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Secondary succession is influenced by belowground insect herbivory on a productive site

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Abstract We investigated the effects of insect herbivory on a plant community of a productive old-field community by applying foliar and soil insecticides in a full factorial design. During the first 3 years of succession, insecticide treatments had only minor effects on total cover abundance and species richness. However, species ranking within the plant community was strongly affected by soil insecticide but not by foliar insecticide. Creeping thistle, *Cirsium arvense*, dominated the experimental plots with reduced root herbivory, while square-stemmed willow-herb, *Epilobium adnatum*, dominated the control and the plots with foliar insecticide. When soil insecticide was applied, cover abundance of monocarpic forbs increased and cover abundance of polycarpic herbs decreased compared to the control. However, this effect was due to a few abundant plant species and is not based on a consistent difference between life history groups. Instead, application of soil insecticide promoted persistence of species that established at the start of succession, and suppressed species that established in the following years. We conclude that below-ground herbivory reduces competitive ability of resident species and, thus, facilitates

colonization by late-successional species. Hence, soil insects can exert strong top-down effects on the vegetation of productive sites by affecting dominant plant species and altering competitive balances.

Keywords Insect exclusion · Plant community structure · Phytophagy · Fretwell-Oksanen hypothesis

Introduction

The effect of invertebrate herbivores on growth, reproduction and fitness of plant individuals and populations (see Crawley 1997) is well known. The impact of insect herbivory on plant communities, however, is supposed to be low when compared with grazing and browsing by vertebrates (Crawley 1989). Several experiments using insecticides provided convincing evidence that insect herbivores can affect biomass, cover abundance, species composition and species richness of plant communities (e.g., Brown 1982, 1990; Brown and Gange 1992, 1999; Brown et al. 1987, 1988; Gibson et al. 1987; Mulder et al. 1999; Schmitz 2003). Some other studies failed to demonstrate such effects (Hendrix et al. 1988; Gibson et al. 1990). The available results suggest that the impact of insects on plant communities may depend on the particular plant community. One explanation for the differential responses is offered by the Fretwell-Oksanen model. Based on empirical data from vertebrate-grazing systems, Fretwell (1977, 1987), Oksanen et al. (1981) and Oksanen (1990) predict a hump shaped curve of herbivore impact: only at intermediate levels of productivity should herbivores reach densities sufficiently high to affect the plant community. Oksanen et al. (1981) and Oksanen (1990) emphasised that their model applies only to vertebrates and made several reservations against the applicability to invertebrates. Some studies support the validity of the Fretwell-Oksanen model for invertebrate herbivores (Fraser and Grime 1997, 1998). However, broad empirical evidence is still not available (Oksanen and Oksanen 2000; Polis et al. 2000; Schädler et al.

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2003a). Particularly, the lack of experiments from productive sites weakens any conclusions about the importance of insect herbivores in natural systems substantially.

Mechanisms regulating soil food webs seem to differ in their importance and patterns from above-ground food-webs (Wardle 2002). Brown and Gange (1989a, 1992) applied different types of insecticides to distinguish between the effects of above- and below-ground herbivory. The exclusion of above-ground insects favoured the establishment of perennial grasses whereas the exclusion of below-ground insects favoured perennial herbs whereas annual herbs were favoured by both treatments. Furthermore, the speed of succession increased following the application of foliar insecticide but decreased following the application of soil insecticide. Up to now, this independent manipulation of above-ground and below-ground herbivores has not been replicated. Hence, our knowledge about the role of soil insects in plant communities is based on the results of one single study. Thus, it is not possible to draw any general conclusions on the impact of below- and above-ground herbivores on the structure and dynamics of plant communities. Therefore, the main objectives of our study were to answer the following questions:

1. Do insect herbivores control species richness and cover abundance of a plant community on a productive site?
2. Do insect herbivores affect plant species differentially according to their life history, and do they change species ranking or species composition?
3. Do insect herbivores change the speed of succession?
4. Do above- and below-ground insect herbivores affect the plant community differently?

Materials and methods

Test for insecticide side effects

Insecticides may have confounding effects on insect exclusion experiments due to toxic or stimulatory influences on plants (Brown et al. 1987). Even if insecticides have been tested for side effects the results are usually not published in detail. Therefore, we performed a greenhouse experiment on two plant species common on our experimental plots (see below): *Chenopodium album* and *Fallopia convolvulus*. The former responded positively and the latter responded negatively to insecticide treatments during the first year of the experiment. We planted seedlings of the two species individually in pots (11.5 cm diameter, 9 cm height) that were filled with sterilised soil from the experimental site. Fifteen seedlings of each species were randomly assigned to each of the following treatments: control, foliar insecticide (dimethoate) and soil insecticide (chlorpyrifos). Concentrations and application rates of insecticides were the same as in the field experiment (see below). For each species, the 3 treatments \times 15 replicates = 45 pots were arranged in a randomised design in an unheated greenhouse. We used plastic cages with nylon mesh to protect plants from herbivory. Plants were watered every 2 days to 100% field capacity of the soil. After 8 weeks, when the plants started to flower, above-ground parts were harvested, dried at 60°C and weighed.

Study site and experimental design

We conducted the field experiment in central Germany (Bad Lauchstädt near Halle, Saxony-Anhalt, Germany; 110 m a.s.l., mean annual precipitation: 490 mm, mean annual temperature: 8.8°C). The soil is a Chernosem characterized by a pH of 7.0 and a high nutrient supply (total C 1.89 \pm 0.08%, total N 0.16 \pm 0.01%, NO₃⁻ 1.09 \pm 0.2 mg/100 g soil, NH₄⁺ 0.03 \pm 0.02 mg/100 g soil, P₂O₄³⁻ 46.8 \pm 7.9 mg/kg soil, K⁺ 176.2 \pm 25.4 mg/kg soil; means across experimental plots \pm SD). In July of the first year of succession, we measured an above-ground biomass of more than 1 kg m⁻² on a part of the experimental plots. This is twice as much as the most productive site of other insect exclusion studies (see Schädler et al. 2003a). Epigeal insect fauna is dominated by aphids (34% of all individuals) and curculionids (approx. 20%) (Witsack et al. 1995). Heteroptera, Diptera, Carabidae and Hymenoptera (all 3–8%) are further abundant taxa which are at least in part phytophagous.

