

Patterns in species composition of arable field boundary vegetation

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SUMMARY

Vegetation composition in contrasting field boundary plots was analysed by means of transects perpendicular to the arable field 3 years after establishment. Plots were established on the outer meters of an arable field next to a pre-existing field boundary and sown with (1) a mixture of 30 forbs, (2) *Lolium perenne** and (3) plots left regenerating naturally. Tall, competitive species concentrated biomass production in a zone within 1 m from the arable field, while small, stress tolerant species were predominantly found in a zone 3–4 m from the field. The tall species were able to increase total vegetation biomass production significantly in the zone bordering the arable field, probably by means of capturing nutrients from the arable field. The two major arable weeds found in the boundary plots, *Elymus repens* and *Cirsium arvense*, colonized the plots with different strategies but both were seriously reduced in vigour when plots were sown with *Lolium perenne* or with forbs at the onset of the experiment. Species richness in the forbs-plots was relatively high but rather low in the grass- and regeneration-plots caused by a very limited colonization of potential field boundary species; only two species colonizing the boundary plots were new to the original field boundary, while 30% of the species from the original field boundary were not found in the boundary plots after 3 years. This limited colonization ability may seriously hamper efforts to restore field boundary diversity.

Key-words: arable weeds, biomass gradient, distribution patterns, field boundary vegetation, species-richness.

INTRODUCTION

Field boundaries have been an important aspect of the human environment since the introduction of agriculture. Arable fields logically end somewhere and people in different areas developed different boundary structures according to specific needs such as fencing, wood for domestic use, drainage of excess water or simply to mark the border between two fields. Before the invention of barbed wire most of the boundaries existed of perennial vegetation such as hedgerows or ditch banks, often characterizing

*Nomenclature following Van der Meijden (1990).

the entire landscape. Furthermore, as they usually comprise the largest areas of perennial vegetation amid annually cultivated fields, they are an important component in the agricultural ecosystem providing a habitat for many plant species and food, shelter, overwintering sites or corridors between habitats for a multitude of animal species (Hooper 1987; Bennet *et al.* 1994; Dennis *et al.* 1994; Parish *et al.* 1994, 1995).

The intensification of the agriculture since the 1950s has resulted in a dramatic loss of field boundary habitats in western Europe, while the remaining boundaries in the agricultural landscape have suffered a serious decline in diversity (Boatman 1992; Freemark & Boutin 1995). Since 1985 there has been an increased interest in the functionality of field boundaries in the agricultural ecosystem and in the factors that control diversity in them (e.g. Marshall & Birnie 1985; Way & Greig-Smith 1987; Boatman 1994).

The farmers' perception of field boundaries is pivotal to the condition of field boundaries, as they are primarily involved in the management and maintenance practices. In general, field boundaries are viewed by farmers as sources of pests and weeds (Marshall & Smith 1987) and are managed accordingly. Of the farmers interviewed by Boatman (1992), Marshall & Smith (1987) and De Snoo & Wegener Sleeswijk (1993) 62%, 60% and 59%, respectively, sprayed their field boundaries, usually with broad spectrum herbicides, in attempts to control perceived weed problems. Indeed, a number of plant species that may seriously hamper crop growth can have populations in both the field boundary and in the crop edge, for instance *Bromus sterilis*, *Cirsium arvense*, *Elymus repens* and *Galium aparine* (Boatman 1989; Marshall 1989; Theaker *et al.* 1995). Therefore, an analysis of the factors affecting field boundary diversity has to include their effects on weed abundance in that boundary.

So far, few studies have tried to relate agricultural practices with the species composition of arable field boundary vegetation. A major difficulty in such attempts is the low level of diversity in most modern field boundaries. Experimental treatments which might have negative effects in botanically rich field boundaries may fail to give any effects in modern species-poor field boundaries (Marshall 1987). Furthermore, since interest in field boundaries is of rather recent date, historical data of the composition of field boundary vegetation, which could have been used as a point of reference, are lacking. Thus there is great need for knowledge of the potential botanical richness and the main factors affecting it in arable field boundaries.

The present study reports on vegetation composition in newly created 4-m-wide field boundary plots bordering an original boundary 3 years after establishment. Management regime of the new boundary vegetation was favourable to establishment of a species-rich vegetation so that the results of the present study may function as a point of reference for future studies on this and other experiments. Furthermore, comparisons made between vegetation composition close to and further from the arable field may identify factors related to agriculture that cause botanical change in field boundary vegetation. Thus, data were collected in order to answer the following questions:

- 1 Is the composition of arable field boundary vegetation affected by agriculture related factors (e.g. herbicide drift, fertilizer application)?
- 2 Is it possible to restore a high species-richness in a perennial vegetation bordering the arable field?

MATERIAL AND METHODS

Sites

In April 1993, experimental field boundaries were established on three fields in the vicinity of Wageningen as part of a joint research programme with participants in France, The Netherlands and the United Kingdom (Marshall *et al.* 1994). The original boundaries of two of the fields were ditch banks while the third field was bordered by an unpaved road. All pre-existing boundaries were at least 1.5 m wide, had a grassy vegetation on sandy soils which was managed by flail-mower once a year without removing the cuttings. This type of management was maintained throughout the experiment. Species present in the original boundary are given in Table 1a. Crop rotation as well as fertilizer and herbicide inputs for the three fields are given in Table 2. Fertilizer was applied with a pneumatic fertilizer spreader while pesticides were applied with a tractor-mounted air-assisted hydraulic sprayer.

