

Plant succession in perennial grass strips and effects on the diversity of leafhoppers (Homoptera, Auchenorrhyncha)

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Abstract

The biodiversity of agroecosystems may be enhanced by increasing species richness and structural diversity of vegetation by creating perennial strips. Aims of the study were (1) to describe the plant succession of perennial strips in northern conditions; (2) to clarify the difference in insect fauna between cereal fields and perennial strips; (3) to determine the effect of succession on leafhoppers in perennial strips; and (4) to compare the leafhopper fauna of perennial strips with that of other uncultivated biotopes. Three perennial grass strips (12 m wide, 420 m long) were sown in the middle of cereal fields (15 ha) in 1991 with a seed mixture of timothy (*Phleum pratense*), meadow fescue (*Festuca pratensis*), red clover (*Trifolium pratense*) and white clover (*Trifolium repens*). The perennial strips were not mown or renewed after the establishment. In 1992 and 1993 barley and in 1994 spring wheat were grown in the surrounding fields.

The composition of plant cover in the grass strips changed over four seasons. The total number of plant species decreased from 23 species in 1992 to 10 in 1995. The change resulted from the dramatic decrease of annual weeds after the first year. Furthermore, the total plant cover declined slightly. The cover of *P. pratense* increased, whereas that of *T. pratense* and *T. repens* decreased. The plant species typical of early succession were annual weeds including *Tripleurospermum inodorum* and *Thlaspi arvense*. In the last year, perennial weeds such as *Cirsium arvense* and *Elymus repens* became common.

Leafhopper abundance and species number were higher in perennial grass strips than in cereal fields. Furthermore, the species composition varied between habitats. Year-to-year fluctuations in leafhopper catches were large. Leafhopper abundance and diversity (Shannon index) were highest in 1993 when 192 sweep net samples contained a total 4680 specimens belonging to 37 species. The plant species richness of the grass strips did not correlate with the abundance and species richness of leafhoppers, which seemed to be more dependent on other factors. Although the plant species number in grass strips decreased clearly during succession, changes in species richness of leafhoppers were not so great. Factors affecting the leafhopper community are discussed. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Auchenorrhyncha; Biodiversity; Succession; Grass strip; Finland

1. Introduction

Intensive agriculture has changed the agricultural landscape. Crops are grown in large fields as monocultures, and natural habitats have decreased. Today, more attention is paid to the diversification of agroecosystems and different management practices, e.g.

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perennial strips, have become more and more popular (Nentwig, 1989; Thomas et al., 1992). The main purpose of the strips is to increase the numbers of natural enemies and their potential for natural control. Furthermore, the biodiversity of agroecosystem including the insect diversity is enhanced by increasing the species richness and structural diversity of plants (Murdoch et al., 1972; Lawton, 1983). A diversified plant community offers more microhabitats and facultative host species for herbivores and increases the abundance of alternative prey species for polyphagous predators (Andersson, 1990). Therefore it is supposed that strips can increase the biodiversity of fields. Another important function of perennial strips is to act as a buffer zone for decreasing erosion and leaching of nutrients.

Compared with cultivated fields, which are ecosystems maintained by human activity at an early stage of succession (Ryszkowski, 1979), perennial strips and other man-made semi-natural habitats may change during succession. A change in the species composition and structure of vegetation changes the environment of insects (e.g. microclimates, food supplies and hiding places). Therefore long-term studies concerning insect fauna and succession of strips are required.

Because it is not feasible to determine the biodiversity of the wider insect fauna in the agroecosystem, the study concentrated on leafhoppers (Hom., Auchenorrhyncha). The effects of perennial strips on polyphagous predators are presented elsewhere (Huusela-Veistola, 1998). Auchenorrhyncha is one of the best known taxa in the fields in Finland, and over 60 species occur in cereals (Raatikainen, 1971, 1972; Raatikainen and Vasarainen, 1971, 1973, 1976). Leafhoppers are an important insect group in the field ecosystem and are herbivorous (sap-feeding) and day-active insects. Most species in cereal fields are oligophagous and their main host plants are gramineous species. They damage plants directly by feeding or indirectly as vectors of a variety of plant pathogens, e.g. oat sterile dwarf virus (Raatikainen, 1970). Natural enemies include insect predators and parasitoids (Waloff, 1980), but leafhoppers are also food for many other animals, e.g. birds and shrews in the agroecosystem. Therefore, a diverse leafhopper fauna may support a greater general diversity of the agroecosystem.

The aims of the study were

1. to describe the plant succession of perennial strips in northern conditions where short growing seasons and snowy winters are typical;
2. to clarify the difference in insect fauna between cereal and grass strips (e.g. do strips increase leafhopper diversity in the field ecosystem?);
3. to determine the effect of succession on leafhoppers in perennial strips (e.g. do strips have only a short-term effect on leafhopper diversity?); and
4. to compare the leafhopper fauna of perennial strips with that of other uncultivated biotopes.

2. Materials and methods

2.1. Experimental design

The effects of perennial grass strips on the insect fauna in the cereal ecosystem were studied within the Nummela project in 1992–1995 at the Institute of Plant Protection, Agricultural Research Centre of Finland (Huusela-Veistola, 1998). In a large-scale field experiment, the effects of two pesticide regimes (conventional and reduced) and two cultivation systems (customary, integrated system) of cereal production on insect fauna were studied (Huusela-Veistola and Kurppa, 1996; Huusela-Veistola, 1996, 1998). Additional elements constituted the perennial grass strips, the purpose of which was to increase habitat diversity.