The experimental site was used as an arable field until 1997. The last crop was barley. The field was ploughed in November 1997 and harrowed in February 1998. Subsequently, vegetation developed from the seed bank, root fragments in the soil and from propagules from outside. The experimental site is separated from the surroundings by a 5 m wide strip of undisturbed vegetation.

The experiment was arranged in a fully factorial randomised block design using 12 blocks each with 8 plots of 3 \times 3 m. Plots and blocks are separated by 2 m wide walkways. Insecticides were applied separately and in combination (four possible treatments randomly assigned to two plots within each block). The density of above-ground insects on the experimental plots was controlled by spraying a Perfekthion solution every 14 days (BASF, dimethoate 40% w/w; 2 ml diluted in 1 l water, 170 ml per plot). With the development of the vegetation, the concentration was increased (3 ml in 1 l water). Below-ground insects were controlled by applying a Hortex suspension every 4 weeks on the soil surface (Celaflor, chlorpyrifos 2% w/w; 45 g in 1 l water, 1 l per plot). Controls were treated with water only. Both insecticides are known to be very effective (Clements et al. 1986; Brown and Gange 1989a; Frampton 1999; Jagers op Akkerhuis et al. 1999; Scheu and Alpei, unpublished data). Since broad-spectrum insecticides (e.g., organophosphates) are widely used in agriculture their effectiveness has been documented and evaluated in a large body of literature. These insecticides were designed to have only a small impact on non-target organisms including plants. They can, therefore, be expected to produce less side-effects within the scope of ecological experiments than, for instance, mechanical exclusion of insects using cages. Hence, these two insecticides became standard substances for the experimental reduction of insect densities (e.g., Brown et al. 1988; Brown and Gange 1989a; Edwards et al. 2000; Fraser 1998; Fraser and Grime 1997; Hulme 1996; Schmitz 2003). Therefore, we did not assess their efficiency on our plots, also in order not to affect the development of vegetation. Both substances act non-selectively and are, therefore, not suspected to alter the composition of insect fauna (Tomlin 1994). Moreover, they have no effect on mammals and birds (Barrett 1968; Barrett and Darnell 1967; Dell'Omo and Shore 1996; Jackson 1952; Solomon 2001), enchytraeids (Brown and Gange 1989b), nematodes (Anonymous 1985) and the microflora (Domsch 1992; Spokes et al. 1981). In an additional treatment, we applied the molluscicide Limax every 4 weeks (Stähler Agrochemie, metaldehyde 60 g/kg, 5.4 g per plot) to exclude molluscs from half of the plots. However, we did not find any slugs or snails on our plots during the first 3 years of the experiment. Furthermore, we could not detect any direct effect of metaldehyde on plants in a greenhouse experiment and, therefore, we excluded the molluscicide treatment from the analysis, which increases the power of the statistical analysis.

Sampling of the vegetation

The vegetation was sampled in 10 of the 12 blocks using the point quadrat method eight times from May to October in 1998 and

1999, and five times from May to September in 2000 (Greig-Smith 1983). A sampling frame of 1 m² was placed onto the central square meter of each plot. The frame was regularly subdivided into 49 quadrats (14.3 cm × 14.3 cm). A stratified random sampling was applied by placing a pin of 3 mm diameter at a random position within each of these quadrats and recording the number of touches by plant species (living plant parts only). The sum of touches across the 49 quadrats was used as an estimate of cover abundance (Brown and Gange 1989a).

Statistical analyses

For the statistical analysis of the greenhouse experiment, we used one-way ANOVAs (three treatments: control, foliar insecticide, soil insecticide) on the log-transformed biomass data of the two plant species (Proc GLM in SAS/STAT 8.0; SAS, Cary, N.C.).

Since estimates of cover abundance in the field experiment are count data (number of touches) we used a square root transformation to approach heteroscedasticity (Bartlett's test). For each year a repeated measures ANOVA was applied to the data. The sequential nature of the data (measurements taken more closely in time are more strongly correlated) may result in inefficient analyses by traditional forms of ANOVA (Little et al. 1998). Therefore, we used a general linear mixed model (Proc MIXED in SAS/STAT 8.0) and a first-order auto-regressive covariance structure which was selected by Akaike's Information Criterion (Burnham and Anderson 1998). This approach provides better Type I error control than traditional tests (Keselman et al. 1999). Statistical analyses were performed for the total number of touches, for the sum of touches of life history groups (see below), and for the number of touches of those species within each life history group that were recorded in more than a third of the plots. Significance for individual plant species was adjusted by a sequential Bonferroni method within each life history group (Sokal and Rohlf 1997).

The classification in annual and perennial plants (e.g., Brown and Gange 1989a; Wilcox 1998) was unsuitable for our study because many plant species on our plots were facultative annuals, biennials or perennials. Therefore, we distinguished between polycarpic and monocarpic species. Furthermore, it may be inappropriate to analyse the sum of touches of a life history group because the response of a dominant species can obscure the response of other, less abundant species in the same life history group. Hence, we applied a nested ANOVA (Proc GLM in SAS/STAT 8.0) to the yearly mean cover abundance of individual plant species. Species were nested within the factor life history group and considered as a random factor. A significant interaction between life history and treatment would then indicate differences in the mean response of monocarpic versus polycarpic species. We compared these results with the repeated measures ANOVA of the sum of touches for each life history group. In all analyses, block effect was considered as a fixed factor and interactions with block were pooled in the error term (see Newman et al. 1997).

In order to quantify the response of the plant community, we performed a discriminant analysis on mean cover abundance (square root transformed) of plant species using the data for each plot across all 3 years (SPSS 10.0.7; SPSS, Chicago, Ill.). Data were grouped according to treatments and years, and *F* tests for the Mahalanobis distances between groups were calculated. For each year, significance levels of the comparisons between the four treatments were corrected using the Bonferroni method.

