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Effect of early succession in wildflower areas on bug assemblages (Insecta: Heteroptera)

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Key words. Early succession, Heteroptera, species composition, species richness, annual plants, perennial plants, vegetation structure, wildflower areas

Abstract. One way of reducing the rapid decline in biological diversity in agricultural landscapes is to establish wildflower areas. The species richness and abundance of heteropteran bugs in twenty 1- to 4-year-old wildflower areas and winter wheat fields were compared, and the effects of succession in the wildflower areas investigated. Vegetation and environmental parameters (plant species richness, vegetation structure, flower abundance, field size, surrounding landscape) and their effects on bug species were explored. Total species richness and abundance of bugs were significantly lower in wheat fields than in wildflower areas but did not differ in the wildflower areas of different ages. The numbers of zoophagous bugs in the wildflower areas were positively correlated with the age of the wildflower areas. Correspondence analysis showed that the bug species composition in the winter wheat fields was very similar but strongly separated from that in the wildflower areas. The species composition of bugs in the wildflower areas became increasingly dissimilar with advancing successional age. In a partial canonical correspondence analysis, the bug assemblage was significantly associated with the number of perennial plant species, the number of annual plant species and vegetation structure, which accounted for 13.4%, 12.6% and 7.2% of the variance, respectively. As wildflower areas clearly increased heteropteran diversity on arable land and bug species composition changed with increasing successional stage, the establishment of a mosaic of wildflower areas of different age is recommended as it enables the survival of heteropteran bugs with different life history traits.

INTRODUCTION

Due to the intensification of agriculture in recent decades and the rapid change in landscape structure, biological diversity in agricultural landscapes has declined (Tscharntke, 1998; Marshall & Moonen, 2002). While arable field size and crop yield have increased there has been a loss or reduction in the size and an increasing isolation of semi-natural and natural biotopes (Harrison & Bruna, 1999). Natural areas adjacent to arable crops are essential for animals since they provide refuges for hibernation and transition zones between habitats on arable land (Wiedemeier & Duelli, 1999). Several methods are now being introduced to counteract this rapid decline in biological diversity. In the European Union, set-aside programmes have been established to enhance the animal and plant diversity of farmland and prevent overproduction of crops (Kleijn et al., 2001). Apart from its economic aspects, set-aside is considered an important contribution to nature conservation in agroecosystems (Corbet, 1995). Swiss agricultural policy subsidizes various types of ecological compensation areas where farmers apply specific forms of management (e.g. extensively managed grasslands, hedges, orchards, conservation headlands, wildflower areas).

This study focuses on bug assemblages (Heteroptera) in winter wheat fields (*Triticum aestivum* Linnaeus), the most frequently cultivated crop in Switzerland, and in 1- to 4-year-old wildflower areas, one type of ecological compensation area. Since wildflowers attract high numbers of beneficial arthropods, like hoverflies (Syrphidae), ladybirds (Coccinellidae), staphylinid beetles (Staphylinidae) and carabid beetles (Carabidae) (Heitzmann & Nentwig, 1993; Frank, 1999; Frank & Reichhart, 2004), they not only enhance biological diversity but also enhance the biological control of agricultural pests by increasing the diversity and abundance, as well as the reproduction and nutritional condition of beneficial arthropods (Lys & Nentwig, 1992; Barone & Frank, 2003). While arthropod diversity generally increases with habitat age from early to late successional stages (Brown & Southwood, 1983; Siemann et al., 1999), effects of succession on insect diversity over four years in wildflower areas have not been previously investigated.

Investigating the influence of vegetation parameters and environmental constraints on insect diversity in wildflower areas can be used to quantify the effect of attempts to enhance biodiversity in agricultural landscapes. While colonization is the dominating process in the initial phase of a secondary succession, environmental constraints, changes in plant communities and internal dynamics soon gain in importance and determine the species composition of arthropod communities (Steffan-Dewenter & Tscharntke, 1997; Belyea & Lancaster, 1999). For example, both spider abundance and species richness are positively correlated with vegetation height and density in field margins (Baines et al., 1998). Southwood et al. (1979) reported an initial increase in richness of plants and bugs (Heteroptera) in the early stages of secondary

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TABLE 1. The total numbers of adult individuals (ind) and species (sp) of the different families of bugs occurring in winter wheat fields (ww) and in 1- to 4-year-old wildflower areas (wa1–4). Numbers are for four samples per site. *n* = number of sites per habitat type.

Family	all sites (n = 20)		wheat ww (n = 4)		wildflower areas wa1 (n = 4)		wa2 (n = 4)		wa3 (n = 4)		wa4 (n = 4)	
	ind	sp	ind	sp	ind	sp	ind	sp	ind	sp	ind	sp
Anthocoridae	65	3	8	1	25	3	7	3	18	3	7	1
Coreidae	7	1	0	0	4	1	2	1	1	1	0	0
Cydnidae	2	1	0	0	1	1	0	0	0	0	1	1
Lygaeidae	37	6	0	0	1	1	24	2	6	2	6	4
Miridae	1919	28	33	7	163	17	602	17	699	15	422	17
Nabidae	94	8	6	3	7	4	7	4	18	4	56	6
Pentatomidae	42	9	3	2	23	4	8	4	3	2	5	4
Piesmatidae	40	1	0	0	36	1	3	1	1	1	0	0
Rhopalidae	74	4	0	0	4	4	10	2	36	2	24	2
Saldidae	1	1	0	0	0	0	1	1	0	0	0	0
Scutelleridae	4	2	1	1	0	0	1	1	0	0	2	1
Sum	2285	64	51	14	264	36	665	36	782	30	523	36