The experimental field was situated on the Nummela Experimental Farm of MTT in Jokioinen (60°52'N, 23°25'E) about 120 km north-west of Helsinki. Before the field experiment, fields were under conventional grain and grass production and cattle pasture. The perennial grass strips (12 m wide, 420 m long) were situated in the middle of cereal fields (15 ha). In practice, three individual strips were sown in 1991 with a 'green fallow seed mixture' which consisted of timothy (*Phleum pratense* L.), meadow fescue (*Festuca pratensis* Hudson), red clover (*Trifolium pratense* L.) and white clover (*T. repens* L.). The perennial strips were not mown or renewed after the establishment. A 4 m wide strip of *Phacelia tanacetifolia* Bentham was added beside the shelter belts in 1992. Sowing of the *Phacelia* strip was repeated annually. In 1992 and 1993 barley (cv. 'Arra') and in 1994 spring wheat (cv. 'Satu') were grown in

the surrounding fields. The layout of the experiment is described in Huusela-Veistola (1998).

In 1991, the leafhopper fauna from adjacent biotopes was monitored covering eight (seven in oats) sampling dates from 18 June to 7 August 1991. Samples were taken from cultivated fields (oats, oats and grass, winter wheat, grassland) as well as from uncultivated biotopes (abandoned field, headland, ditch bank, edge of forest) in Jokioinen near the strip study sites.

2.2. Botanical composition of grass strips

Each strip was divided into two blocks according to the field plot experiment when samples were taken and analysed. In July each year eight sample squares (1 m²) per block were analysed from the perennial grass strips. Percentages of total plant cover and species composition were estimated visually altogether from 16 samples per individual strip. Furthermore, plant species found outside the sample squares were listed.

2.3. Monitoring of arthropods

Leafhoppers in the grass strips and the fields were collected with sweep nets. The diameter of the net was 30 cm and one sweep net sample consisted of 60 sweeps. Four sweep net samples per block were taken from the grass strips and from cereal fields. In 1992, only one sample per block was taken from the grass strips. In 1995, only perennial strips from four blocks were swept. The distance between cereal and grass samples was 50 m. Table 1 gives details of the sampling programme.

After capture, the samples were frozen for a day and the leafhoppers were removed to 70% alcohol for storage. Leafhoppers were identified to species and polymorphic species to morphs. Because juveniles could not be identified reliably, the analysis was limited to adult catches only. *Macrostelus* sp. females could not be determined by species and they were allocated to 'separate species' in the analysis. Generally they could be divided into species in the same ratios as their males (Raatikainen and Vasarainen, 1971), but this could not be done as there were no males in the sample. The nomenclature of Auchenorrhyncha complied with Ossiannilsson (1983).

Table 1
Leafhopper sampling programme and effective temperature sum >+5°C (day degrees) in 1992–1995^a

	Sampling	Date	Effective temperature sum (dd)
1992	1	11 June	327
	2	24 June	453
	3	26 June	474
	4	06 July	566
	5	15 July	674
	6	23 July	770
	7	13 August	1005
1993	1	30 June	499
	2	09 July	575
	3	20 July	713
	4	30 July	815
1994	1	29 June	332
	2	14 July	530
	3	25 July	676
	4	12 August	937
1995	1	16 June	356
	2	30 June	503
	3	14 July	623
	4	27 July	763

^a In 1995, samples taken only from grass strips.

2.4. Statistical analyses

In the plant data, dependent variables were total plant cover, cover of individual plant species, species richness, diversity (Shannon $H' = -\sum p_i \ln p_i$ where p_i is the proportion of i th species in the pooled data) and evenness (Hill $E' = (\sum p_i^2)^{-1} / \exp H'$). Total catch of leafhoppers, species richness, abundance of individual species, diversity (Shannon H') and evenness (Hill E') were dependent variables in the leafhopper data. For statistical analysis the data was log- or arcsin(square root)-transformed as necessary to satisfy the conditions of normality and homogeneity of variances.

Effective temperature sum (>+5°C) of the growing season in southern Finland is approximately 1300 dd (day degrees). The leafhopper data was divided into two periods: early summer (0–650 dd) and later summer (650–1300 dd). Means by block period and year were used in analyses except for species richness when total species richness by block was used. The analyses were performed by the MIXED procedure of the SAS/STAT Software (Littell et al., 1996). In the

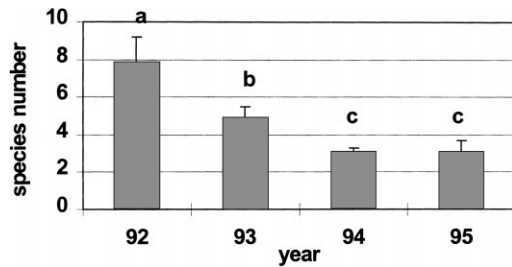


Fig. 1. Number of plant species (mean±S.D.) in perennial strips in 1992–1995. Years with different letters differed significantly, $p < 0.05$ (Tukey's test).

model, year and period were fixed factors and strip and block(strip) and their interactions were random factors. Satterthwaite's approximation was used in degrees of freedom if one of the covariance parameter estimates was zero. If the main effects were statistically significant in ANOVA, Tukey's HSD test was used to determine significances between levels.