Results

Pesticide side effects

When plants were treated with insecticides in the greenhouse, mean dry mass at the end of experiment was slightly lower compared to the control (*Chenopodium album*: control 1.09±0.05 g, dimethoate: 0.99±0.07 g, chlorpyrifos: 0.97±0.08 g; means ± SE; *Fallopia convolvulus*: control: 1.91±0.11 g, dimethoate: 1.79±0.09 g, chlorpyrifos: 1.62±0.11 g). However, these differences were not significant (ANOVA, *P* > 0.1).

General floristic composition

About 80 plant species were recorded during the first 3 years of succession. Most of the species were monocarpic, with *C. album* dominating the field in the first year. The timing of plough and harrow influenced the floristic composition of our field. Spring-germinating species (*C. album*, *Fallopia convolvulus*) dominated the community in the first year, whereas species germinating in autumn (*Coryza canadensis*, *Lactuca serriola*) became more frequent in the second season. Other common monocarpic species were *Tripleurospermum maritimum*, *Stellaria media*, *Soncus asper*, *Sysimbrium loeselii* and *Galium aparine* in the second and *C. canadensis* in the third season. The only abundant polycarpic species in the first year was *Cirsium arvense*, which developed predominantly from root fragments. In the second and third years, the clonal polycarpic herbs *C. arvense* and *Epilobium adnatum* dominated the community. At the beginning of the third year, a number of polycarpic herbs established (*E. parviflorum*, *Picris hieracoides*, *Solidago*

Table 1 Results of the repeated measures ANOVA (*F*-values) of the effect of insecticide treatments (*FI* foliar insecticide, *SI* soil insecticide) on cover abundance and species richness during 3 years on a highly productive old field. Degrees of freedom in the within-subject model vary with the number of measures. Significance (*P*) levels of the effects are denoted with (*) *P*<0.1; * *P*<0.05; ** *P*<0.01 and *** *P*<0.001

		FI	SI	FI×SI	Time	Time×FI	Time×SI	Time×FI×SI	
	<i>df</i>	<i>F</i> -values			<i>df</i>	<i>F</i> -values			
1998									
Species richness	1, 67	3.19(*)	0.20	0.51	7, 532	73.55***	0.94	1.29	0.76
Cover abundance	1, 67	4.35*	5.76*	0.01	7, 532	532.5***	0.17	1.04	1.23
1999									
Species richness	1, 67	2.58	0.01	0.35	7, 532	85.77***	1.33	1.10	1.11
Cover abundance	1, 67	0.21	2.06	0.48	7, 532	175.7***	0.87	3.58***	0.28
2000									
Species richness	1, 67	0.14	0.95	0.01	4, 304	2.56*	0.72	3.90**	0.29
Cover abundance	1, 67	0.57	0.14	1.83	4, 304	111.4***	0.36	2.51*	0.61

canadensis). Grasses were generally rare with a proportion of less than 1% of the total cover abundance.

Effects on total cover abundance and species richness

In the first year of succession, application of foliar insecticide as well as application of soil insecticide resulted in an increase of cover abundance of the plant community (Table 1, Fig. 1). The magnitude of this effect, however, was rather low (foliar insecticide: 5% and soil insecticide: 8% during the peak of cover abundance in July). In the second season, only application of soil insecticide increased total cover abundance by up to 15%. However, the main effect was not significant but showed a highly significant interaction with time. This interaction was also found in the third year and was caused by differences in the phenology of dominant plant species (see below).

Species richness reached a maximum in summer in the first 2 years but in the third year, it followed a flat line owing to the higher proportion of perennials. In the first year, the mean number of species differed only slightly between experimental treatments (Table 1, Fig. 1). In fact, at the time of peak biomass the number of species increased from five to six when foliar insecticide was applied. The results of the second and third year did not indicate any difference of plant species richness between experimental treatments. However, in the third year the interaction between soil treatment and time was highly significant. A possible explanation is a temporary increase of species richness with the application of soil insecticide during the germination peaks in spring and autumn. Similar to the mean number of species, the cumulative number of species did not differ between treatments, irrespective of whether the data were pooled for individual years or across the 3 years (ANOVA, all $P < 0.3$).

Effects on life history groups and plant species

We analysed the effect of insecticide application on plant life history groups in two ways. First, we compared the cover abundance of monocarpic and polycarpic species using the sum of touches across all respective species. In this case, the two life history groups showed a different response to soil insecticide application. In the first year, monocarpic forbs showed no response, while polycarpic herbs increased slightly when soil insecticide was applied. In the second and third year, cover abundance of monocarpic forbs increased when treated with soil insecticide but polycarpic herbs showed the opposite response (Table 2, Fig. 2).

Second, we compared the mean response of monocarpic and polycarpic species using cover abundance of individual plant species nested within life history groups. If cover abundance of each species was averaged for each year, 10 species in the second year and 12 species in the third year were sufficiently frequent for a nested ANOVA. The monocarpic forbs were *C. canadensis*, *G. aparine*, *L. serriola*, *S. media* and *T. maritimum* in both years, *Chenopodium album*, *F. convolvulus* and *S. asper* in the second year, and *C. vulgare* and *S. loeselii* in the third year. The perennial herbs were *Cirsium arvense* and *E. adnatum* in both years, and, additionally, *E. parviflorum*, *P. hieracoides* and *S. canadensis* in the third year. We revealed no significant interactions between treatment and life history group, either in the first or in the second year (Table 3). Thus, in contrast to the sum of touches of all respective species, the mean response to insecticide application did not differ between the two life history groups. However, plant species within each life history group differed considerably in their particular response to soil insecticide as indicated by a highly significant species \times soil insecticide interaction.