Treatments

Three types of experimental field boundary plots were established in the former crop edge, all $8 \times 4 \text{ m}^2$ large, parallel to and bordering the pre-existing field boundary. The first type were plots sown with a mixture of 30 species of forbs (Table 1b). Species were selected from a range of vegetation types representing possible stages in succession on fallow arable land under a mowing regime (Schmidt, 1993): perennial forbs from open, nutrient rich and more or less disturbed vegetation; perennial forbs from dry, open to closed grassland vegetation; and perennial forbs from moist, closed grassland vegetation. Furthermore, these species had to occur on sandy, slightly acid soils, had to flower attractively and sufficient seeds had to be available. Seeds of most of the species were collected around Wageningen in 1992. Some seeds were purchased from De Cruythoeck, a company specializing in native wild species. The aim of this treatment was to establish a boundary type with a high species-richness which, although highly artificially established, may function as a point of reference concerning potential species-richness. For simplicity, this plot will hereafter be referred to as the forbs-plot. The second type were plots sown with *Lolium perenne*. This treatment was included because it is known to be a good weed suppressor in the early stages of arable fallow. The third type were plots allowed to regenerate naturally. On each field three replicates were created with the three treatments randomized within the replicates (resulting in a total of 3 fields \times 3 replicates \times 3 plot types = 27 plots). All plots were mown once a year in autumn and cuttings were removed. Care was taken to reduce seed dispersal between plots due to removal of the cuttings.

The effects of agriculture-related factors causing botanical change were expected to diminish with increasing distance from the arable field. Therefore vegetation composition was determined by means of transects perpendicular to the arable field. In August 1995, transects of $4 \times 0.5 \text{ m}^2$ (eight $0.5 \times 0.5 \text{ m}^2$ subplots) were set out over the total width of each newly created boundary plot. Aboveground biomass of each subplot was cut, separated into species and dry weight was determined after drying for 48 hours at 80°C .

Analysis

Within the field-stratum each plot type was replicated nine times. Since the performance of a species depends on both its own biomass production and the biomass production

Table 1. (a) Grassland species occurring in the pre-existing boundaries of three fields at a maximum distance of 5 m from the newly created boundary plots. (b) Species sown to the herbs boundary plots. Seeding rate of the mixture was 1 g m^{-2} . The percentage of total seed weight is given for each species

(a) Fields	Bornsesteeg	Keijenberg	(b) Sown species	(%)
Amfoort				
	<i>Agrostis capillaris</i>	<i>Achillea millefolium</i>	<i>Campanula rotundifolia</i>	2.6
	<i>Anemona nemorosa</i> *	<i>Agrostis capillaris</i>	<i>Centaurea jacea</i>	8.1
	<i>Angelica sylvestris</i> *	<i>Arrhenatherum elatius</i>	<i>Chaerophyllum temulum</i>	5.2
	<i>Arthriscus sylvestris</i> *	<i>Artemisia vulgaris</i>	<i>Cichorium intybus</i>	1.6
	<i>Arrhenatherum elatius</i>	<i>Bromus hordeaceus</i>	<i>Crepis capillaris</i>	0.1
	<i>Cardamine pratensis</i> *	<i>Carduus crispus</i>	<i>Crepis biennis</i>	1.9
	<i>Cerastium fon. ssp. vulgare</i>	<i>Chaerophyllum temulum</i>	<i>Daucus carota</i>	3.4
	<i>Cirsium arvense</i>	<i>Cirsium arvense</i>	<i>Euphrasia stricta</i> †	0.8
	<i>Dactylis glomerata</i>	<i>Crepis capillaris</i>	<i>Galium mollugo</i>	0.7
	<i>Elymus repens</i>	<i>Dactylis glomerata</i>	<i>Galium verum ssp. verum</i>	0.6
	<i>Equisetum arvense</i>	<i>Elymus repens</i>	<i>Hieracium pilosella</i>	1.8
	<i>Festuca rub. ssp. commutata</i>	<i>Festuca rubra ssp. commutata</i>	<i>Hypericum perforatum</i>	3.2
	<i>Galium aparine</i>	<i>Holcus lanatus</i>	<i>Hypochaeris radicata</i>	2.1
	<i>Holcus lanatus</i>	<i>Holcus mollis</i>	<i>Jasione montana</i> †	0.3
	<i>Holcus mollis</i>	<i>Lolium album</i> *	<i>Lathyrus pratensis</i> †	2.1
	<i>Juncus effusus</i>	<i>Leontodon autumnalis</i>	<i>Leontodon autumnalis</i>	4.0
	<i>Galium aparine</i>	<i>Lolium perenne</i>	<i>Leonurus cardiaca</i>	1.6
	<i>Holcus lanatus</i>	<i>Plantago lanceolata</i>	<i>Leucanthemum vulgare</i>	2.0
	<i>Juncus effusus</i>	<i>Poa trivialis</i>	<i>Linaria vulgaris</i>	0.9
	<i>Lolium perenne</i>	<i>Potentilla argentea</i>	<i>Lotus corn. ssp. corniculatus</i>	0.7
	<i>Lotus uliginosus</i> *	<i>Ranunculus reptans</i> *	<i>Lysimachia vulgare</i> †	1.3
	<i>Lolium perenne</i>	<i>Ranunculus repens</i>	<i>Malva moschata</i>	18.1
	<i>Lotus uliginosus</i> *	<i>Rumex acetosella</i>	<i>Medicago lupulina</i> †	1.9
	<i>Poa pratense</i> *	<i>Rumex acetosella</i>	<i>Picris hieracioides</i>	0.4
	<i>Poa trivialis</i>	<i>Rumex obt. ssp. obtusifolius</i>	<i>Pimpinella saxifraga</i>	5.2
	<i>Ranunculus acris</i> *	<i>Sambucus nigra</i> *	<i>Saponaria officinalis</i>	16.1
	<i>Ranunculus repens</i>	<i>Stellaria holostea</i>	<i>Silene latifolia ssp. alba</i>	5.4
	<i>Rubus fruticosus</i> *	<i>Trifolium repens</i>	<i>Tanacetum vulgare</i>	5.2
	<i>Rumex acetosa</i>	<i>Urtica dioica</i>	<i>Trifolium arvense</i> †	0.5
	<i>Rumex crispus</i> *	<i>Valeriana officinalis</i>	<i>Trifolium dubium</i>	2.2
	<i>Rumex obt. ssp. obtusifolius</i>	<i>Vicia hirsuta</i>		
	<i>Sambucus nigra</i> *	<i>Vicia sativa ssp. nigra</i>		
	<i>Stellaria holostea</i>			
	<i>Trifolium repens</i>			
	<i>Urtica dioica</i>			
	<i>Valeriana officinalis</i>			
	<i>Vicia hirsuta</i>			
	<i>Vicia sativa ssp. nigra</i>			
	<i>Vicia sepium</i> *			

*Species which were not found in the experimentally established plots after 3 years; †sown species that did not establish at all; ‡sown species establishing only in the first year.