Patterns in whole assemblages were investigated through CANOCO (Ter Braak, 1987) by applying detrended correspondence analysis (DCA) to plant and leafhopper data. DCA is a divisive ordination technique which is based on reciprocal averaging (Hill and Gauch, 1980). Before the analysis, the data was pooled by blocks.

Similarities of leafhopper communities between different habitats were studied using index of percentage similarity by Renkonen (1938) ($PS = \sum \min(p_{ij}, p_{ik})$) where p_{ij} is the proportion of species i in sample j).

3. Results

3.1. Succession of perennial strips

The composition of plant cover in grass strips changed over the four seasons. Species number decreased dramatically during succession (Fig. 1, ANOVA $df=3, 6, F=28.28, p < 0.001$). The total number of plant species in sample squares decreased from 23 species in 1992 to 10 in 1995. The change was caused by a dramatic decrease of annual weeds after the first year. Furthermore, the total plant cover decreased from 78 to 57%. The cover of *Phleum pratense* increased from 8 to 35%, whereas that of *Trifolium pratense* and *T. repens* decreased dramatically (Table 2). The nearly total disappearance of the *Trifolium* species during winter 1993–1994 was probably caused by voles (Arvo Myllymäki, personal communication, 1999). The cover of *Festuca pratensis* did not change significantly during the experiment (Table 2). Overall, the percentage of monocotyledons increased during succession (Fig. 2, ANOVA $df=3, 6, F=28.28, p < 0.001$), whereas the percentage of dicotyledons decreased (Fig. 3, ANOVA $df=3, 8, F=25.69, p < 0.001$). Generally, the plant composition of the first 2 years (1992 and 1993) differed from the last 2 years (1994 and 1995). In the last year (1995) the plant cover was dominated by *P. pratense*. Diversity (Shannon H') decreased during succession, but evenness (Hill E') did not differ among years (Table 2).

In DCA of plant data the successive years clustered clearly according to the first axes (Fig. 4). Of the sown

Table 2
Percentages of plant cover and diversity in grass strips (mean±standard deviation)^a

	Mean±S.D.				df	F	P
	1992	1993	1994	1995			
<i>Phleum pratense</i> (%)	7.6±4.5 a	16.5±3.2 a	34.3±4.8 b	34.6±7.4 b	3, 8	30.52	0.0001
<i>Festuca pratensis</i> (%)	12.0±3.4	18.1±5.5	22.8±9.1	15.0±5.6	3, 6.46	3.51	0.0834
<i>Trifolium repens</i> (%)	13.4±5.7 a	11.7±6.1 a	0±0 b	0.3±0.5 b	3, 6	43.98	0.0002
<i>Trifolium pratense</i> (%)	36.5±18.4 a	29.9±7.1 ab	6.0±9.1 bc	0.3±0.5 c	3, 7.39	9.70	0.0060
Total plant cover (%)	78.2±12.1 a	78.0±7.3 a	65.2±8.5 b	57.0±13.4 b	3, 15	15.61	0.0001
Shannon's H'	1.47±0.27 a	1.41±0.10 ab	0.98±0.14 ab	0.92±0.24 b	3, 8	6.3	0.0168
Hill's E'	0.76±0.11	0.88±0.03	0.88±0.04	0.86±0.05	3, 6	2.6	0.1478

^a Variation between years was tested by ANOVA, differences between pairs of years was tested by Tukey's test (means with the same letter are not significantly different). Satterthwaite's approximation used in degrees of freedom.

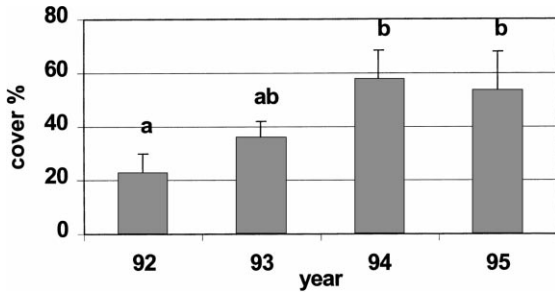


Fig. 2. Cover of monocotyledons (mean±S.D.) in perennial strips in 1992–1995. Years with different letters differed significantly, $p < 0.05$ (Tukey’s test).

species, *Trifolium* sp. were typical in the beginning and *P. pratense* dominated in the last 2 years. The plant species typical of early succession were annual weeds such as *Tripleurospermum inodorum* Shultz Bip. and *Thlaspi arvense* L. In the last year, perennial weeds including *Cirsium arvense* (L.) and *Elymus repens* (L.) became common. Two blocks clustered separately from the others in 1992. In these blocks the total plant cover was lowest and the percentage of grasses highest.

3.2. Difference in leafhopper fauna between perennial strips and cereal field

Leafhopper abundance was higher in perennial grass strips than in cereal fields, although the difference was statistically significant only in 1994 (Fig. 5). Leafhopper abundance varied among seasons. The total sum of leafhoppers was highest in 1993, when 192 sweep net samples contained a total 4680 speci-

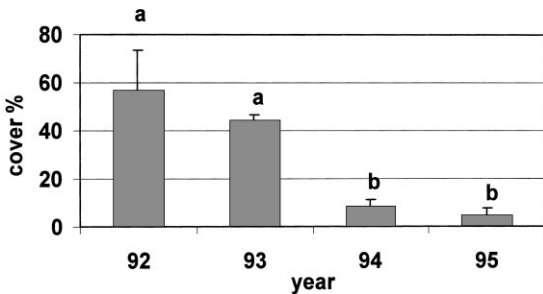


Fig. 3. Cover of dicotyledons (mean±S.D.) in perennial grass strips in 1992–1995. Years with different letters differed significantly, $p < 0.05$ (Tukey’s test).