Analysing plant species individually revealed that the positive effect of soil insecticide on monocarpic forbs “as

Fig. 1 Seasonal dynamics of **a** species richness and **b** total cover abundance (mean across plots) in relation to insecticide treatments during the first 3 years of succession. The y-axis is square-root scaled. Black circle control, triangle foliar insecticide, inverted open triangle soil insecticide, open square both insecticides

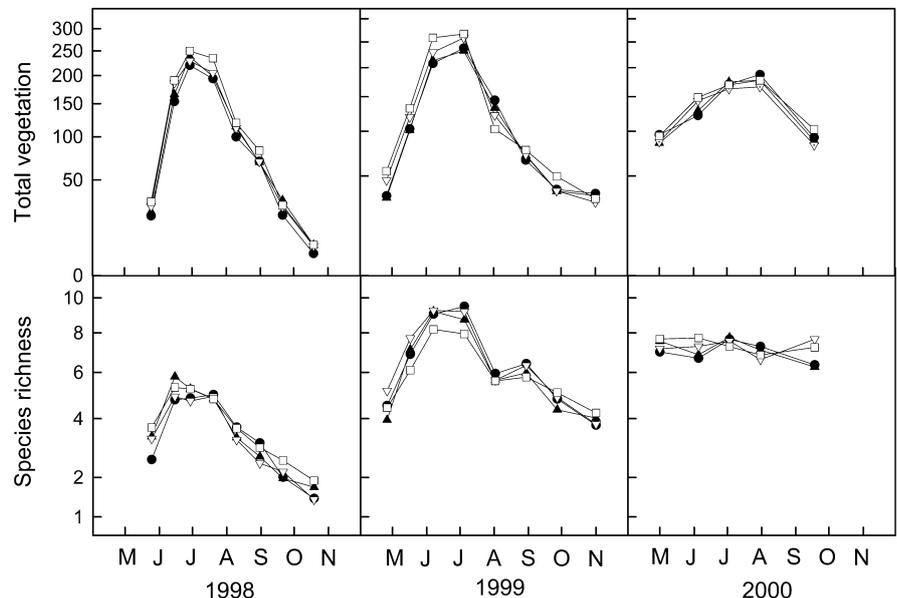


Table 2 Results of the repeated measures ANOVA (F-values) of the effect of insecticide treatments (*FI* foliar insecticide, *SI* soil insecticide) on cover abundance of plant species and plant life history groupings during 3 years of succession on a highly productive old-field. Degrees of freedom in the within-subject

model vary with the numbers of measures in the analysis. Significance (*P*) levels of the effects are denoted with (*)*P*<0.1; **P*<0.05; ***P*<0.01 and ****P*<0.001 (for plant species after sequential Bonferroni correction)

	<i>df</i>	FI <i>F</i> -values	SI	FI×SI	<i>df</i>	Time <i>F</i> -values	Time×FI	Time×SI	Time×FI×SI
1998									
Monocarpic forbs	1, 67	1.94	0.20	0.12	7, 532	384.3***	0.87	1.60	1.35
<i>Chenopodium album</i>	1, 67	0.76	0.01	3.54	6, 456	221.7***	1.33	0.86	2.26*
<i>Fallopia convolvulus</i>	1, 67	0.95	1.14	0.20	3, 228	74.85***	1.29	1.18	0.47
Polycarpic herbs	1, 67	0.29	3.18(*)	0.01	7, 532	56.46***	0.66	0.62	0.88
<i>Cirsium arvense</i>	1, 67	0.35	3.19(*)	0.01	7, 532	60.12***	0.48	0.69	0.81
1999									
Monocarpic forbs	1, 67	0.01	9.06***	2.09	7, 532	126.4***	1.75(*)	0.77	0.34
<i>Chenopodium album</i>	1, 67	0.06	60.76***	0.04	4, 304	58.60***	0.79	14.71***	0.58
<i>Lactuca serriola</i>	1, 67	7.00**	0.63	1.85	4,304	23.14***	2.3	0.18	0.83
<i>Stellaria media</i>	1, 67	0.37	6.85*	1.38	4, 304	47.65***	2.11	2.26	3.6*
<i>Sonchus asper</i>	1, 67	0.86	14.34**	0.62	2, 152	20.21***	2.49	3.44	0.80
<i>Conyza canadensis</i>	1, 67	5.74(*)	0.80	2.33	5, 380	17.13***	0.71	1.17	0.15
Polycarpic herbs	1, 67	0.67	7.64**	1.57	7, 532	93.97***	0.52	5.32***	0.25
<i>Cirsium arvense</i>	1, 67	1.08	15.61***	0.69	7, 532	80.90***	1.67	0.68	0.5
<i>Epilobium adnatum</i>	1, 67	0.35	117.7***	0.43	7, 532	45.20***	0.64	12.73***	0.38
2000									
Monocarpic forbs	1, 67	1.30	58.74***	1.87	4, 304	73.60***	0.65	3.22*	0.59
<i>Lactuca serriola</i>	1, 67	0.68	2.31	0.08	2, 152	4.45*	3.29*	1.47	0.86
<i>Tripleurosp. maritimum</i>	1, 67	0.52	10.82**	1.94	4, 304	23.27***	0.16	1.31	0.25
<i>Galium aparine</i>	1, 67	0.18	30.66***	0.01	4, 304	20.28***	1.49	14.63***	0.52
<i>Conyza canadensis</i>	1, 67	1.16	2.77	0.01	4, 304	117.8***	1.60	7.09***	0.98
<i>Stellaria media</i>	1, 67	0.10	23.60***	0.71	2, 152	78.14***	0.68	3.70(*)	0.46
Polycarpic herbs	1, 67	0.74	87.52***	0.83	4, 304	56.25***	0.38	4.00***	0.91
<i>Cirsium arvense</i>	1, 67	1.82	17.81***	1.50	4, 304	48.74***	0.47	3.55*	0.50
<i>Epilobium adnatum</i>	1, 67	4.18(*)	358.3***	1.46	4, 304	33.58***	0.62	3.33**	0.92

Fig. 2 Seasonal development of cover abundance (means across plots) for **a** monocarpic forbs and **b** polycarpic herbs (sum of cover abundance of all species) in relation to insecticide treatments during the first 3 years of succession. The *y*-axis is square-root scaled. Symbols as in Fig. 1

