Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community

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We tested the hypothesis that selective feeding by insect herbivores in an old-field plant community induces a shift of community structure towards less palatable plant species with lower leaf and litter tissue quality and may therefore affect nutrient cycling.

Leaf palatability of 20 herbaceous plant species which are common during the early successional stages of an old-field plant community was assayed using the generalist herbivores *Deroceras reticulatum* (Mollusca: Agriolomacidae) and *Acheta domesticus* (Ensifera: Gryllidae). Palatability was positively correlated with nitrogen content, specific leaf area and water content of leaves and negatively correlated with leaf carbon content and leaf C/N-ratio.

Specific decomposition rates were assessed in a litter bag experiment. Decomposition was positively correlated with nitrogen content of litter, specific leaf area and water content of living leaves and negatively correlated with leaf C/N-ratio.

When using phylogentically independent contrasts the correlations between palatability and decomposition versus leaf and litter traits remained significant (except for specific leaf area) and may therefore reflect functional relationships.

As palatability and decomposition show similar correlations to leaf and litter traits, the correlation between leaf palatability and litter decomposition rate was also significant, and this held even in a phylogenetically controlled analysis. This correlation highlights the possible effects of invertebrate herbivory on resource dynamics.

In a two-year experiment we reduced the density of above-ground and below-ground insect herbivores in an early successional old-field community in a two-factorial design by insecticide application. The palatability ranking of plants showed no relationship with the specific change of cover abundance of plants due to the reduction of above- or below-ground herbivory. Thus, changes in the dominance structure as well as potentially associated changes in the resource dynamics are not the result of differences in palatability between plant species. This highlights fundamental differences between the effects of insect herbivory on ecosystems and published results from vertebrate-grazing systems.

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By changing competition regimes and dominance hierarchies between plant species, invertebrate herbivores may impose strong influences on the structure of terrestrial plant communities (Brown and Gange 1989a, Carson and Root 1999, Schädler et al. 2003). These changes are commonly explained by selective feeding of herbivores on particular plant species. Selective feeding by generalist herbivores is supposed to be closely related to functional traits of plants, e.g. growth rates, resource allocation patterns, nutrient uptake and reten-

tion. Usually, these traits are related to differences in the carbon/nitrogen-ratio of the leaf tissue. In general, plant palatability increases with a decreasing carbon/nitrogen ratio (Mattson 1980, Strong et al. 1984, Hartley and Jones 1997, Griffin et al. 1998). However, all the parameters listed above are also crucial for litter decomposition (Swift et al. 1979, Melillo et al. 1982, Berg et al. 1996, Cornelissen and Thompson 1997, Cotrufo et al. 1998). Carbon-based secondary compounds such as phenolics and lignin are important controls of palatability and decomposability. Hence a close relationship between palatability and decomposition should exist, even if leaf traits may differ between living leaves and litter (Aerts 1996). Grime et al. (1996) showed that litter decomposition and leaf palatability are closely correlated across a broad array of vascular plant species. That study strongly supports the view that palatability and decomposition rate are determined in a similar way by chemical, morphological and physiological leaf traits. Hence, anti-herbivore defence may generate a link between above-ground and below-ground processes (Grime et al. 1996, Bardgett et al. 1998). However, phylogenetically related plant taxa often share secondary compounds which may influence phytophagy, palatability and decomposition (Frenzel and Brandl 1998, Hendriks et al. 1999). Relationships between species traits may therefore be determined more by phylogeny than by ecology (Felsenstein 1985, Harvey and Pagel 1991, Silvertown and Dodd 1996). Thus, a phylogenetically controlled analysis is mandatory to disentangle phylogenetical from functional relationships.

If insects prefer plants of a high nutritional quality, then herbivory may cause a shift in the composition of plant communities towards less palatable species and consequently to less degradable phytomass which should slow down rates of nutrient cycling (Pastor and Cohen 1997). In recent years, the importance of litter decomposition as an interface between above- and below-ground processes in ecosystems became increasingly recognized (Pastor and Cohen 1997, Wardle et al. 1997, Bardgett et al. 1998, Bardgett and Shine 1999, Nilsson et al. 1999, Van der Putten et al. 2001). For invertebrates, however, studies on the relationship between palatability, litter decomposition and leaf traits have never been analysed in correlation to herbivore-induced changes in plant abundance. In an experiment we reduced the density of above- and below-ground insect herbivores on an abandoned field. We correlated changes in the abundance of the most common plant species with their palatability and leaf and litter traits.

The main objectives of our study were to answer the following questions:

1. What are the relationships between plant palatability, litter decomposition rates and functional leaf traits across common species in an old-field plant community and how are this relationships influenced by the phylogeny of plants?
2. Are there predictable effects of plant palatability on insect herbivore-induced changes in the cover abundance of plant species?