succession following fallow, and inferred that the greater structural diversity of the vegetation in the later stages is important in keeping numbers of bug species high, while the numbers of plant species decreased. Furthermore, plant species diversity is a determinant of arthropod diversity in different types of semi-natural habitats (Brown & Southwood, 1983; Sanderson, 1992; Greiler, 1994; Siemann et al., 1998; Di Giulio et al., 2001). In wildflower areas, bug species richness and abundance are positively correlated with the number of perennial plant species (Ullrich, 2001).

Heteroptera are an ideal indicator group for insect diversity because (i) both nymphs and adults live in the same habitat and respond to changes in botanical diversity (Otto, 1996) and (ii) are an ecologically very diverse group including both phytophagous and zoophagous species with different degrees of food specialization, mobility and kinds of life cycle (Dolling, 1991).

The goals of this investigation were (i) to determine bug species richness and abundance in winter wheat fields and 1- to 4-year-old wildflower areas as well as the successional trends in species richness and abundance, (ii) to compare the similarity of bug species composition in winter wheat fields and wildflower areas of different ages and (iii) to identify vegetation and environmental parameters affecting bug assemblage. This was done to provide new information for policy makers managing schemes establishing semi-natural habitats in agricultural landscapes.

MATERIAL AND METHODS

Research area and study sites

The study was carried out from May to August 2001 around Bern (Swiss plateau) and Solothurn (Bucheggberg), an intensively used arable region in Switzerland. The research area is about 500 km^2, with maximum dimensions north – south of 27 km and east – west of 19 km. Sixteen wildflower areas of four ages (four replicates of each) were studied: 1-year-old areas were sown at the beginning of May 2001, 2- to 4-year-old areas were sown in April 1998 to 2000. Wildflower areas (a term synonymous with wildflower or weed strips) either run through or along the edge of an arable field and had a minimum width of 3 m; they were sown with a recommended mixture of indigenous arable weeds, meadow and ruderal plant species (Günter, 2000), but not fertilized or treated with pesticides. They were maintained for two to six years and from the second year on, one half of each area was mown in rotation yearly after the flowering period. We were not able to study wildflower areas older than four years because from the fourth year onwards grassy vegetation begins to dominate and farmers usually remove them. All the wildflower areas were adjacent to crop fields and established where cereals were grown previously. The most frequently cultivated crop in Switzerland, winter wheat (*T. aestivum*) was used as a control. The four wheat fields sampled were sown in October 2000 with maize (*Zea mays* Linnaeus) as the previous crop. None of the wheat fields were sprayed with insecticides. The minimum distance between two study sites was 500 m. The twenty study sites were in the same climate zone providing similar site conditions in terms of altitude, mean annual rainfall and temperature. The wildflower areas of different ages and the winter wheat fields were intermingled within the research area to avoid spatial autocorrelation. Their size ranged from 0.22 to 2.7 ha with a mean of 0.8 ha. The five habitat types did not differ significantly in size (ANOVA: F = 2.73, P = 0.069, n = 20).

Methods used to sample bugs

Samples were taken on four occasions between the beginning of May and mid-August 2001. Only the uncut part of the wildflower areas was sampled and sampling was restricted to periods when conditions were favourable for bug activity, i.e. periods between 10:00 a.m. and 17:30 p.m. when the minimum air temperature was 15°C, it was sunny and not windy, and the vegetation was dry. The order in which the fields were sampled was not always the same. The heteropteran bugs were collected using a standardised sweep-net method (Otto, 1996). The sweep-net had a diameter of 40 cm and was fitted with a heavy cloth net suitable for use in coarse vegetation. Each sample consisted of 100 sweeps made through the vegetation at a constant pace along a transect of about 80 m. The net was emptied after