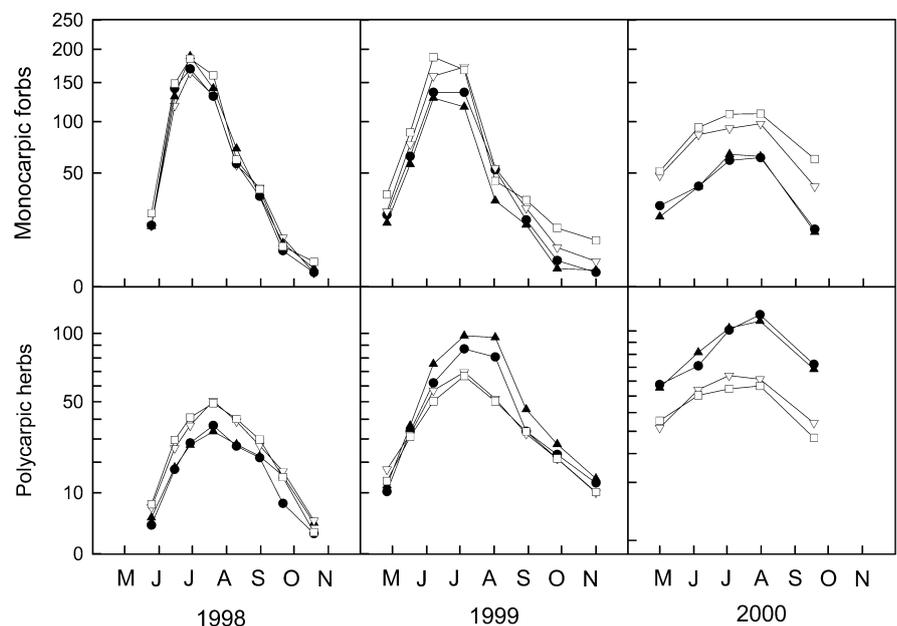
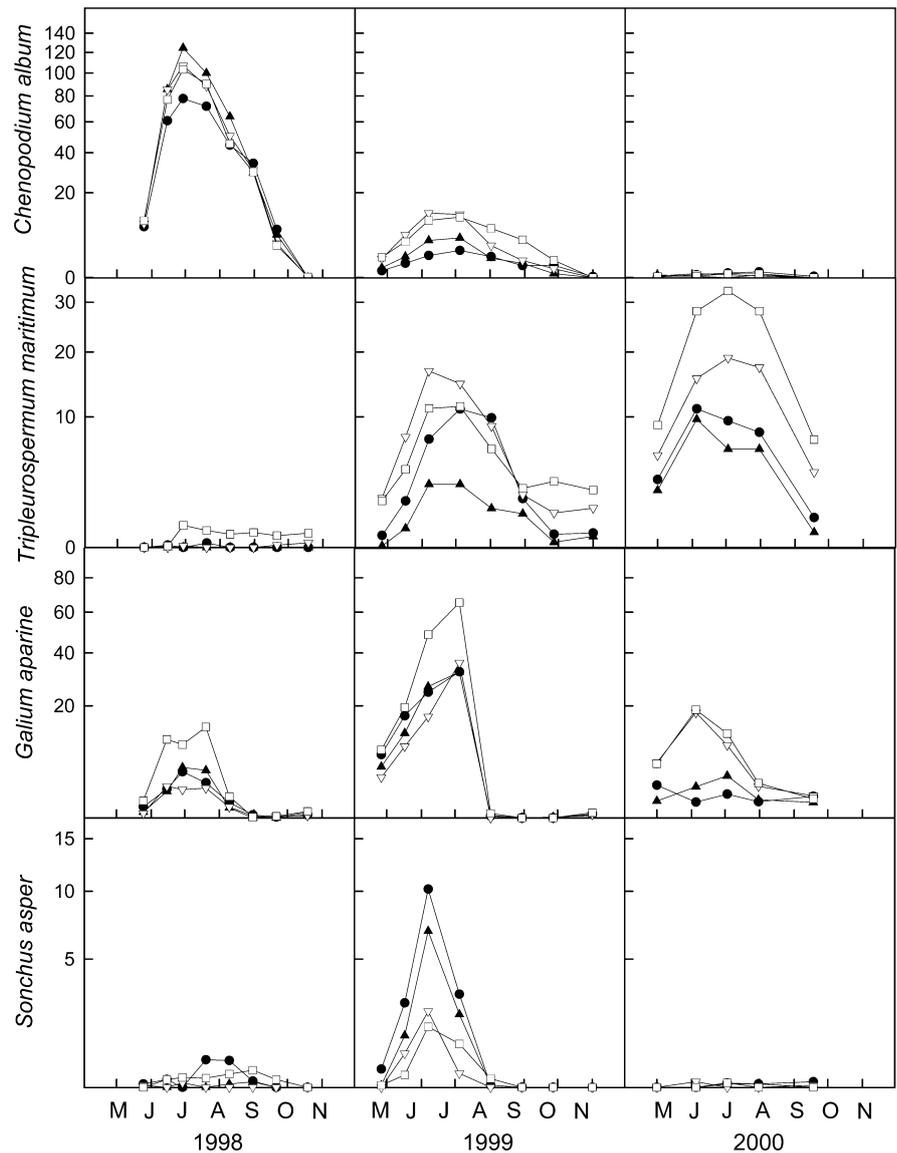


Table 3 Results of the nested ANOVA of the effects of insecticide treatments on cover abundance of plant life history groupings with plant species nested in life history. Terms indicated by upper case letters were tested against the term with the accordant lower case letter, all other terms were tested against the residual mean squares

Source of variation	1999				2000			
	df	SS	F	P	df	SS	F	P
Foliar insecticide (FI)	1	0.13	0.04	0.66	1	0.04	0.03	0.87
Soil insecticide (SI)	1	5.64	1.77	0.18	1	0.04	0.03	0.87
FI×SI	1	0.16	0.05	0.82	1	0.03	0.02	0.89
Block	9	25.78	0.90	0.53	9	11.66	0.78	0.64
Life history ^A	1	632.73	13.51	0.006	1	44.39	0.16	0.69
FI×life history ^B	1	0.45	0.20	0.67	1	1.85	0.99	0.34
SI×life history ^C	1	35.40	0.67	0.24	1	118.19	2.98	0.12
FI×SI×life history ^D	1	2.30	2.23	0.17	1	1.59	0.72	0.42
Species (life history) ^a	8	374.72	14.69	<0.001	8	2,718	163.1	<0.001
FI×species (life history) ^b	8	17.92	0.70	0.68	8	18.71	1.12	0.34
SI×species (life history) ^c	8	176.13	6.90	<0.001	8	392.26	23.77	<0.001
FI×SI×species (life history) ^d	8	8.24	0.32	0.96	8	22.16	1.33	0.21
Residual	751	2,394			903	1,505		