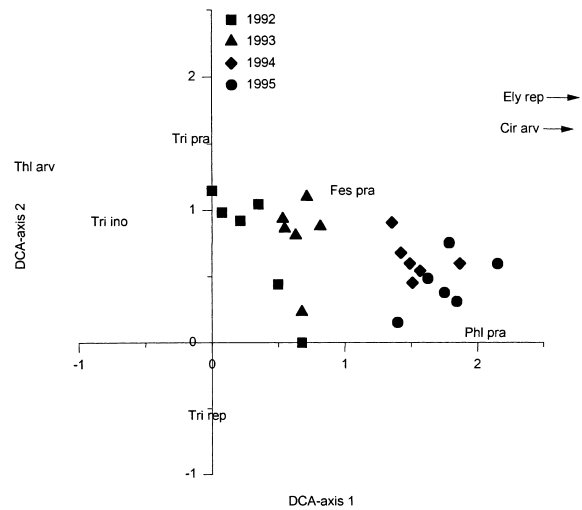


Fig. 4. Plant communities of perennial strips on the first two axes of DCA ordination. Eigenvalue of first and second axes are 0.4107 and 0.1122, respectively. Only dominant species plotted. Abbreviations for species are: Cir arv=*Cirsium arvense*, Ely rep=*Elymus repens*, Fes pra=*Festuca pratensis*, Phl pra=*Phleum pratense*, Thl arv=*Thlaspi arvense*, Tri ino=*Tripleurospermum inodorum*, Tri pra=*Trifolium pratense*, Tri rep=*Trifolium repens*.

mens belonging to 37 species. Part of the variation in species number was explained by the size of total catch (Fig. 6; 1992: $p < 0.001$, 1993: $p < 0.001$). In 1992, the species number of the strips did not differ statistically significantly from that of the fields (ANCOVA $df = 2, 9, F = 1.15, p = 0.246$). However, in 1992 less samples were taken from grass strips than from fields which may have decreased the probability of discovering rare species. In 1993, the species number in the strips was higher than in the field (Fig. 6, ANCOVA $df = 2,$

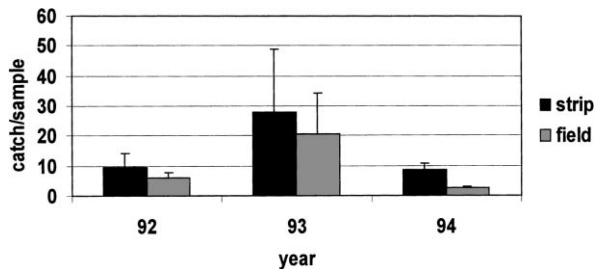


Fig. 5. Abundance of leafhoppers (mean±S.D.) in the field and in the perennial strip in 1992–1994. (Anova: 1992 and 1993 not significant, 1994: $p < 0.05$).

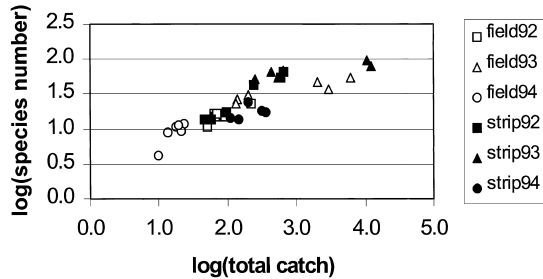


Fig. 6. Total catch and species number of leafhoppers in the field and in the perennial strip in 1992–1994.

9, $F=140.43$, $p<0.001$). In 1994, reliable comparison of species number between field and strip was not possible because interaction $\log(\text{total catch}) \times \log(\text{species number})$ was statistically significant (ANOVA $df=1, 3$, $F=16.02$, $p=0.028$) and the total catches of the strip were distinct from those of the field (Fig. 6).

Species composition varied between habitats. *Verdanus abdominalis* (F.) (35.8%), *Paluda flaveola* (Boh.) (20.2%) and *Elymana sulphurella* (Zett.) (9.9%) were the dominant species in grass strips. Field catches were dominated by *Macrostes laevis* (Rib.) (42.3%) and *Macrostes cristatus* (Rib.) (15.9%). In 1992, *Javesella pellucida* (F.), too, was common in field catches (20.4%). Eight leafhopper species which are known to be vectors of virus or mycoplasma (Raatikainen, 1970; Lindsten et al., 1970) were found

both from the grass strips and the field. However, the percentage of harmful species was clearly higher in the field catches (80%) than in the strip catches (32%).

The percentage of brachypterous morphs was higher in grass strips (1992: 69.3%; 1993: 54.7%; 1994: 52.9%) than in the field (0.9, 7.7 and 6.1%, respectively). Brachypterous forms of *Dicranotropis hamata* (Boh.) and *Megadelphax sordidulus* (Stål) occurred nearly exclusively in the grass strips. Among dimorphic species, brachypterous females dominated in the grass strips and macropterous males in the field.

Species composition of leafhoppers in the grass strips was quite similar to sweep net samples taken from adjacent uncultivated biotopes in 1991. According to Renkonen's similarity index, the leafhopper fauna of grass strips resembled that of the abandoned field, headland and edge of forest, whereas the leafhopper fauna of cereal fields resembled that of cultivated biotopes (Table 3). Table 4 presents a list of leafhopper species taken in sweep net samples from the experiment (field and strip) and adjacent biotopes.