Table 2. Fertilizer and herbicide inputs in three fields bordering the new field boundary plots. Numbers in superscript indicate different applications of herbicides within a season

Field	Amfoort	Bornsesteeg	Keijenberg
Crop in 1993	<i>Spring Wheat</i>	<i>Winter Wheat</i>	<i>Triticale</i>
Herbicides	Certrol Combin (4l/ha)	Starane ¹ (2l/ha) MCPA ² (1l/ha)	MCPA (1.5l/ha) MCPP (1.5l/ha) Starane (0.5 l/ha)
Fertilizer	70 kg N/ha 65 kg P/ha 165 kg K/ha	190 kg N/ha 0 kg P/ha 0 kg K/ha	65 kg N/ha 0 kg P/ha 75 kg K/ha
Crop in 1994	<i>Sugar Beet</i>	<i>Potato</i>	<i>Phacelia</i> (Set-aside)
Herbicides	Betanal ¹ (2l/ha) Goltix ¹ (2kg/ha) Betanal ² (2l/ha) Tramat ² (1.5l/ha) Goltix ² (1kg/ha)	Butisan ¹ (1l/ha) Patoran ¹ (3l/ha) MCPA ² (1l/ha) Gramoxone ³ Reglone ³ (2.5l/ha)	— (2.5l/ha)
Fertilizer	150 kg N/ha 40 kg P/ha 165 kg K/ha	195 kg N/ha 20 kg P/ha 115 kg K/ha	65 kg N/ha 25 kg P/ha 125 kg K/ha
Crop in 1995	<i>Potato</i>	<i>Spring Wheat</i>	<i>Silage Maize</i>
Herbicides	Boxer (3l/ha) Patoran (1.5l/ha)	MCPA (2l/ha) MCPP (2l/ha)	Lentagran EC (2l/ha) Atrazin (1.5l/ha)
Fertilizer	100 kg N/ha 40 kg P/ha 100 kg K/ha	80 kg N/ha 0 kg P/ha 50 kg K/ha	200 kg N/ha 55 kg P/ha 280 kg K/ha

of the surrounding vegetation, the performance of a species is expressed proportional to the total biomass production of the subplot. Proportional yields summarize the relative vegetative success of a species and may be considered as the relative ecological performance (Austin & Austin 1980).

Individual species were analysed separately for each treatment plot and, as the biomass data for individual species did not meet the assumptions for ANOVA due to a large number of zeros, a Monte Carlo approach was used to analyse for significant differences caused by subplot position (Sokal & Rohlf 1981). Data of total vegetation biomass and species numbers were analysed by nested ANOVA with the subplot treatment nested within the plot type treatment.

RESULTS

Of the 53 field boundary species listed in Table 1a, 16 species did not manage to colonize the experimental plots within the 3 years of this experiment, while only two species (*Carex ovalis* and *Anthoxanthum odoratum*) encountered in the experimental boundary plots in 1995 had not been found at the onset of the experiment in either the original field boundary or the arable field.

Herbicides were mostly applied once or twice a year (Table 2) but visual damage to the field boundary vegetation was not observed in any of the years, with the exception

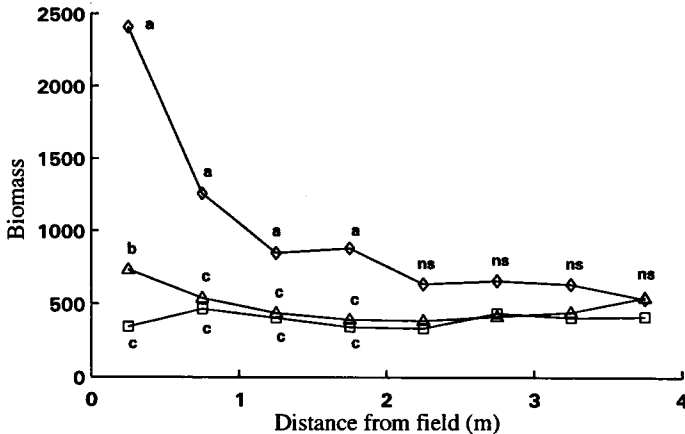


Fig. 2. Biomass production of the total vegetation ($\text{g}\cdot\text{m}^{-2}$) across experimental field boundary plots sown with forbs (\diamond), *Lolium perenne* (\square) or left regenerating (\triangle). Different characters indicate significant differences between similar subplots in different plot types ($P < 0.05$).

of a single occasion when part of the vegetation hanging over the arable field showed curling of leaves and shoots following an application of a MCPA/MCPP mixture.

While the initial conditions of the three plot types did not differ systematically with respect to fertility or soil seed bank (since the plot types were randomized within the nine blocks), the vegetation composition and more surprisingly the vegetation structure, height and biomass production contrasted sharply at the end of the third growing season (Fig. 1a–c). Biomass production of the three plot types differed significantly between 0 and 2 m from the arable field but was not statistically different from 2 to 4 m (Fig. 2). From 0–2 m, the forbs-plots always yielded higher than the other plot types while at 0.25 m biomass production of the regeneration-plot was also higher than that of the grass-plots. A comparison of biomass production within plot types showed a significant increase in biomass production at the subplot bordering the arable field for both the forbs- and the regeneration-plots while the grass-plots did not produce any trend in biomass yields (Tables 3, 4 and 5).