Fig. 3 Seasonal development of cover abundance (means across plots) for five common monocarpic forbs in relation to insecticide treatments during the first 3 years of succession. The y-axis is square-root scaled. Symbols as in Fig. 1



a whole" was obviously caused by strong positive responses of *C. album*, *T. maritimum* and *G. aparine* (Table 2, Fig. 3). However, some of the less abundant species like *L. serriola* and *S. asper* (Table 2, Fig. 3) showed negative responses. Such negative responses were only evident for some of the species which established in the second year of succession. In contrast, positive responses were exclusively found for some of the first-year species.

Similarly, the positive effect of reduced root herbivory on the sum of touches of all polycarpic herbs in the first year and their negative response in the following years was caused by different responses of the two most abundant herbs *E. adnatum* and *C. arvense*. *C. arvense* showed a slight positive response to the application of soil insecticide even in the first year. This effect was even more evident in the second and third years of succession (Table 2, Fig. 4). In contrast, *E. adnatum* established at the end of the first year from seeds and showed a negative response to the application of soil insecticide in the following years (Table 2, Fig. 4). Due to the strong responses of these two species, species ranking within the plant community changed completely. *C. arvense* was dominant in plots treated with soil insecticide, whereas *E. adnatum* dominated the other plots. Furthermore, *E. adnatum* reached its maximum cover abundance 1 month later than *C. arvense* (Fig. 4). This caused a shift in the dynamics of total cover abundance with temporarily lower values on the soil insecticide plots in August, explaining the soil insecticide \times time interaction noted above. In general, soil insecticide had a strong impact on abundance patterns of plant species, whereas the application of above-ground insecticide affected community structure only slightly (Fig. 5).

Effects on plant community dynamics

The ordination of cover abundance of plant species using a discriminant analysis revealed a broad overlap of all four treatments in the first year of succession ($P > 0.3$ for all pair-wise Mahalanobis distances after Bonferroni correction; Fig. 6). In the second and in the third year, however, the plots treated with soil insecticide (including the combination with above-ground insecticide) were clearly separated from the control plots and the plots treated with above-ground insecticide only ($P < 0.001$ for all pair-wise comparisons). In contrast, no significant distance was found between the control and the foliar insecticide treatment as well as between the soil insecticide and the combination treatment ($P > 0.3$). Obviously, variate 1 is related to the dynamics of succession across years. Between-year differences in variate 1 are smaller for the plots treated with soil insecticide indicating a reduced speed of succession compared to the other plots. Separation along variate 2 may be related to complex changes in community structure but was much less pronounced.

Discussion

With respect to our initial questions, we can summarize our experimental results as follows. Our experiment carried out on a productive site revealed only weak effects of insecticide application on cover abundance and species richness of the plant community. Plant life history groups did not show consistent differences in their response to insecticide treatments. Rank order of species within the plant community, however, was strongly affected by the application of soil insecticide. Persistence of early successional plant species was promoted and colonization by later-successional species was retarded owing to soil insecticide, thus obviously decelerating the speed of

Fig. 4 Seasonal development of cover abundance (mean across plots) for two common polycarpic herbs in relation to insecticide treatments during the first 3 years of succession. The y-axis is square-root scaled. Symbols as in Fig. 1