3.3. Changes of leafhopper assemblage in grass strips

The succession of vegetation in grass strips did not greatly affect leafhopper numbers. Year-to-year fluctuations in leafhopper catches were high. Leafhopper

Table 3

Renkonen's similarity indices of leafhopper fauna in the experiment (field and strip) in 1992–1995 with leafhopper fauna of adjacent biotopes in 1991

	Field-92	Strip-92	Field-93	Strip-93	Field-94	Strip-94	Strip-95
Grass	0.296	0.478 ^a	0.263	0.230	0.297	0.219	0.175
Silage grass	0.366 ^a	0.471 ^a	0.266	0.231	0.348 ^a	0.223	0.180
Oat	0.481 ^a	0.298	0.251	0.039	0.180	0.038	0.051
Oat+grass	0.332 ^a	0.484 ^a	0.316 ^a	0.228	0.390 ^a	0.298	0.160
Winter wheat	0.361 ^a	0.338 ^a	0.227	0.022	0.153	0.016	0.036
Ditch bank	0.094	0.268	0.066	0.126	0.207	0.180	0.064
Forest edge	0.132	0.397 ^a	0.081	0.321 ^a	0.265	0.272	0.291
Abandoned field	0.112	0.448 ^a	0.054	0.264	0.249	0.286	0.122
Headland	0.170	0.596 ^a	0.108	0.377 ^a	0.426 ^a	0.437 ^a	0.297
Field-92	1	0.461 ^a	0.637 ^a	0.102	0.516 ^a	0.071	0.073
Strip-92		1	0.366 ^a	0.434 ^a	0.584 ^a	0.446 ^a	0.266
Field-93			1	0.121	0.391 ^a	0.096	0.078
Strip-93				1	0.371 ^a	0.638 ^a	0.711 ^a
Field-94					1	0.459 ^a	0.267
Strip-94						1	0.551 ^a
Strip-95							1

^a Indicate values >0.3 .

Table 4

Presence/absence table of leafhopper species in sweep samples collected from the experiment (field and strip) in 1992–1994 and from different biotopes in 1991^a

	Strip	Field	DB	H	EF	A	O	OG	G	S	W
<i>Achorotile albosignata</i> (Dahlb.)	–	+	–	–	–	–	–	–	–	–	–
<i>Aguriahana germari</i> (Zett.)	+	–	–	–	–	–	–	–	–	–	–
<i>Anoscopus flavostriatus</i> (Don.)	+	+	–	–	–	–	–	–	–	–	–
<i>Aphrodes bicincta</i> (Schrnk.)	–	–	–	+	–	–	–	–	–	–	–
<i>Aphrodes makarovi</i> Zachv.	+	–	–	–	–	–	–	–	–	–	–
<i>Arthaldeus pascuellus</i> (Fall.)	+	+	+	+	+	+	–	–	+	+	–
<i>Athysanus argentarius</i> Metc.	+	+	–	–	–	–	–	–	–	–	–
<i>Athysanus quadrum</i> Boh.	–	–	–	–	+	–	–	–	–	–	–
<i>Balclutha punctata</i> (F.)	+	+	+	+	+	+	+	–	+	+	+
<i>Cicadella viridis</i> (L.)	–	+	–	–	–	–	–	–	–	–	–
<i>Cicadula</i> sp. Zett.	+	–	+	+	+	–	–	–	+	–	–
<i>Cixius similis</i> Kbm.	–	–	–	–	+	+	–	–	–	–	–
<i>Criomorpha albomarginatus</i> Curt.	–	–	–	–	+	–	–	–	–	–	–
<i>Criomorpha</i> sp. Curt.	–	–	–	–	+	–	–	–	–	–	–
<i>Deltocephalus pulicaris</i> (Fall.)	+	+	–	+	+	–	–	–	–	–	–
<i>Dicranotropis hamata</i> (Boh.)	+	+	+	+	+	+	–	+	+	+	–
<i>Dikraneura aridella</i> (Sahlb.)	–	–	–	–	+	–	–	–	–	–	–
<i>Doliotettix lunulatus</i> (Zett.)	+	+	–	–	–	–	–	–	–	–	–
<i>Doratura stylata</i> (Boh.)	–	–	–	+	–	–	–	–	–	–	–
<i>Elymana sulphurella</i> (Zett.)	+	+	+	+	+	+	–	+	+	+	–
<i>Empoasca smaragdula</i> (Fall.)	+	+	–	–	–	–	–	–	–	–	–
<i>Eupteryx cyclops</i> Mats.	–	–	+	–	+	–	–	–	–	–	–
<i>Eupteryx origani</i> Zachv.	+	–	–	+	+	–	–	+	–	–	–
<i>Eupteryx</i> sp. Curt.	+	–	+	+	–	–	–	–	–	–	–
<i>Euscelis distinguendus</i> (Kbm.)	+	–	–	–	–	–	–	–	–	–	–
<i>Evacanthus interruptus</i> (L.)	+	+	+	–	+	–	–	–	+	–	–
<i>Graphocraerus ventralis</i> (Fall.)	+	+	–	+	+	+	–	+	–	–	–
<i>Grypotes puncticollis</i> (H.-S.)	–	+	–	–	–	–	–	–	–	–	–
<i>Idiocerus</i> sp. Lewis	–	–	+	–	–	–	–	–	–	–	–
<i>Jassargus flori</i> (Fieb.)	+	–	–	–	–	–	–	–	–	–	–
<i>Javesella discolor</i> (Boh.)	–	+	–	–	–	–	–	–	+	–	+
<i>Javesella dubia</i> (Kbm.)	+	+	–	–	–	–	–	–	+	–	–
<i>Javesella obscurella</i> (Boh.)	+	+	+	+	+	–	+	+	+	+	+
<i>Javesella pellucida</i> (F.)	+	+	+	+	+	+	+	+	+	+	+
<i>Lebradea flavovirens</i> (Gill. & Bak.)	+	+	+	–	–	–	–	–	–	–	–
<i>Macropsis</i> sp. Lew.	–	–	+	–	–	–	–	–	–	–	–
<i>Macrostes cristatus</i> (Rib.)	+	+	–	–	–	–	+	+	–	–	–
<i>Macrostes fieberi</i> (Edw.)	–	+	–	–	–	–	–	–	–	–	–
<i>Macrostes laevis</i> (Rib.)	+	+	+	+	+	–	+	+	+	+	+
<i>Macrostes septemnotatus</i> (Fall.)	–	–	+	–	–	–	–	–	–	–	–
<i>Macrostes sexnotatus</i> (Fall.)	–	+	–	–	–	–	–	–	–	–	–
<i>Macrostes</i> sp. Fieb.	+	+	–	–	–	–	–	–	–	–	–
<i>Macustus griseus</i> (Zett.)	+	–	–	–	–	–	–	–	–	–	–
<i>Megadelphax sordidulus</i> (Stål)	+	+	–	–	–	–	–	–	–	–	–
<i>Mocuellus metrius</i> (Fl.)	+	+	+	–	–	–	–	–	–	–	–
<i>Muellerianella brevipennis</i> (Boh.)	+	+	–	–	–	–	–	–	–	–	–
<i>Neophilaenus lineatus</i> (L.)	–	+	+	+	+	–	–	–	–	–	–
<i>Paluda flaveola</i> (Boh.)	+	+	+	+	+	–	–	+	–	–	–
<i>Philaenus spumarius</i> (L.)	+	–	+	+	+	+	+	–	+	–	+
<i>Planaphrodes bifasciata</i> (L.)	+	–	–	+	–	–	–	–	–	–	–
<i>Psamnotettix</i> sp. Hpt.	+	+	+	–	–	–	+	–	–	–	–
<i>Psamnotettix alienus</i> (Dahlb.)	+	+	–	–	–	–	+	–	–	–	–