Averaged over the total transect the mean number of species were, with $5.9 \text{ sp./}0.25\text{m}^2$, lowest in the grass-plots, significantly higher in the regeneration-plots (8.6 , $P < 0.05$) and highest in the forbs-plots (13.7 , $P < 0.001$). Close to the arable field (0–1.25 m), however, species numbers were not significantly different between forbs- and regeneration-plots while in the grass-plots they were significantly lower. Further from the arable field (1.75–3.75 m) species numbers of the forbs-plots became significantly higher than those of the grass- and regeneration-plots (Fig. 3). Within plot types species-richness showed a more varied picture (Tables 3, 4 and 5). In general, in the forbs-plots species numbers between 0 and 0.75 m were significantly lower than between 0.75 and 3.75 m from the arable field. In the *L. perenne* sown plots a steady and significant increase in species numbers was observed with increasing distance from the field and in the regeneration plots the 0.75 and 1.25 m subplots differed significantly (higher) from the 3.75 subplot only (Tables 3, 4 and 5).

While in the grass- and regeneration-plots no significant relationship existed between total biomass production and species-richness, in the forbs-plots a significant negative regression was found (Fig. 4). This relationship was determined mainly by a limited

Table 3. The distribution of some of the most common species (in percentage of total biomass), total biomass production and number of species in relation to distance from the field in plots sown with a *forbs* mixture (species with an asterisk) in spring 1993. *n* = frequency, total number of sampled subplots is 72. *P*-values (Monte-Carlo randomization test) are given for differences between distances. Biomass and species number data were analysed by means of ANOVA, different characters indicate significant differences

Distance	<i>n</i> (%)	0.25	0.75	1.25	1.75	2.25	2.75	3.25	3.75	<i>P</i> -value
<i>Agrostis capillaris</i>	(29)	0.3	0.1	0.1	0	0.1	0	1.1	8.0	(0.000)
<i>Campanula rotundifolia</i> *	(24)	0.02	0.05	0.02	0.06	0.09	0.02	0.47	0.07	(0.981)
<i>Centaurea jacea</i> *	(93)	12.6	17.8	30.3	21.9	27.1	13.4	15.8	14.1	(0.089)
<i>Cichorium intybus</i> *	(31)	3.5	1.2	2.0	0.2	0.5	0	0	0.4	(0.243)
<i>Dactylis glomerata</i>	(29)	0	0.2	0.2	0.5	1.0	0.7	3.9	1.1	(0.283)
<i>Daucus carota</i> *	(36)	0	0	0.01	0.01	0.01	0	0.06	0.25	(0.056)
<i>Elymus repens</i>	(49)	0	0	0.1	0.4	0.5	0.9	1.6	4.2	(0.000)
<i>Festuca rubra</i> ssp. <i>commutata</i>	(32)	0	0	0	0.1	0.1	0.3	2.1	12.4	(0.000)
<i>Galium mollugo</i> *	(83)	1.8	5.7	4.2	3.2	4.8	3.3	1.8	2.2	(0.822)
<i>Galium verum</i> ssp. <i>verum</i> *	(60)	0.5	0.5	0.4	1.4	1.1	1.0	0.2	0.2	(0.541)
<i>Hieracium pilosella</i> *	(21)	0	0	0	0.01	0.02	0.01	0.15	0.28	(0.018)
<i>Holcus lanatus</i>	(40)	0.4	0.6	0.3	0.2	3.0	5.2	10.5	9.2	(0.006)
<i>Hypericum perforatum</i> *	(39)	0.4	0.8	1.8	0.7	3.8	2.3	0.7	0	(0.170)
<i>Hypochaeris radicata</i> *	(32)	0.1	0.3	0.1	0.5	0.1	0.2	0.7	1.4	(0.108)
<i>Leucanthemum vulgare</i> *	(90)	1.7	9.8	9.7	16.6	8.9	14.1	8.8	15.9	(0.085)
<i>Linaria vulgaris</i> *	(25)	0.3	0.1	0.1	0.2	0.1	0.3	0.8	0	(0.945)
<i>Malva moschata</i> *	(35)	0.3	0.2	0.4	0.7	0.3	0.4	0.4	0	(0.970)
<i>Picris hieracitoides</i> *	(28)	0	0.8	0.3	2.3	0.2	0.4	0.5	0	(0.246)
<i>Saponaria officinalis</i> *	(99)	8.4	6.3	13.1	7.3	12.8	12.5	4.8	2.9	(0.004)
<i>Silene latifolia</i> ssp. <i>alba</i> *	(65)	8.7	12.4	7.8	12.3	2.2	8.4	9.1	5.1	(0.743)
<i>Tanacetum vulgare</i> *	(94)	59.6	40.7	25.9	24.6	26.1	26.4	20.2	3.5	(0.000)
<i>Vicia hirsuta</i>	(28)	0.1	0.2	0.4	0.7	0.2	0.2	0.4	0.7	(0.543)
Total biomass (g/m ²)		2408.4 ^a	1259.6 ^b	848.4 ^c	882.0 ^c	636.0 ^{cd}	658.0 ^{cd}	634.0 ^{cd}	534.8 ^d	
No. species		11.8 ^d	10.7 ^d	12.4 ^{cd}	14.6 ^b	14.7 ^b	15.2 ^{ab}	16.7 ^a	13.9 ^{bc}	

Table 4. The distribution of some of the most common species (in percentage of total biomass), total biomass production and number of species in relation to distance from the field in plots sown in spring 1993. Species with an asterisk are species originally sown in the forbs plots. n = frequency, total number of sampled subplots is 72. P -values (Monte Carlo randomization test) are given for differences between distances. Biomass and species number data were analysed by means of ANOVA, different characters indicate significant differences