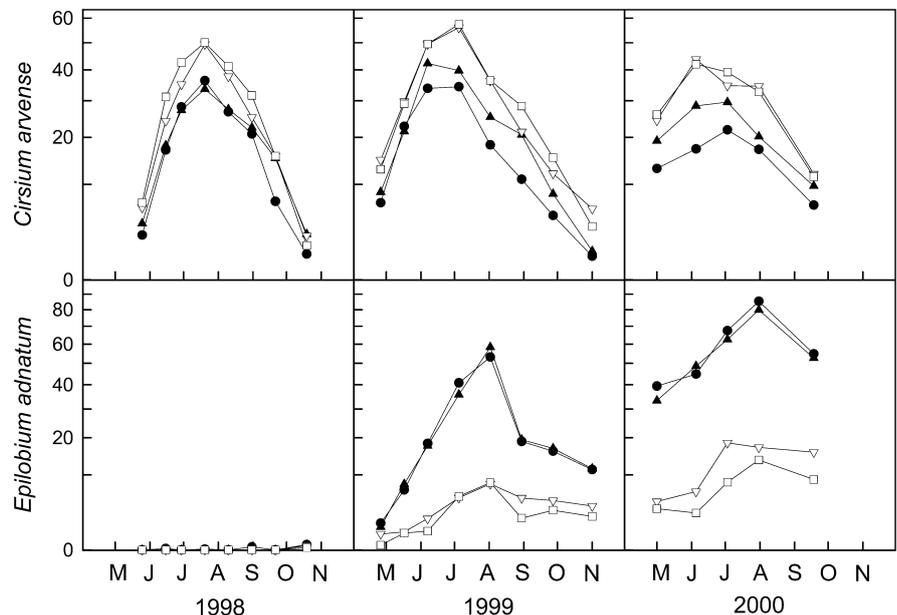
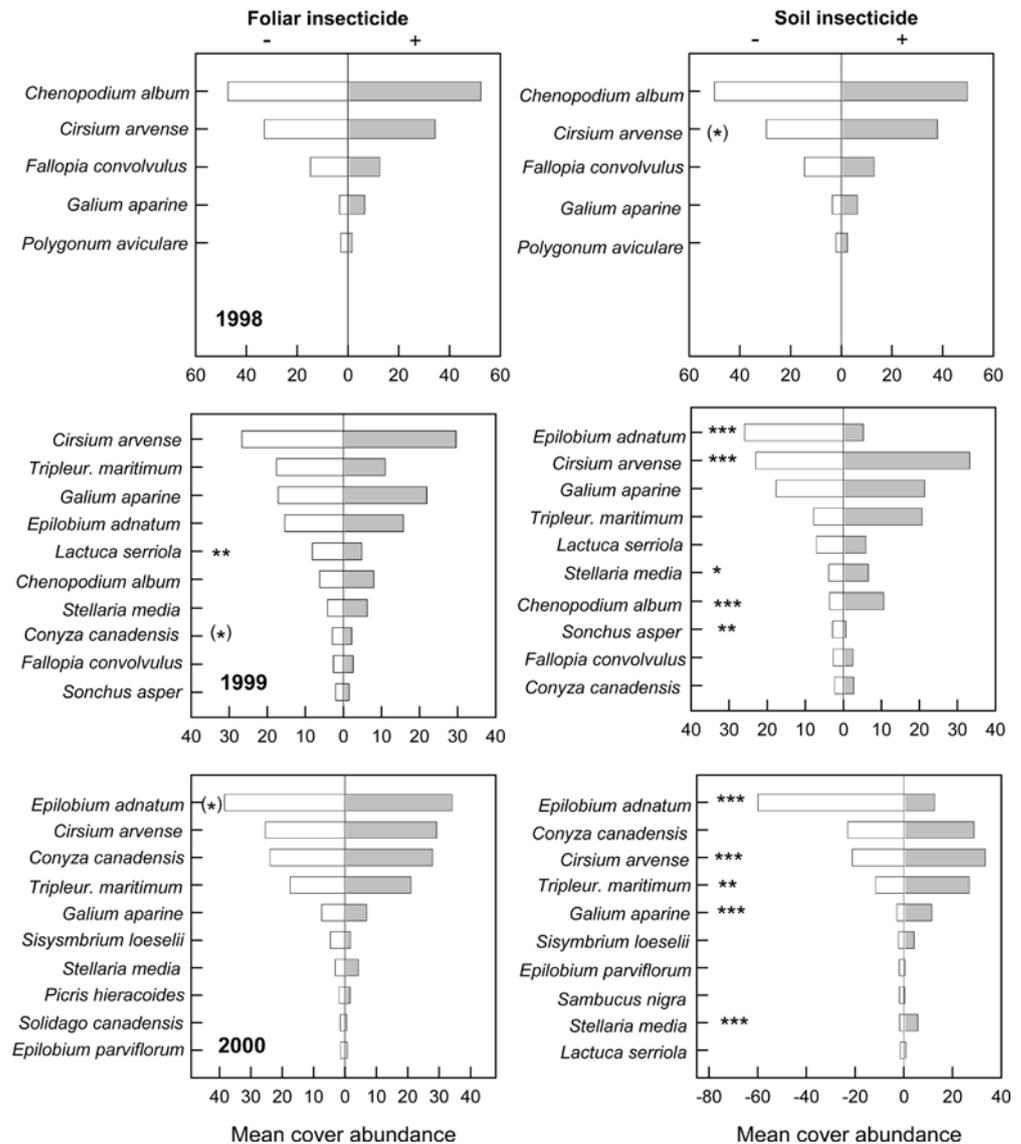


Fig. 5 Cover abundance of frequent plant species in the old-field community in relation to insecticide treatments during the first three years of succession (plot means per year). In the first year, only very few plant species were common on the experimental plots and only these five species are given. Note different scaling in different graphs. Significance levels after Bonferroni correction from the repeated-measures ANOVA are given as *) for $P < 0.1$, * for $P < 0.05$, ** for $P < 0.01$ and *** for $P < 0.001$. Note different scales of x-axes



succession. In general, application of below-ground insecticide had a much stronger impact on the plant community than application of above-ground insecticide.

Cover abundance and species richness of the plant community

In our study, the reduction in the density of above-ground insects and of soil insects caused only a slight increase of cover abundance in the very early stage of secondary succession. In later stages, neither soil insecticide nor foliar insecticide had any influence on total cover abundance of the plant community. As indicated by the close correlation between cover abundance and leaf area index, the point quadrat method provides a good estimate for standing crop (Jung et al. 2000) and, thus, the above results are obviously not biased by the sampling method. Furthermore, the two insecticides are not likely to exert phytotoxic or stimulatory effects if applied as recom-

mended (Brown and Gange 1989a; Fraser and Grime 1997; Ganade and Brown 1997; Tomlin 1994). Although Gange et al. (1992) reported an inhibition of seed germination by dimethoate for some annual forbs we consider this effect to be of minor importance. First, dimethoate was sprayed on above-ground plant parts and should, therefore, not affect germination of seeds in the soil. Second, cover abundance and species richness were positively affected by dimethoate application during the first year of succession. Hence, if dimethoate inhibits germination, our results give conservative estimates of the true effect of insect herbivory. Third, the results of our greenhouse experiment indicate that both insecticides had no impact on plant growth.

Several studies report strong effects of above-ground as well as below-ground insects on plant community biomass or cover abundance (Brown et al. 1988; Brown and Gange 1989a; Carson and Root 1999, 2000) whereas other experiments did not reveal such effects (Hendrix et al. 1988; Hulme 1996). In only a few studies has the