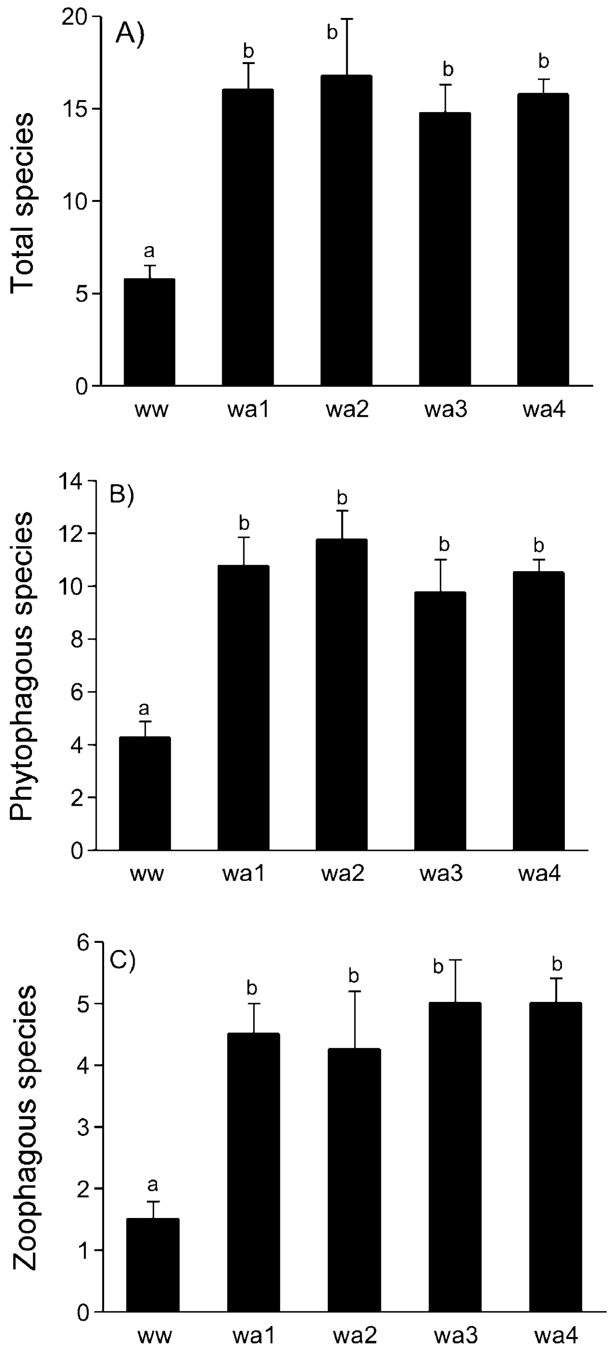

Fig. 1. Mean ± SE number of A) total bug species, B) phytophagous bug species and C) zoophagous bug species in winter wheat fields (ww) and 1- to 4-year-old wildflower areas (wa1–4). Different letters denote significant differences (Tukey's honestly significant difference [HSD] test, $P < 0.05$, $n = 20$).

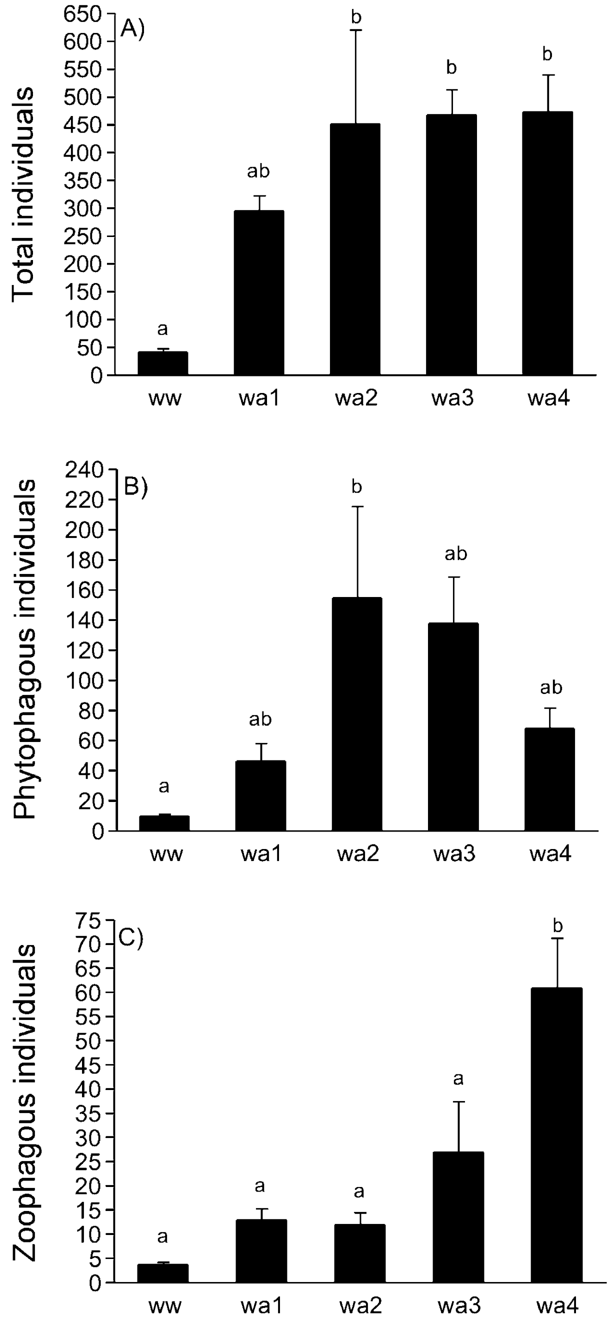

Fig. 2. Mean ± SE number of A) total bug individuals, B) phytophagous bug individuals and C) zoophagous bug individuals in winter wheat fields (ww) and 1- to 4-year-old wildflower areas (wa1–4). Different letters denote significant differences (Tukey's HSD test, $P < 0.05$, $n = 20$). Note that for A) larvae were included, and for B) and C) larvae were excluded.

every 25th sweep and the bugs were killed immediately with diethylether ($C_4H_{10}O$).