Distance	n (%)	0-25	0-75	1-25	1-75	2-25	2-75	3-25	3-75	P -value
<i>Achillea millefolium</i>	(25)	0-3	4-8	4-1	0-9	1-1	1-2	0-4	0	(0-211)
<i>Agrostis capillaris</i>	(24)	0	0	0-1	0	1-2	0-8	4-3	8-6	(0-000)
<i>Artemisia vulgaris</i>	(15)	0	4-5	0-1	0	0-4	5-9	5-9	6-8	(0-701)
<i>Cirsium arvense</i>	(15)	4-1	3-0	1-7	3-0	1-6	1-0	0	1-1	(0-939)
<i>Crepis capillaris*</i>	(19)	0	3-5	3-5	2-7	3-0	2-1	0-4	0	(0-302)
<i>Dactylis glomerata</i>	(19)	0	0	0	0	0-1	0	2-8	0-3	(0-182)
<i>Elymus repens</i>	(39)	0	0	0-1	0	0-2	1-9	6-4	8-8	(0-000)
<i>Equisetum arvense</i>	(19)	0	0	0	0-2	0-6	0-4	0-8	1-6	(0-001)
<i>Erigeron canadensis</i>	(25)	0-1	0-1	0-5	0-4	0-1	0	0-1	0	(0-164)
<i>Festuca rubra</i> ssp. <i>commutata</i>	(15)	0	0	0	0	0	0-4	0-2	6-1	(0-000)
<i>Holcus lanatus</i>	(38)	3-4	8-0	5-2	7-4	9-9	17-7	20-6	14-2	(0-093)
<i>Holcus mollis</i>	(13)	0-7	0	0-4	0	0	0-6	4-9	13-5	(0-001)
<i>Lolium perenne</i>	(99)	84-9	71-6	76-7	75-0	69-5	54-9	47-9	27-2	(0-000)
<i>Rumex acetosa</i>	(14)	0-1	0-1	0-4	0-9	0	0-7	1-4	0	(0-530)
<i>Trifolium repens</i>	(17)	0	0-2	0	0	0	0	0-1	0	(0-191)
<i>Vicia hirsuta</i>	(40)	4-0	1-4	4-5	2-7	4-7	1-8	1-4	2-1	(0-882)
<i>Vicia sativa</i> ssp. <i>nigra</i>	(18)	0-3	1-1	0-6	1-3	1-3	0	0	0	(0-094)
Total biomass (g/m ²)		343-6	466-0	404-8	342-4	334-0	438-4	408-0	414-8	
No. species		3-6 ^d	4-9 ^{cd}	5-6 ^{bc}	5-6 ^{bc}	7-0 ^{ab}	5-7 ^{bc}	6-6 ^{abc}	7-8 ^a	

Table 5. The distribution of some of the most common species (in percentage of total biomass), total biomass production and number of species in relation to distance from the field in plots left *regenerating* since spring 1993. Species with an asterisk are species originally sown in the forbs plots. n = frequency, total number of sampled subplots is 72. P -values (Monte Carlo randomization test) are given for differences between distances. Biomass and species number data were analysed by means of ANOVA, different characters indicate significant differences

Distance	n (%)	0-25	0-75	1-25	1-75	2-25	2-75	3-25	3-75	P -value
Species										
<i>Achillea millefolium</i>	(29)	7-7	10-5	8-3	8-5	6-3	3-7	0-3	0	(0-188)
<i>Agrostis capillaris</i>	(38)	3-4	7-5	0-1	2-0	1-5	3-4	5-2	9-3	(0-742)
<i>Arrhenatherum elatius</i>	(11)	0	0	7-2	8-5	10-5	7-3	10-1	7-9	(0-487)
<i>Artemisia vulgaris</i>	(15)	8-8	0-1	1-3	0-9	0-3	1-6	0-9	1-0	(0-902)
<i>Bromus hordeaceus</i>	(11)	4-6	5-3	5-4	6-1	7-0	3-0	2-5	0-1	(1-000)
<i>Cirsium arvense</i>	(36)	15-1	11-0	10-0	5-7	4-4	2-4	0-8	0-1	(0-001)
<i>Crepis capillaris</i> *	(19)	0-1	0-1	0-9	0-4	0	0	0-2	0	(0-095)
<i>Dactylis glomerata</i>	(31)	0-1	0-3	0-1	0-1	0-8	1-0	0	2-2	(0-077)
<i>Daucus carota</i> *	(11)	0-02	0-03	0-02	0	0-65	0	1-09	0	(0-963)
<i>Elymus repens</i>	(69)	3-3	3-4	2-1	1-1	2-4	7-8	11-8	13-1	(0-023)
<i>Epilobium ciliatum</i>	(22)	2-3	3-5	0-3	0-1	0-6	0-2	0-1	0	(0-165)
<i>Equisetum arvense</i>	(13)	0	0-2	0-2	0-4	0-9	1-2	0-8	0-3	(0-892)
<i>Erigeron canadensis</i>	(21)	0-7	0-3	0	0-4	0-4	0-4	0	0	(0-358)
<i>Festuca rubra</i> ssp. <i>commutata</i>	(33)	0	0	0-3	0-4	6-1	16-1	18-2	20-7	(0-000)
<i>Holcus lanatus</i>	(64)	14-3	23-1	39-0	56-2	41-2	34-6	27-8	13-7	(0-001)
<i>Holcus mollis</i>	(15)	0	0	0	0	0-1	1-1	7-6	21-2	(0-001)
<i>Hypochoeris radicata</i> *	(31)	0-1	1-0	3-1	0-2	0-3	0-1	0-1	0-1	(0-059)
<i>Juncus effusus</i>	(19)	0	0-9	1-2	0-2	0	0-1	0	0	(0-177)
<i>Leontodon autumnalis</i>	(11)	4-4	0-05	0-02	0	0	0-02	0-04	0	(0-202)
<i>Ranunculus repens</i>	(49)	2-0	1-5	1-6	0-2	0-1	0	0-1	0	(0-134)
<i>Rumex acetosa</i>	(21)	0	0-1	0-9	0-3	0-7	0-9	0-8	1-4	(0-674)
<i>Rumex obt. ssp. obtusifolius</i>	(29)	19-0	11-7	6-2	0-6	3-7	5-8	8-1	6-9	(0-562)
<i>Trifolium repens</i>	(24)	0	0	0	0-2	1-0	0-6	0-4	0-4	(0-003)
<i>Urtica dioica</i>	(14)	2-7	3-1	1-1	0	0	0	0	0	(0-036)
<i>Vicia hirsuta</i>	(31)	0-3	1-6	2-4	1-1	0-7	0-6	0-4	0	(0-025)
<i>Vicia sativa</i> ssp. <i>nigra</i>	(17)	0-4	0-5	0-5	0-2	0-1	0-1	0-2	0	(0-288)
Total biomass (g/m ²)		732-0 ^a	539-2 ^{ab}	438-4 ^b	393-6 ^b	386-4 ^b	415-6 ^b	444-8 ^b	544-4 ^{ab}	
No. species		8-7 ^{ab}	9-8 ^a	9-4 ^a	8-4 ^{ab}	8-4 ^{ab}	8-6 ^{ab}	8-6 ^{ab}	6-9 ^b	