Table 4 (Continued).

	Strip	Field	DB	H	EF	A	O	OG	G	S	W
<i>Psammotettix confinis</i> (Dahlb.)	+	+	–	–	–	–	–	–	–	–	–
<i>Rhopalopyx preysleri</i> (H.-S.)	+	+	+	+	–	–	–	–	–	–	–
<i>Sonronius dahlbomi</i> (Zett.)	+	–	+	–	–	–	–	–	–	–	–
<i>Stiroma bicarinata</i> (H.-S.)	+	+	+	+	+	–	–	–	+	+	–
<i>Streptanus aemulans</i> (Kbm.)	+	–	–	–	–	–	–	–	–	–	–
<i>Streptanus sordidus</i> (Zett.)	+	–	–	–	+	–	–	–	–	–	–
<i>Typhlocyba</i> sp. Germ.	–	–	+	–	–	–	–	–	–	–	–
<i>Verdanus abdominalis</i> (F.)	+	+	+	+	+	+	+	+	+	+	–
<i>Xanthodelphax stramineus</i> (Stål)	–	+	–	–	+	–	–	–	–	–	–
<i>Zycina</i> sp. Fieb.	–	–	–	–	–	–	–	–	–	–	+

^a DB=ditch bank, H=headland, EF=edge of forest, A=abandoned field, O=oat, OG=oat and grass, G=grassland, S=silage grass, W=winter wheat.

abundance was highest in 1993. There was a statistically significant interaction between period and year in abundance of leafhoppers (Fig. 7, Table 5). The abundance of leafhoppers differed between periods. Variation among years was greater in late summer.

There was a statistically significant interaction between total catch and year in terms of species richness (Table 5, Fig. 8). Part of the variation in species number was explained by the size of the total catch in 1992 and 1994, but not in 1993 and 1995. Species number was highest in 1993 and lowest in 1995. Diversity (Shannon H') was statistically different among years, highest in 1993, but evenness (Hill E') did not differ significantly between factors (Table 5).

In DCA of leafhopper data, successive years clustered, but not as in the plant data (Fig. 9). In 1992, two blocks were separated from the rest, because in these blocks the species number was higher and species

composition differed from other blocks. The same blocks also differed in plant composition in 1992 (c.f. Fig. 4). In 1992, the leafhopper fauna of grass strips resembled that of fields, because the numbers of *Macrostoteles* species were high. The other years clustered more clearly. Years 1993 and 1995 formed a separate group. In both years, *Paluda flaveola* was