The minimum distance of a transect from the field edge was 3 m, in narrow areas 2 m. The first and second transects ran parallel to one another with the inner one 3 m from the field edge. The following two samples were taken in a prolongation of the first and second transect. The abundance (total number of adults and larvae per site), species richness (total number of adult bug species per site) and species composition based on the number of individuals per species at each site, were analysed. Bug larvae from the first sample were too small for identification and were not taken into account. Based on the information on species ecology in the literature (Wachmann, 1989; Di Giulio et al., 2000), zoophagous (i.e. predators including phyto-zoophagous) and phytophagous species were identified and analysed separately. For the analyses of trophic groups only adult bugs were used. Bugs were determined using entomological handbooks and publications (Wagner, 1952, 1966, 1967, 1970; Stichel,

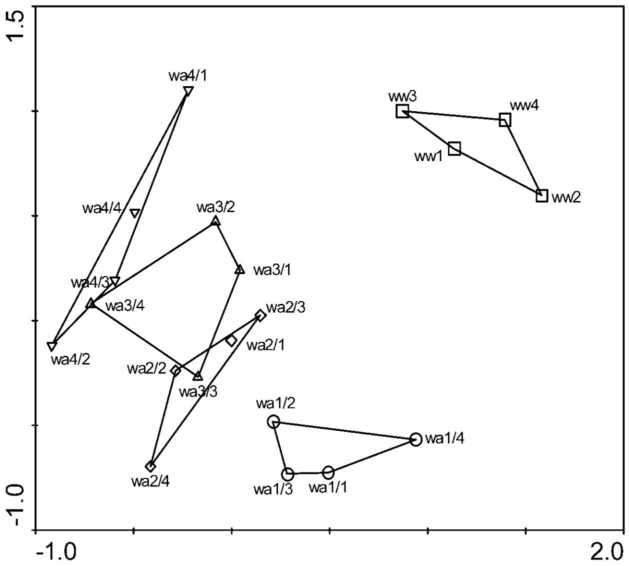

Fig. 3. Correspondence analysis (CA) ordination to compare the similarity of bug species composition in winter wheat fields (□ ww), 1-year-old wildflower areas (○ wa1), 2-year-old wildflower areas (◇ wa2), 3-year-old wildflower areas (△ wa3) and 4-year-old wildflower areas (▽ wa4). The four replicates from each habitat type are enveloped to make similarities among habitat types more apparent. The replicates are indicated by numbers following the symbol for habitat type (ww, wa1–4).

1955–1962; Rieger, 1978, 1985; Péricart, 1987, 1999a,b,c) and the nomenclature follows Günther & Schuster (2000).

Vegetation and environmental parameters

In order to determine the influence of vegetation on the bug assemblage plant species richness, flower abundance and vegetation structure were analysed. Plant species richness was mapped once in June 2001 on five 4 m × 4 m squares located regularly in each sampling area. The plant species were separated into annual and perennial species and used for data analyses. Flower abundance and vegetation structure were surveyed five times during the bug sampling period. The sample sites were located every 2 m along a 50 m transect, resulting in 26 sub samples. Flower abundance was estimated in 30 cm × 30 cm squares using the following scale: 0 = 0 flowers, 1 = 1–25, 2 = 26–50, 3 = 51–75, 4 = 76–100, 5 = >100 flowers / 900 cm^2. A modified point quadrat method was used to investigate vegetation structure. This quantitative method is widely used to measure plant cover, which is a good criterion for estimating vegetation changes (e.g. Mueller-Dombois & Ellenberg, 1974; Greig-Smith, 1983). The point quadrat technique is suitable for sampling meadows of high structural complexity and species diversity (Stampfli, 1991), but not for the coarse vegetation of wildflower areas. Furthermore, we were interested in the structural complexity of the vegetation not in plant species composition. Thus we simplified the point quadrat method in three ways: (i) the sampling was carried out along a transect, (ii) a 150 cm long iron rod, measuring 8 mm in diameter, was used instead of a needle and (iii) individual plant species were not taken into account. The iron rod was marked at 15 cm (soil level), 55 cm (40 cm mark), 95 cm (80 cm mark) and 135 cm (120 cm mark). It was inserted 15 cm vertically into the soil and every plant that was in contact with the rod was counted, beginning at the top. Between two marks, it was difficult to record more than 15 contacts in dense grassy vegetation. For the analyses, the arithmetic mean of the plant parts touching the iron rod in the five sub samples, each consisting of 26 replicates was used.

The field size and surrounding landscape were mapped in June 2001. The latter was surveyed by measuring the area of semi-natural landscape (extensively managed meadows, wildflower areas, ruderal sites, orchards, hedges, woodlands, single trees) in a 150 m strip around each site. Field size and percentage of the area of adjoining landscape that was semi-natural were used in the statistical analyses.

Statistical analyses

For the analyses of the data, all samples were pooled, resulting in one sample per site. To achieve normal distribution and homogeneity of variance (Zar, 1996), flower abundance, field size, and the number of zoophagous and phytophagous bugs were log_{10}-transformed and percentage of semi-natural landscape was arcsine-square root transformed. One-way-ANOVA was conducted using the programme Systat 10.0 to ascertain differences in bug species richness and abundance, and in vegetation and environmental variables among habitat types. Tukey's honestly significant difference (HSD) test was carried out for multiple comparisons. Spearman's correlation coefficient was used to test for successional trends in bug species richness and abundance. For that, wheat fields were excluded from the analysis because they were not considered as part of the succession. In addition, multivariate statistics were performed to characterize the bug assemblage in the different areas using the programme Canoco 4.5 (Ter Braak & Šmilauer, 2002). Species represented by less than five individuals were omitted to minimise random effects and sampling errors (Pfiffner & Luka, 2003). Multivariate statistics were performed using log_{10}-transformed species data and without downweighting of rare species. Ordination by correspondence analysis (CA) was used to compare the similarity of the bug species composition in the winter wheat fields and wildflower areas of different ages. The influence of all vegetation and environmental parameters on the bug assemblage was analysed using canonical correspondence analysis (CCA). Thereafter, a partial CCA was performed with those parameters that significantly accounted for any of the variance. The amount of the variance explained by each parameter was calculated separately, after eliminating the variance due to the other (partialled) parameters, which were used as covariables (Borcard et al., 1992). The significance of each parameter in the partial CCA was obtained by a Monte Carlo test run with 499 permutations.