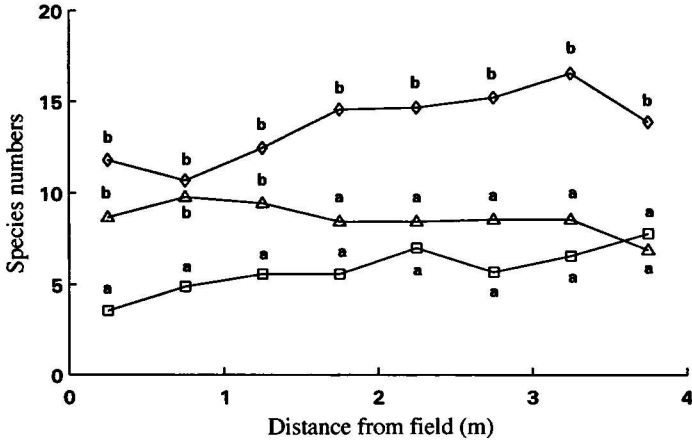


Fig. 3. Numbers of species (0.25 m^{-2}) across experimental field boundary plots sown with forbs (◇), *Lolium perenne* (□) or left regenerating (△). Different characters indicate significant differences between similar subplots in different plot types ($P < 0.05$).

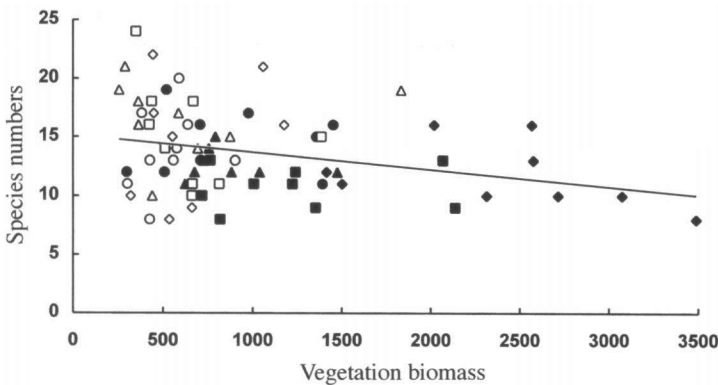


Fig. 4. Relationship between vegetation biomass production (g.m^{-2}) and species numbers (0.25 m^{-2}) in the forbs-plots. Regression significant ($P < 0.01$). ◇: 0.25 subplot, ■ (0.75), ▲ (1.25), ● (1.75); ◇ (2.25), □ (2.75), △ (3.25), ○ (3.75).

number of plots with very high biomass production and low species numbers, all of them located within 1 m from the arable field.

For individual species, four types of distribution patterns could be distinguished (Tables 3, 4 and 5): I. species showing a random distribution pattern, such as *Galium mollugo* in the forbs-plots, *Vicia hirsuta* in the grass-plots and *Agrostis capillaris* in the regeneration-plots; II. species significantly increasing in relative abundance with increasing distance from the arable field. Examples are the species *Hieracium pilosella* in the forbs-plots, *A. capillaris* in the grass-plots and *Festuca rubra* ssp. *commutata* in the regeneration-plots; III. species significantly decreasing in abundance with increasing distance from the arable field. The most striking example was *Tanacetum vulgare* in the forbs-plots which decreased in mean relative performance from 60% of the total biomass at 0.25 m from the arable field to 4% at 3.75 m, despite the fact that it was sown evenly and established accordingly in the first year. *L. perenne* and *C. arvensis* showed similar patterns in the grass- and regeneration-plots respectively, and in particular the pattern

of *C. arvense*, which established only by rhizomatous growth, is peculiar since it originated from the pre-existing boundary. Thus in within 3 years it grew through the 4-m-wide regeneration-plots and concentrated aboveground biomass production in a zone within 1.5 m from the arable field; IV. species with a significantly higher abundance in the middle of the plot. In particular, *Holcus lanatus* in the regeneration-plots and *Saponaria officinalis* in forbs-plots.

Although most annual weeds had been able to produce very large quantities of seeds in the first season, these species were virtually absent in the third year. The most common arable weeds that persisted in the boundary plots after two years were *Elymus repens*, followed by *V. hirsuta* and *C. arvense*, respectively. Based on their mean relative performance, however, *E. repens* and *C. arvense* were the only weedy species of significance in the boundary plots. On average they remained minor components of the vegetation, never contributing more than c. 15% of the total vegetation; however, in individual subplots they occasionally dominated the vegetation with mean relative performances of 80 and 79%, respectively. Figure 5a and b shows that, although the two species displayed opposite distribution patterns, both species had their highest mean relative performance in the regeneration-plots and the lowest in the forbs-plots. Averaged over the transect, biomass production of *C. arvense* declined from 33.4 g/m² in the regeneration-plots to 7.5 g/m² in the grass-plots (difference significant at $P < 0.05$) and to 0.1 g/m² in the forbs-plots (difference between grass- and forbs-plots: $P < 0.01$). Biomass production of *E. repens* was with 27.7 g/m² significantly higher ($P < 0.05$) in the regeneration plots than in the grass-plots (9.0 g/m²) and the forbs-plots (5.8 g/m²). Biomass production of the grass- and the forbs-plots did not differ significantly. The biomass production of *E. repens* and *C. arvense* did not differ significantly in the regeneration- and the grass-plots but *E. repens* was more successful in the forbs-plots ($P < 0.001$).

