of propagules. For most species in the soil seed bank the linear elements should probably be considered simply as a habitat rather than a corridor. In contrast to Forman (1995) we would like to reserve the concept of 'corridor' for linear landscape elements which to a significant degree function as conduits. The linear elements of the landscape are clearly also important habitats for a substantial number of species which are not present in the soil seed bank, e.g. *Festuca pratensis, Phleum pratensis* and *Anthriscus sylvestris.*

The divergence between the species composition of the soil seed bank and the aboveground vegetation demonstrates the necessity of sampling both to obtain a representative estimate of the real vascular plant diversity present in the linear habitats.

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