RESULTS

Bug species richness and abundance in the wildflower areas of different ages

Altogether 6887 individuals consisting of 2285 adults and 4602 larvae of 64 bug species were recorded (Table 1), including one specimen of the lygaeid *Emblethis denticollis* Horváth, found in a 1-year-old wildflower area, which has not previously been recorded for Switzerland (Günther et al., 1982; Péricart, 1987; Günther & Schuster, 2000). The total numbers of species of bugs and of phytophagous and zoophagous species were significantly lower in wheat fields than in 1- to 4-year-old wildflower areas, with no differences among 1- to 4-year-old wildflower areas (Fig. 1A–C). The total number of bugs per site differed between wheat and 2- to 4-year-old wildflower areas, but there was no significant difference in bug abundance between 1- to 4-year-old wildflower areas

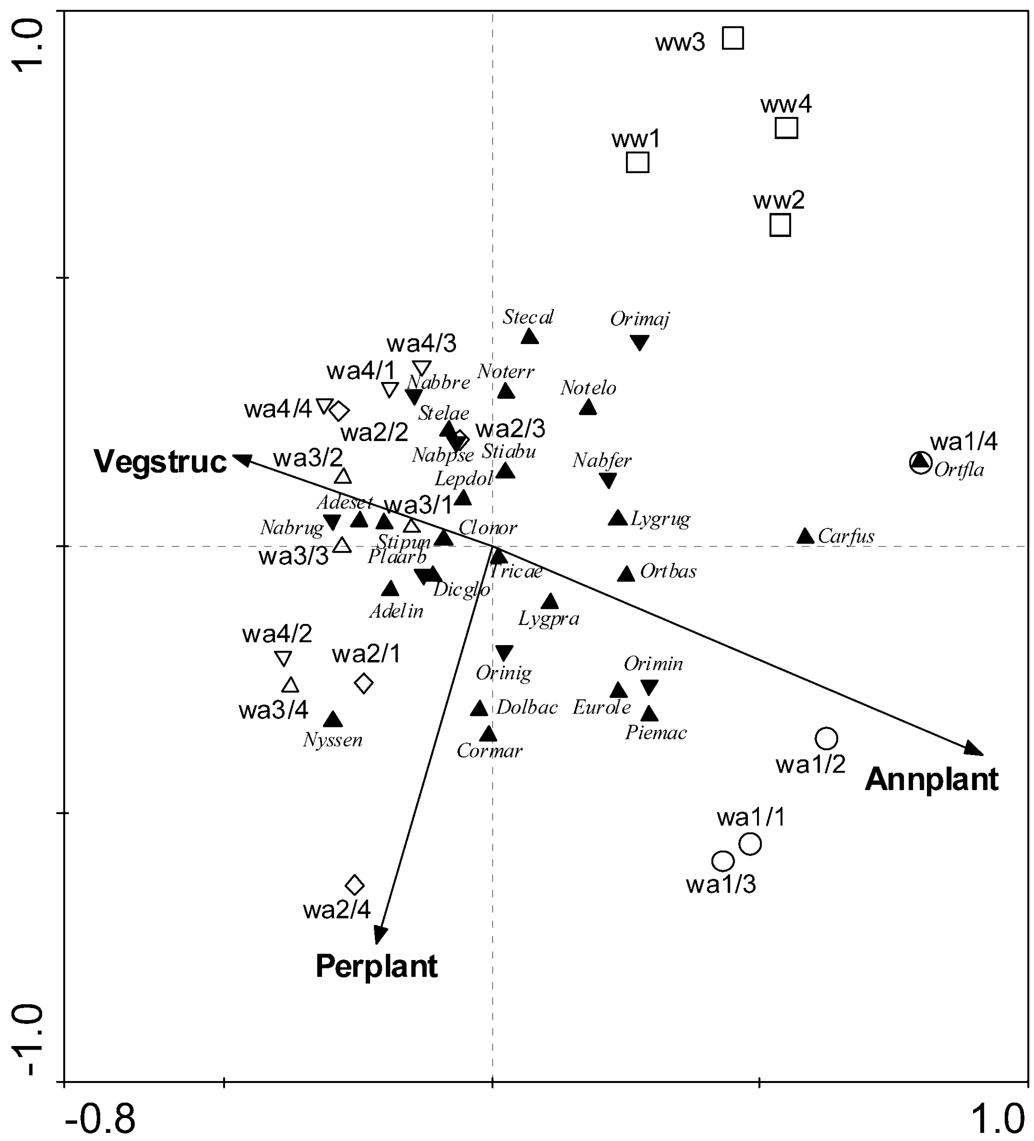

Fig. 4. Partial canonical correspondence analysis (CCA) ordination showing the influence of perennial plant species richness (Perplant), annual plant species richness (Annplant) and vegetation structure (Vegstruc) on phytophagous (▲) and zoophagous (▼) bug species, in the different habitat types (symbols as in Fig. 3). For species abbreviations see Table 2.

and between wheat fields and first year wildflower areas (Fig. 2A). While the abundance of phytophagous bugs was highest in 2-year-old wildflower areas and seemed to be less in 3- and 4-year-old areas, zoophagous individuals appeared to continuously increase from 2- to 4-year-old areas (Fig. 2B–C). The number of zoophagous bug individuals was positively correlated with the age of wildflower areas (Spearman $r_s = 0.70$, $P = 0.003$, $n = 16$).