DISCUSSION

Although the establishment of most of the sown species, including species with low competitive ability, was good, the number of species colonizing the new field boundary plots was low. Only two species were completely new to the field margin and 16, all common to very common species, failed to establish from within a 5 m distance. Similar observations were made by Graham & Hutchings (1988) and Smith & MacDonald (1989) and must be related to the absence of a seed bank and the limited dispersal ability of species characteristic of a perennial grassy vegetation (Hume & Archibold 1986; Van Dorp 1996)

A remarkable result was the increase in biomass production near the arable field in the forbs- and regeneration-plots, which was not found in the grass-plots. Both the regeneration- and the forbs-plots were characterized by a limited number of species with peak mean relative performance close to the arable field which were absent in the grass plots. In the forbs-plots *T. vulgare* and in the regeneration-plots *C. arvense* and *Urtica dioica* have in common that they are very tall and strong competitors (Grime *et al.* 1988). Kleijn (1996) found that this type of species was able to capture nutrient resources efficiently from the arable field and use it for increased biomass production in the boundary while species of low stature were less able to do so. Campbell *et al.* (1991) and Grime (1994) found species to contrast in their scale of root foraging. Tall, dominant plant species such as *U. dioica* were found to actively adjust root and shoot growth into locally resource-rich zones while low-growing species such as *Campanula*

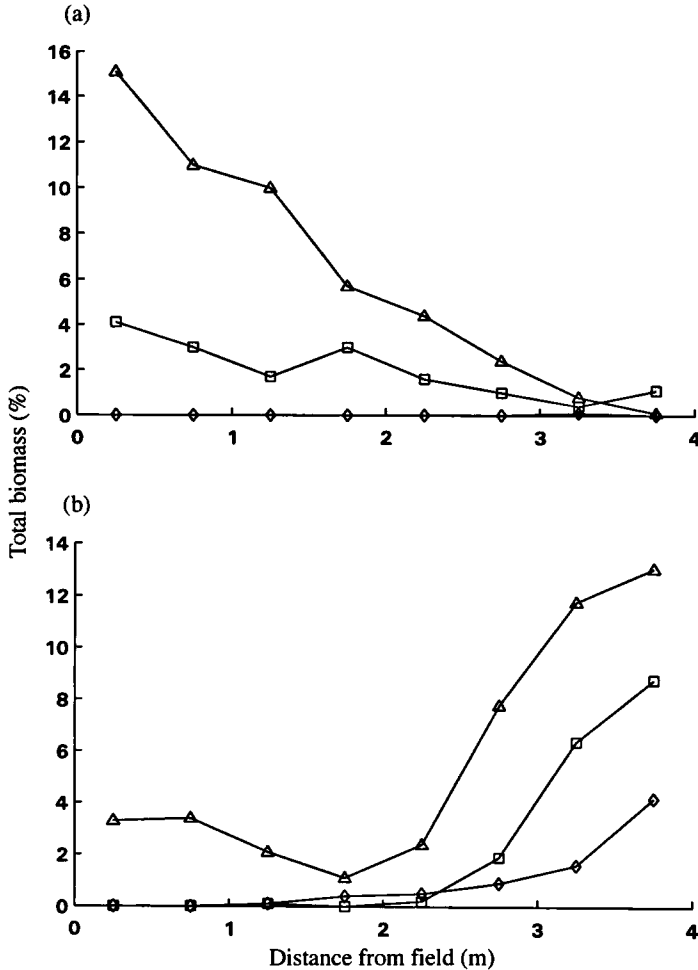


Fig. 5. Mean relative ecological performance (biomass species in subplot/total biomass in subplot \times 100%) across the experimental field boundary plots for two weedy species: (a) *Cirsium arvense* and (b) *Elymus repens*. Forbs plots: ◇; *Lolium perenne* plots: □; regeneration plots: △.

rotundifolia rather depended on capturing pulses of resources in nutrient-poor environments more efficiently. Thus, it is likely that the success of tall, competitive species in the field boundary plots is related to their ability to use nutrient resources from the arable field for increased biomass production in the boundary. *T. vulgare* indeed grew roots well over 70 cm into the arable field (Fig. 6) while its clonal growth habit may explain why the biomass increase was detectable so far from the arable field in the forbs-plots: a single clone can easily cover 1.5 m with its roots and rhizomes. Presence of these species in the forbs- and regeneration-plots and their absence in the grass-plots is probably the cause for the differential occurrence of the biomass increase in the boundary plots. The distribution pattern displayed by, for instance, *Hieracium pilosella*, an increasing mean relative performance with increasing distance from the arable field, will be the indirect result of the increase in aboveground biomass production in the zone near the arable field. In contrast to the grass species showing similar patterns (the result