Table 5
Succession of leafhopper abundance, species richness and diversity in grass strips (Anova table)^a

	df	F	P	Significance ^b
<i>Total abundance</i>				
Year	3, 4.98	6.71	0.0336	*
Period	1, 2.18	0.20	0.6968	ns
Year×Period	3, 5.38	32.81	0.0007	***
<i>Shannon H'</i>				
Year	3, 13	7.53	0.0036	**
Period	1, 10.9	0.30	0.5977	ns
Year×Period	3, 10.9	0.89	0.4758	ns
<i>Hill E'</i>				
Year	3, 10.7	0.84	0.5012	ns
Period	1, 2.77	0.29	0.6325	ns
Year×Period	3, 9.05	1.08	0.4065	ns
<i>Species richness</i>				
Log(Total catch)	1, 16	15.15	0.0013	**
Year	3, 17.5	7.12	0.0025	**
Log(Total catch)×Year	3, 18.5	5.59	0.0067	**
Period	1, 14.9	8.28	0.0116	*
Year×Period	3, 14.7	1.42	0.2761	ns

^a In analyses of species richness, log(total catch) and its interaction with year were added to the model. Satterthwaite's approximation used in degrees of freedom.

^b * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns $p \geq 0.05$.

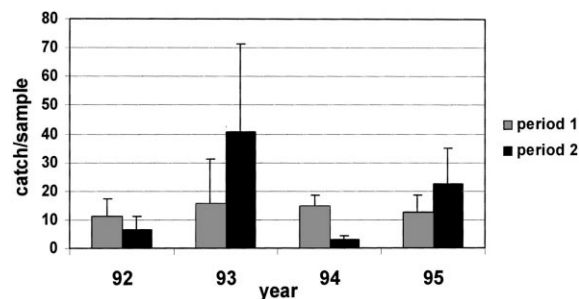


Fig. 7. Abundance of leafhoppers (mean±S.D.) in the perennial strips in 1992–1995. (Period 1=early summer, Period 2=late summer).

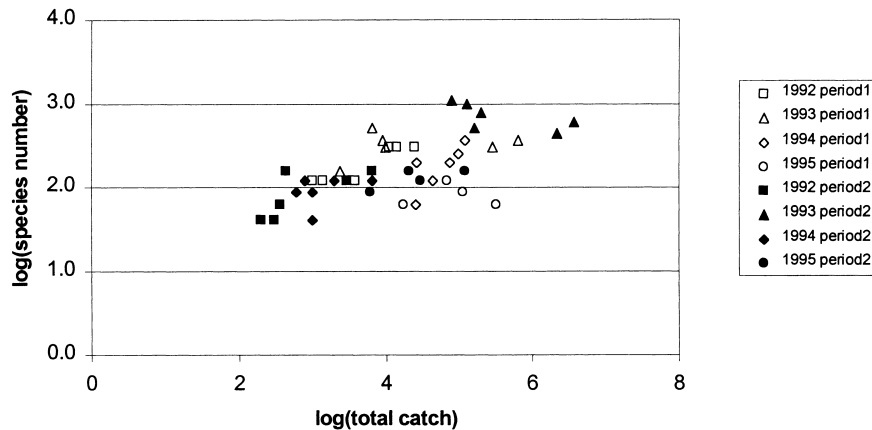


Fig. 8. Total catch and species number of leafhoppers in perennial strips in 1992–1995 (Period 1=early summer, Period 2=later summer).

the second dominant species. The leafhopper species typical of the first year were *Macrostes laevis* and *Javesella pellucida*, and in the last year *Verdanus abdominalis* and *Paluda flaveola*.

The plant species richness of the grass strips did not correlate with leafhopper abundance (Pearson

$R=-0.197$, $df=20$, $p=0.381$) or species richness ($R=0.063$, $df=20$, $p=0.780$). The number or abundance of gramineous species also did not correlate with leafhopper species number ($R=0.031$, $df=20$, $p=0.892$, $R=-0.171$, $df=20$, $p=0.445$, respectively) or leafhopper abundance ($R=-0.046$, $df=20$, $p=0.840$, $R=-0.142$, $df=20$, $p=0.530$, respectively).

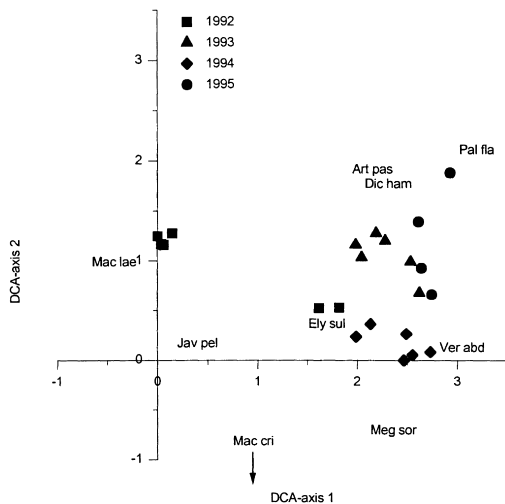


Fig. 9. Leafhopper communities of perennial strips on the first two axes of DCA ordination. Eigenvalue of first and second axes are 0.4045 and 0.1701, respectively. Only dominant species plotted. Abbreviations for species are: Art pas=*Arthaldeus pascuellus*, Ely sul=*Elymana sulphurella*, Dic ham=*Dicranotropis hamata*, Jav pel=*Javesella pellucida*, Mac cri=*Macrostes cristatus*, Mac lae=*Macrostes laevis*, Meg sor=*Megadelphax sordidulus*, Ver abd=*Verdanus abdominalis*.