Characterization of bug assemblages

In the correspondence analysis (CA) the cumulative percentage explained by the first two axes was 35.3%. The bug species present in the winter wheat fields were very similar but strongly separated by axis 1 from those in 1-year-old wildflower areas, and by axis 2 from those in the older wildflower areas (Fig. 3). The similarity in bug species composition decreased with the age of the wildflower areas, i.e. the youngest and oldest areas differed the most. The canonical correspondence analysis (CCA) model, which included all vegetation and environmental parameters, explained 45.1% of the total variance in bug assemblage. The three vegetation parameters that significantly contributed to the model (numbers of perennial and annual plant species, and vegetation structure) were introduced in a partial CCA to rank them according to explained variance. The number of perennial plant species explained 13.4% ($F = 3.15$, $P = 0.002$), the number of annual plant species 12.6% ($F = 2.95$, $P = 0.002$) and vegetation structure 7.2% of the variance ($F = 1.70$, $P = 0.016$). The results of the partial CCA ordination are presented in Fig. 4. A further CCA model including all vegetation and environmental parameters, but not discriminating between annual and perennial plant species, explained 31.4% of the total variance of the bug assemblage. The only significant explanatory parameter was the number of plant species, which accounted for

TABLE 2. Number of individuals of the most abundant bug species in winter wheat fields (ww) and 1- to 4-year-old wildflower areas (wa1–4). The abbreviations are those used in Fig. 4.

Family, species	Abbreviation	ww	wa1	wa2	wa3	wa4	Total
ANTHOCORIDAE							
Orius majusculus Reuter	*Orimaj*	8	2	2	2	0	14
Orius niger Wolff	*Orinig*	0	7	3	13	7	30
Orius minutus Linnaeus	*Orimin*	0	16	2	3	0	21
COREIDAE							
Coreus marginatus Linnaeus	*Cormar*	0	4	2	1	0	7
LYGAEIDAE							
Nysius senecionis Schilling	*Nyssen*	0	0	23	5	2	30
MIRIDAE							
Adelphocoris lineolatus Goeze	*Adelin*	0	1	25	3	46	75
Adelphocoris seticornis Fabricius	*Adeset*	0	0	3	11	28	42
Closterotomus norwegicus Gmelin	*Clonor*	2	10	47	294	54	407
Dicyphus globulifer Fallén	*Dicglo*	0	20	412	201	69	702
Leptopterna dolobrata Linnaeus	*Lepdol*	0	1	1	5	5	12
Lygus pratensis Linnaeus	*Lygpra*	1	23	15	10	1	50
Lygus rugulipennis Poppius	*Lygrug*	10	50	5	8	2	75
Notostira elongata Geoffroy	*Notelo*	1	1	0	0	19	21
Notostira erratica Linnaeus	*Noterr*	3	1	1	1	10	16
Orthops basalis Costa	*Ortbas*	0	3	6	0	0	9
Orthotylus flavosparsus Sahlberg	*Ortfla*	0	28	0	0	0	28
Plagiognathus arbustorum Fabricius	*Plaarb*	0	18	23	121	178	340
Stenodema calcarata Fallén	*Stecal*	13	0	2	4	1	20
Stenodema laevigata Linnaeus	*Stelae*	3	0	5	36	2	46
Trigonotylus caelestialium Kirkaldy	*Tricae*	0	2	51	1	0	54
NABIDAE							
Nabis brevis H. Scholz	*Nabbre*	0	0	1	0	20	21
Nabis ferus Linnaeus	*Nabfer*	1	3	3	0	0	7
Nabis pseudoferus Remane	*Nabpse*	4	2	2	10	18	36
Nabis rugosus Linnaeus	*Nabrug*	0	0	0	5	15	20
PENTATOMIDAE							
Carpocoris fuscispinus Boheman	*Carfus*	2	5	0	0	0	7
Dolycoris baccarum Linnaeus	*Dolbac*	0	4	3	2	2	11
Eurydema oleracea Linnaeus	*Eurole*	0	13	3	0	1	17
PIESMATIDAE							
Piesma maculatum Laporte	*Piemac*	0	36	3	1	0	40
RHOPALIDAE							
Stictopleurus abutilon Rossi	*Stiabu*	0	1	1	3	1	6
Stictopleurus punctatonervosus Goeze	*Stipun*	0	1	9	33	23	66