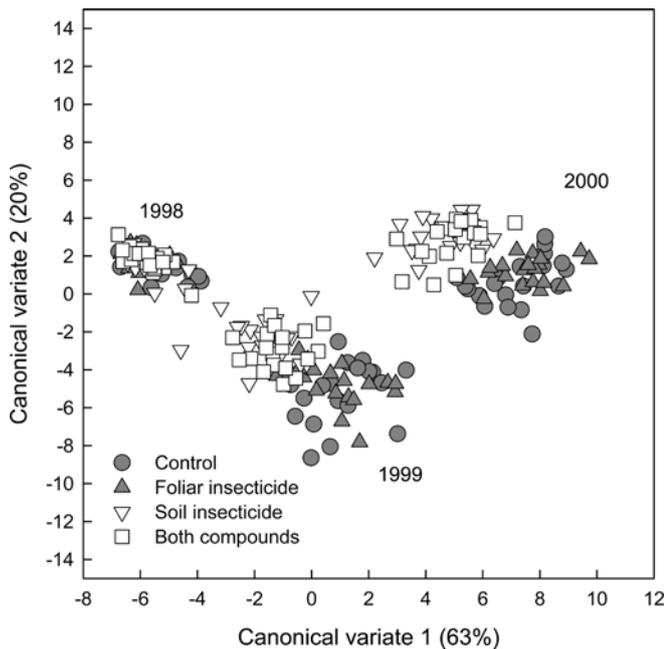


Fig. 6 Discriminant analysis of cover abundance data of species (plot means per year). Plots were grouped according to treatment and year

differential response of plant communities been analysed in relation to the productivity of experimental sites (Fraser 1998; Fraser and Grime 1997; Uriarte and Schmitz 1998). Based on vertebrate-grazing systems, Fretwell (1977, 1987), Oksanen (1990) and Oksanen et al. (1981) suggested that herbivory should affect plant community biomass only at sites of intermediate productivity. Since herbivores are controlled by resource availability at sites of low productivity and by predation at sites of high productivity, the effect of herbivory should be much reduced towards the lower and the higher ends of the productivity gradient. Since our experiment was carried out on a highly productive site the weak effects of insect herbivory on cover abundance of the plant community are in accordance with the model of Fretwell and Oksanen.

Only during the first year of succession and in only one treatment (above-ground insecticide), did we find a marginally significant increase in the mean number of plant species. The cumulative number of species showed no differences among treatments, either in single years or across 3 years. During phases of germination in spring and autumn of the third year, we observed a temporary increase in species number when soil insecticide was applied. Consistently, Brown and Gange (1989b) found that soil insects particularly attack seedlings and may thus cause a decrease in plant species richness. In their study, the negative effect of below-ground herbivory lasted for the first 4 years of succession (Brown and Gange 1992). Herbivory by above-ground insects, however, decreased plant species richness only in the first year but increased species richness in the following years (Brown and Gange 1992). Experiments in late-successional communities also revealed that above-ground insects can increase plant

species richness (Bach 1994; Brown and Gange 1999; Carson and Root 1999). Two mechanisms may be responsible for this effect. First, insect herbivory can affect plant diversity by reducing the amount of above-ground phytomass and litter cover (Foster and Gross 1998; Wilby and Brown 2001; Xiong and Nilsson 1999). Second, herbivores may enhance plant diversity by selective feeding on dominant species. In general, selective herbivory may change the competitive relationship between plant species (Bentley and Whittaker 1979; Clay 1993; Louda et al. 1990; see also Crutchfield and Potter 1995; Potter et al. 1992). Selective feeding on dominant species may release subordinate ones from competition or allow others to invade the community (Carson and Root 1999; Pacala and Crawley 1992). Indeed, the dominant plant species at our study site (*C. arvensis*) was negatively affected by below-ground insect herbivory. But in contrast to the ideas discussed above, subordinate species were not favoured. Instead, another plant species (*E. adnatum*) became dominant and, as a result, plant species richness did not increase.

Plant species ranking and life history groups

The displacement of one dominant species by another dominant species owing to herbivory by soil insects led to a complete shift in species ranking within the plant community. *C. arvensis* is a widespread perennial weed in the study area, occurring both on fallow land and on arable fields. Across consecutive years, it represents a rather stable resource for specialized insects (Eber and Brandl 2003) which can build up high population densities if the host plant becomes abundant. A large proportion of our *C. arvensis* population showed visible signs of root herbivory (up to 30%) and approximately 4% of the males and 14% of the females were infested by the root-galling weevil *Cleonis pigra* (Coleoptera: Curculionidae; Jung, unpublished data). The damage caused by this insect may have been particularly severe because most *C. arvensis* ramets established from root fragments. In contrast, *E. adnatum* established exclusively from seeds at the end of the first year, and both sexual and vegetative propagation occurred in subsequent years. However, clonal growth in *E. adnatum* takes place by above-ground daughter rosettes which may suffer less from root herbivory during their early stages.

Our results clearly contradict the widespread view that the effect of herbivory on plant species should be contingent on their life history (Brown and Gange 1992). Considering the sum of touches for life history groups, our conclusion would be quite different from that of Brown and Gange (1992) since reducing below-ground insect herbivory delayed the establishment of perennial herbs. However, this difference is based on the response of only one dominant species (*E. adnatum*). In an ANOVA with species nested in life history groups, we could not find consistent effects of insecticide treatments on life history groups. Rather, plant species that were abundant in

the first year (e.g., *C. arvense*, *Chenopodium album*) tended to show a positive response to soil insecticide application. Obviously, these common, early successional species prevented colonization by others (e.g., *E. adnatum* and *S. asper*). Hence, herbivory by soil insects can break the inhibitory effect of resident species.

Plant community dynamics

As discussed above, invertebrate herbivores often suppress the dominant species in plant communities (Crawley 1989; Carson and Root 1999). Thereby, they facilitate the establishment of subordinate plant species and affect plant community structure. These effects may also interact with ecosystem processes or resource availability, and, therefore, generate a high diversity of results (Davidson 1993; Schädler et al. 2003b; Schowalter 1981). For instance, it has been shown that insect herbivory may increase (e.g., Fraser and Grime 1998; Wilcox 1998) or decrease (e.g., Bach 1994; McBrien et al. 1983) the speed of succession. Moreover, the studies of Brown and Gange (1989a, 1992) and Carson and Root (1999, 2000) showed that host choice and timing of herbivore impact are crucial for the speed of succession. In general, our study supports the conclusions of Brown and Gange (1992) that the effects of soil insects on successional dynamics are completely different from the effects of foliar insects. In fact, foliar insects showed only a very slight impact on the vegetation of our highly productive site, whereas soil insects accelerated the speed of succession which is also indicated by the ordination of species composition. Nevertheless, due to the lack of long-term studies it is premature to generalize about the effects of insect herbivores on successional trajectories.

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