4. Discussion

In the present experiment, plant diversity decreased and dominance of perennial grasses increased remarkably during succession, due in part to no mowing or managing of the strips after establishment. Overall, a species-rich and annual-dominated community is difficult to maintain for longer periods without any disturbance by mowing and resowing of plants (Wilcox, 1998). Furthermore, the nutrient rich soil of previously cropped land might affect the composition of plant species and increase the dominance of grasses. Overall, the succession of sown perennial strips resembled that of reserved (abandoned) fields (Hokkanen and Raatikainen, 1977a) although the total plant species number was lower in the strips. Hansson and Fogelfors (1998) recommended that set-aside fields on poor sites should be established by natural succession, and on fertile sites using a cover crop. They recommended mowing on poor sites to prevent invasion of woody species and on fertile sites to increase species diversity.

In spite of a decline in plant species richness during succession, the diversity of leafhoppers did not change as clearly. Overall, grass strips maintained a diverse and abundant leafhopper fauna. Therefore, leafhopper abundance and species richness seem to be more dependent on factors other than plant species richness. Although the plant species diversity in the grass strips decreased, the changes in structure of habitat were not necessarily as great. The effects of structural diversity of vegetation are often impossible to distinguish from the direct effects of plant species richness (Lawton, 1983). However, according to Andrzejewska (1979), destruction of the structure of meadows by mowing and grazing simplifies the species composition of leafhoppers, because the multilayer structure of plant cover can maintain a more diversified phytophage community. Because many grassland leafhoppers are oligophagous, feeding mainly on gramineous plants, decreasing the number of dicotyledons did not affect the species richness of leafhoppers in the grass strips. In the study of Brown et al. (1992), leafhopper assemblies were strongly affected by plant architecture, but not by plant species composition except for a few specialists. Similarly, according to Denno and Roderick (1990), structurally complex grasses, including those with thatch, may support many coexisting species of leafhoppers and other sap-feeders, and there is only little evidence of inter-specific competition. Many leafhopper species have the potential for rapid population growth, but this is usually suppressed by natural enemies (Denno and Roderick, 1990). Because many of their predators and parasitoids are polyphagous or non-specific, the enemies tend to attack grassland leafhopper species in proportion to their abundance (Waloff, 1980), which may partly maintain the high diversity of leafhoppers in grasslands. In particular, number of spiders were high in the grass strips (Huusela-Veistola, 1998).

The species composition of leafhoppers in the grass strips was quite similar to sweep net samples taken from neighbouring habitats in 1991. According to similarity indices, the leafhopper fauna of grass strips resembled that of abandoned fields, headlands and forest edges, whereas the fauna of cereal fields was quite similar to that of different crops and grasslands. Generally, the species found in grass strips were typical of meadows and grasslands. Furthermore, leafhopper communities of the grass strips resembled

assemblages dominated by *Megadelphax sordidula* in early summer and by *Verdanus* (= *Diplocolenus*) *abdominalis* in high summer, typical of older (2–6 years) reserved fields (Hokkanen and Raatikainen, 1977b). These leafhopper communities showed a fairly clear affinity for the *P. pratense* community in reserved fields (Hokkanen and Raatikainen, 1977b). *Macrosteles laevis*, which favour a poor vegetation structure (Brown et al., 1992), was common in grass strips in the first year but not thereafter.

The percentage of brachypterous morphs was clearly higher in perennial grass strips than in the field, which is in accordance with the results of Novotny (1994) where the proportion of brachypters on permanent host plants was significantly higher in undisturbed habitats than in temporary habitats (ruderal host plants). According to Brown (1982, 1986), wing polymorphism is most prevalent in species occurring during the middle stages of plant succession when long-living grasses are common, whereas early successional vegetation is exploited effectively by macropterous species. Generally the production of macropters depends on the population density and host quality. The levels of dispersal (percent macroptery) in field populations are influenced by a variety of factors including host plant architecture, habitat persistence, plant succession and resource isolation (Denno and Roderick, 1990).

Large year-to-year variation in the numbers of leafhoppers between years was also found in other long-term monitoring of farming systems nearby the experimental site (Vasarainen, unpublished data). According to Andrzejewska (1979), weather conditions play an important role in the variation between seasons, but not changes in plant biomass. Brown et al. (1992) reported substantial temporal and spatial variation in abundance of different species in leafhopper assemblies and species richness. Although they explained part of the variation by changes in vegetation structure (architecture and species composition) and by leafhoppers' life-history traits, a substantial part of the variability in leafhopper assemblies could not be explained. Overall, leafhopper populations tend to be labile and the numerical dominance of a species and the species composition of a complex may change with generations (Waloff, 1980).

Although the number of plant species in grass strips decreased clearly during succession, changes in

species richness of leafhoppers were not so dramatic. As leafhoppers favour permanent multilayer habitats, even small and simple permanent grasslands can maintain a diverse community of leafhoppers. Abundant and diverse leafhopper fauna may have a positive influence on populations of polyphagous predators such as spiders, ground beetles and rove beetles. Overall, the abundance of Diptera, Hymenoptera and Heteroptera (Huusela-Veistola and Kurppa, 1996) and especially the abundance of spiders (Huusela-Veistola, 1998) were higher in perennial grass strips than in the fields. Because the requirements of different insect species differ, many kinds of habitats should be included in the agricultural landscape if biodiversity is to be increased or maintained. Although butterflies or pollinators are dependent on diverse flowering plants (Lagerlöf et al., 1992; Dramstad and Fry, 1995; Steffan-Dewenter and Tschardt, 1997), less diverse, but permanent multilayer habitats are important for leafhoppers and spiders.

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