11.8% of the variance ($F = 2.41$, $P = 0.004$). Thus, it was justified to calculate the numbers of species of annuals and perennials separately in order to get more information about the response of certain bug species to plant species richness. Of the most abundant bug species, *Stenodema calcarata* Fallén and the predatory *Orius majusculus* Reuter mainly occurred in winter wheat fields (Table 2) and were negatively associated with perennial plants, which were rarely observed in wheat fields (Table 3). *Piesma maculatum* Laporte, *Eurydema oleracea* Linnaeus, *Orius minutus* Linnaeus, *Carpocoris fuscispinus* Boheman and *Orthotylus flavosparsus* Sahlberg were positively correlated with annual plants (Fig. 4). The number of annual plant species was by far the highest in 1-year-old wildflower areas (Table 3), which were closely related to annuals (Fig. 4). The above species, together with *Lygus pratensis* Linnaeus and *L. rugulipennis* Poppius, comprised a group of species whose abundance within the wildflower areas decreased significantly in the older areas (Spearman $r_s \geq -0.565$, $P \leq 0.023$, $n = 16$). Other species were associated with perennial plant species (e.g. *Nysius senecionis* Schilling, *Coreus marginatus* Linnaeus, *Dolycoris baccarum* Linnaeus, *Orius niger* Wolff) and vegetation structure (e.g. *Adelphocoris seti-*

TABLE 3. Vegetation parameters significantly explaining variance in bug assemblage: mean ± SE number of annual plant species, perennial plant species and vegetation structure in winter wheat fields (ww) and 1- to 4-year-old wildflower areas (wa1–4). Different letters in the same line denote significant differences (Tukey' s HSD test, $P < 0.05$, $n = 20$).

Vegetation parameter	ww	wa1	wa2	wa3	wa4
Annual plant species	10.75 ± 1.65 a	24.00 ± 0.91 b	6.25 ± 1.80 ac	3.25 ± 0.63 c	2.50 ± 0.50 c
Perennial plant species	4.75 ± 1.11 a	23.25 ± 2.50 b	26.00 ± 3.11 b	20.25 ± 1.93 b	20.75 ± 2.29 b
Vegetation structure	4.21 ± 0.29 a	6.57 ± 0.75 ab	9.75 ± 1.21 b	7.21 ± 1.26 ab	9.29 ± 0.79 b

cornis Fabricius, *Nabis rugosus* Linnaeus, *N. brevis*; Fig. 4), which was significantly lower in winter wheat fields than in the 2- and 4-year-old wildflower areas (Table 3). There was a group of species that were more abundant in the older wildflower areas than in younger wildflower areas and wheat fields, and increased in abundance in older wildflower areas (*Plagiognathus arbustorum* Fabricius, *Closterotomus norwegicus* Gmelin, *A. seticornis*, *Nabis pseudoferus* Remane, *Stictopleurus punctatonervosus* Goeze). Except for *C. norwegicus*, these species were significantly positively correlated with successional age ($r_s \geq 0.596$, $P \leq 0.015$, $n = 16$). Finally, two zoophagous species were restricted to the older wildflower areas (*N. brevis*, *N. rugosus*; Table 2), of which the latter species was significantly positively correlated with habitat age ($r_s = 0.760$, $P = 0.001$, $n = 16$).

DISCUSSION

There was a greater species richness and abundance of bugs in wildflower areas than in winter wheat fields. The species richness and abundance of heteropteran bugs did not differ significantly in the wildflower areas of different ages. Correspondence analysis (CA), however, revealed clear distinctions and showed that the bugs in winter wheat fields were similar but distinct from those in the wildflower areas. In the wildflower areas the bugs differed increasingly with increasing age of the areas. Thus, the use of multivariate statistics revealed information on the species composition of the bugs that are not apparent when only species richness or abundance are considered (Jeanneret et al., 1999). The exploration of 1- to 4-year-old wildflower areas within the same year was performed with space-for-time substitution. This method is not applicable when the past has unsuspected effects (Pickett, 1989). By exploring successional effects over a short period of time we ruled out such effects. Space-for-time substitution is used most successfully in systems acknowledged to have strong successional dynamics. As plant recruitment in wildflower areas is known to exhibit clear successional patterns (Günter, 2000), space-for-time substitution is an appropriate method for investigating changes in the species composition of bugs in wildflower areas.

Wheat fields were characterized by highly mobile and ubiquitous species such as *O. majusculus* and *S. calcarata*, which frequently occur on several grasses and crops (Afscharpour, 1960; Wagner, 1967; Wachmann, 1989). The mirid species dominating in the first year of succession were generalists that tend to occur also in wheat fields, e.g. *L. pratensis* or *L. rugulipennis* (Afscharpour, 1960). *Orthotylus flavosparsus*, *E. oleracea*, *O. minutus, C. fuscispinus* and *P. maculatum* were most abundant in the first year of succession in wildflower areas, indicating they are pioneer species. In 3- and 4-year-old wildflower areas more oligophagous or specialised species and species overwintering as eggs were recorded, e.g. *Dicyphus globulifer* Fallén, *Adelphocoris lineolatus* Goeze, *C. norwegicus* or *P. arbustorum* (Wagner, 1952, 1970). Brachypterous to submacropterous forms of zoophagous species, e.g. *N. brevis* and females of the phytophagous mirid *Leptopterna dolobrata* Linnaeus, were moderately abundant in 3- and 4-year-old wildflower areas and less frequently found in young successional stages. Because of their low mobility, they are probably unable to colonise wildflower areas in the first year (Ullrich, 2001).