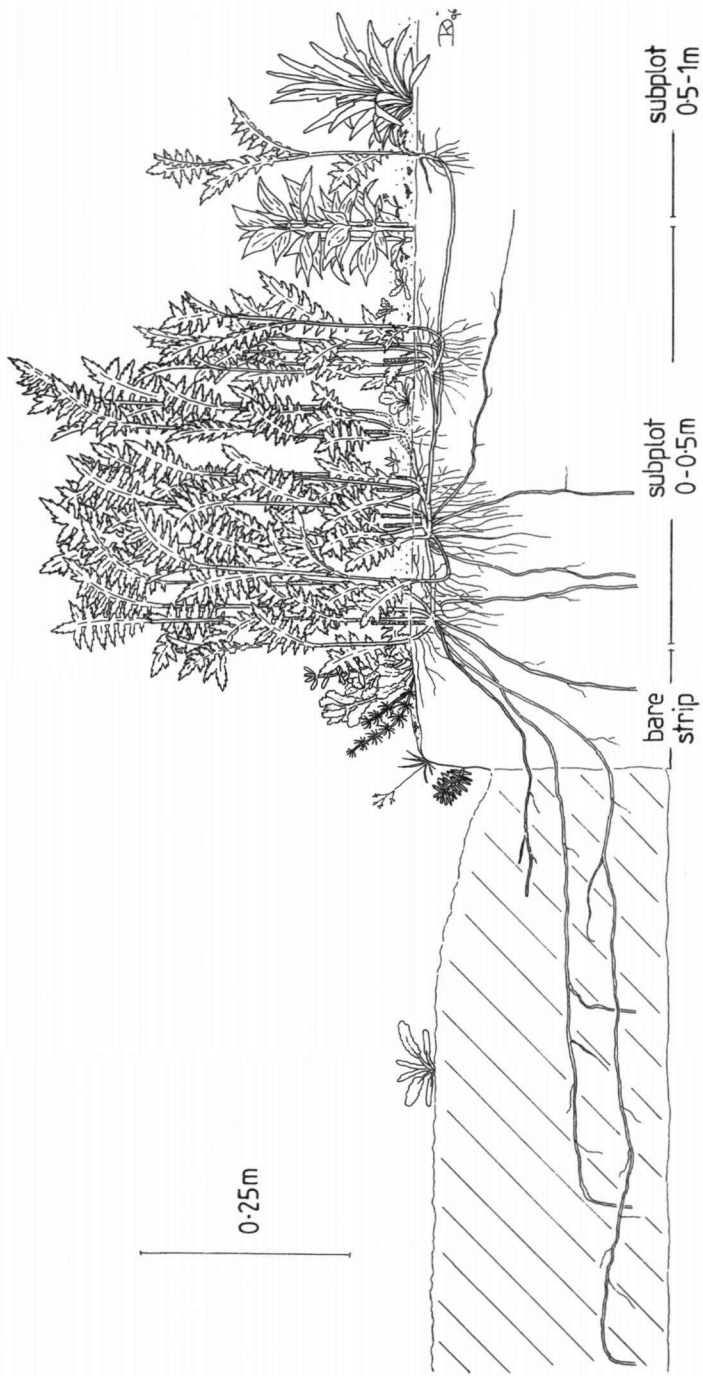


Fig. 6. Distribution of shoots, roots and rhizomes of a single *Tanacetum vulgare* plant dug out on 13 May 1996. Total vegetation is depicted aboveground while belowground only roots and rhizomes of *T. vulgare* are shown. Shaded area is the cultivated soil, ploughed on 7 March 1996.

of the steady but incomplete colonization of the boundary plots from the side of the original boundary) *H. pilosella*, like *T. vulgare*, was distributed evenly over the forbs-plots at the onset of the experiment. Being a very small and prostrate species, *H. pilosella* must have been shaded out in the zone near the arable field and only survived in the areas with the lowest biomass production.

Interpretation of the species numbers data is difficult since the vegetation within the plots is still far from stable. Species from the original boundary, predominantly grasses, are progressively moving into the boundary plots and may increase species numbers on one hand (as is most probably the case in the grass-plots) but on the other hand may decrease species numbers as a small number of grasses replace a higher number of forbs and annual species. Thus, predictions about long-term development of species-richness can not yet be made. However, within the forbs-plots with their initially high and uniform species-richness, species numbers after 3 years proved to be related to vegetation biomass production (Fig. 4). The high productivity of the vegetation near the arable field caused species numbers to decline. This may be caused by the simple fact that more small than large plants, and thus species, can grow on 0.25 m^{-2} (Oksanen 1996). It was, however, also caused by the incapability of small species such as *H. pilosella* to persist in a tall productive vegetation while tall species like *T. vulgare* were able to persist in a low productive vegetation. Most normal field boundaries are not wider than 1 m. Therefore, the vegetation biomass increase resulting from the capture of arable nutrients by a small number of dominant species may be very relevant to the low species-richness observed in most modern field boundaries.

The only weedy species with a significant abundance in the boundary plots in this experiment, *E. repens* and *C. arvensis*, are considered to be the most important boundary related weed species by farmers (De Snoo & Wegener Sleswijk 1993). In this experiment, similar to the findings of Smith & MacDonald (1992), abundance of both species was significantly higher in unsown than in sown boundary plots although they had almost opposite distribution patterns across the boundary plots (Fig. 5a–b). Abundance of these species is largely related to the absence of competition (Bakker 1960; Marshall 1990; Schmidt & Brübach 1993). Maintaining a competitive perennial vegetation therefore seems to be the best option to control these species in arable field boundaries. The use of herbicides in the field boundary vegetation, presently the most common weed control measure in field boundaries, will probably lead to an increase of either one of the species. Since no herbicides exist currently which control both species without killing the entire vegetation, killing one species will create gaps in the vegetation that benefit the other.

The most important agriculture-related factor affecting vegetation composition in this experiment was the abundance of nutrients in the arable field which benefited some species but not others. The biomass increase of a limited number of species resulted in a striking gradient in vegetation height and structure with low numbers of large plants near the arable field and high numbers of small plants near the original boundary (compare Fig. 1a and b). Indirectly species-richness was affected by the gradient in productivity of the vegetation. However, irrespective of any relationship between vegetation productivity and species-richness we could observe that species numbers only reached considerable levels when species were sown. Colonization ability of potential field boundary species was very limited and this might prove to be the most important problem in restoring field boundary diversity. It may take very long indeed before improvement of the habitat results in a more diverse habitat.

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