The abundance of zoophagous bugs increased significantly with increasing age of wildflower areas. This emphasizes the importance of habitat age for natural enemies and possible biological control potential of ecological compensation areas in agroecosystems. By contrast, we did not find any response to successional stage in either total or phytophagous bug abundance, or species richness. Compared with other research on Heteroptera in wildflower areas (Ullrich, 2001), age seemed to be less important in determining total bug species richness and abundance during early succession. Similarly, there is little evidence of early successional change in hemipteran fauna and butterflies (Sanderson, 1992; Steffan-Dewenter & Tscharntke, 1997). Possible reasons for this are differences between regions or in the life history traits of the species studied, e.g. dispersal ability or response to host plant features (Steffan-Dewenter & Tscharntke, 1997). Baines et al. (1998) assume that changes in abundance and species richness of spiders are likely to become detectable over a longer time period, a hypothesis which is supported by White & Hassall (1994) who recorded a clear increase in density and species richness of spiders between one and ten years after fallowing a site.

The bug assemblage was best explained by the numbers of perennial and annual plant species. This indicates that the bug species that are abundant in 1- year-old wildflower areas characterized by annual plants, are different from those occurring in older successional stages with mainly perennial plants. The presence of certain bug species that have a close association with annual plants may be used as an indicator of 1-year-old wildflower areas, which contain significantly more annual plant species than 2- to- 4-year-old areas and winter wheat fields. Our finding that perennial plant species richness can be used to predict bug species composition is supported by other studies on insects and spiders (Tscharntke & Greiler, 1995; Borges & Brown, 2001). Most specialised species of bugs feed on perennial host plants, so preferences for perennial plants as forage emphasize the positive relationship between certain species of bugs and the number of perennial plant species (Ullrich, 2001). In addition, the most abundant bug species in wildflower areas are known to hibernate as eggs and are dependent on their food plants overwintering on the site for development in spring, as they are unable to feed on annuals (Wagner, 1952, 1966; Ullrich, 2001). This hypothesis is supported by our results, since some bug species that hibernate as eggs (e.g. *A. seticornis*, *P. arbustorum*) are negatively associated with the numbers of annual plant species, and positively with numbers of perennials and vegetation structure. As a measure combining vegetation density and the vertical distribution of plant structures, vegetation structure significantly explained part of the species assemblage. This finding confirms other research on arthropods in wildflower areas (Schwab & Dubois, 2002). They found that the vertical distribution affects species richness of spiders and bugs and inferred that the high correlation between bug species richness and light intensity at ground reflects the influence of vegetation density at higher stratifications. White & Hassal (1994) showed that species richness and abundance of ambushers and active hunting spiders correlated significantly with the structural complexity of vegetation. A highly structured vegetation supports large insect populations by providing a greater potential surface for colonisation and more resources for resting, overwintering and oviposition (Price et al., 1980; Lawton & Strong, 1981; Lawton, 1983). These advantages possibly account for the positive response of zoophagous species (e.g. *N. pseudoferus*, *N. rugosus*, *N. brevis*) of bugs, which are dependent on availability of prey and the hiding-places provided by dense vegetation (White & Hassal, 1994), particularly the importance of vegetation structure for zoophagous bugs. Contrary to our results, previous studies on 1- to 7-year-old fallow land and 1- to 10-year-old conservation headlands report an increase in vegetation structure during succession (Brown & Southwood, 1987; White & Hassal, 1994). Unlike naturally developing compensation areas, wildflower areas are sown with a standardised wildflower mixture. Thus we suggest that secondary succession shows different patterns in vegetational change in sown and naturally developing compensation areas. The spatial scale at which landscape heterogeneity was surveyed was based on Ullrich & Edwards (1999), who observed that several bug species inhabiting wildflower areas and crop fields can disperse up to about 140 m. As there are more mobile bugs (Southwood, 1962) landscape heterogeneity was also surveyed at a scale of 300 m. Correspondingly, in a CCA model, which included landscape heterogeneity at a scale of 300 m, bug distribution did not show any response to landscape (data not shown). However, it might be that bugs respond to landscape heterogeneity when measured at scales larger than 300 m, as do moths, members of three hymenopteran pollinator guilds and carabid beetles (Ricketts et al., 2001; Steffan-Dewenter et al., 2002; Purtauf et al., 2005). Among the less mobile species, such as lygaeids, the xerophilic *Peritrechus gracilicornis* Puton and *E. denticollis* occurred in wildflower areas. Augmenting the temporal and spatial constancy of favourable habitat conditions for less mobile and rare species, it might be advantageous to locate new wildflower areas adjacent to non-cropped areas (Southwood et al., 1983; Ullrich, 2001). Furthermore, large regions containing a great diversity of environmental conditions support more species and insects have a better chance of finding suitable habitats, shelter or food in a mosaic of different habitats (Saunders et al., 1991; Duelli & Obrist, 2003).

In general, our results indicate that perennial and annual plant species richness, and vegetation structure are good predictors of the presence of certain bugs. Accordingly, highly structured and species rich vegetation in wildflower areas enhanced the heteropteran diversity in agroecosystems. Since wildflower areas clearly increased the heteropteran diversity of arable land with a greater number of species in the older areas, the creation of a mosaic of wildflower areas of different ages is recommended to restore a high diversity of Heteroptera with several life history traits in agroecosystems. This is a practical recommendation because wildflower areas are part of agri-environment management schemes financially supported by the Swiss government.

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