Methods

Study site

The study site is located in Central Germany (51° 22′ 60N, 11° 50′ 60E, Bad Lauchstädt near Halle, Saxony-Anhalt, Germany 124 m NN), an area of low annual rainfall (480 mm) and a mean annual temperature of 8.8°C. The soil is a Chernosem with a high nutrient level (C-content 1.89%, N-content 0.16%, NO_3^- 1.09 mg/100g soil, NH_4^+ 0.03 mg/100 g soil, $P_2O_4^{3-}$ 46.8 mg/kg soil). The experimental field is a former arable field with barley as the last crop in 1997. The field was ploughed and harrowed in winter 1997 and subsequently the vegetation developed from the seed bank and root fragments.

Palatability test

To obtain a general measure of plant palatability, two taxonomically unrelated plant consumers were used. The garden slug *Deroceras reticulatum* (Müller) is a widespread generalist herbivore in the agricultural landscape of central Europe. Adults of *D. reticulatum* were collected in the surrounding of our experimental old-field. Nymphs of the omnivorous house cricket *Acheta domesticus* L. were obtained from commercial dealers. Both species were kept in the laboratory for one week with a photoperiod of L/D 8/16 and a temperature cycle of 20°C/18°C for *D. reticulatum* and 25°C/20°C for *A. domesticus*. For both species lettuce and for *A. domesticus* oat flakes were provided ad libitum. All animals were starved for 24 h before running the experiment. During this period each cricket individual was kept isolated to avoid cannibalism. At the beginning of the experiment 25 animals of each species were weighed, frozen, dried and weighed again to assess a specific fresh weight/dry weight ratio. Fresh weight was highly correlated to dry weight (*D. reticulatum*: $r^2 = 0.97$, $P < 0.001$; *A. domesticus*: $r^2 = 0.86$, $P < 0.001$), so the individual fresh weights were used for further analysis.

Fully expanded, non-senescing leaves of mature plants were collected at the beginning of July 1999 adjacent to the experimental plots (see below). With few exceptions all leafs came from different plant individuals. We included 20 of the most common dicotyle-

donous herbaceous species. Taxonomy follows Rothmaler (1996). Leaves were slightly moistened with deionised water and stored at 3°C in sealed polythene bags for one day in the case of *Deroceras reticulatum* and two days in the case of *Acheta domesticus*. Discs of 20 mm $\varnothing$ were taken from the leaves avoiding the midrib. Two discs of each species were weighed and placed in a petri dish ($\varnothing$ 9 cm) together with one slug or cricket individual. For small leaves a portion of them representing approximately the same mass as the discs were used. Twenty leaf discs per plant species were weighed and dried to obtain the initial dry mass. We used ten replicates for each plant species and each herbivore. The test ran for 16 hours. The remaining leaf material was dried and weighed. The specific palatability was calculated as the ratio of the leaf dry weight (mg) consumed in relation to herbivore fresh weight (g). The pooled palatability index was calculated as the mean across the two herbivore species.

Decomposition test

Leaf litter of 19 plant species occurring in our old-field community was sampled in July and August from fully grown plants adjacent to the experimental plots. Seventeen of them were also used in the palatability experiment. Freshly senesced litter was collected by hand from the ground or by shaking plants gently. Again litter was collected from as many plant individuals as possible and subsequently pooled for the experiment.

Litter was dried at 50°C to weight constancy and cleaned by brushing. Six replicates of 1.0 ± 0.1 g per species were weighed, slightly moistened with deionised water to avoid break losses and sealed in flat litter-bags made of a polyester net (mesh size 1.55-mm). The inner compartment of the litter bags was about 12×8 cm.

An area of about 400 m^2 of the experimental field was mulched during the end of August. A decomposition bed of 2×10 m was covered with a 20 cm-layer of mulch to avoid germination of plants and allow settlement of decomposer fauna. After two weeks litter bags were placed in a randomised arrangement on bare ground and covered by the mulch layer. Samples were retrieved after 8 weeks, dried to weight constancy, cleaned and weighed. Percentage dry weight loss was used as a measure of plant specific decomposition rate.

Leaf traits

Specific water content, specific leaf area, nitrogen and carbon were measured using about 20 leaves from different individuals. Specific water content was defined as percentage mass loss after drying living leaves to weight constancy at 60°C. Thus, specific water content is complementary to the leaf dry matter content used by Wilson et al. (1999). Specific leaf area was assessed as the ratio of leaf area to leaf dry weight. Twenty leaves per species were measured using a LI-3000 Area Meter (LI-COR inc., Lincoln, Nebraska, USA). Dried leaves and a sub-sample of litter of each plant species were ground in a mill. Total nitrogen- and carbon content was measured with a Elementar Vario EL element analyser (Elementar Analysengeräte GmbH, Hanau, Germany).

Insect exclusion experiment

In February 1998, experimental plots of 3×3 m were arranged in a full factorial randomised block design. The plots are separated from each other by 2 m wide walkways and from the surrounding agricultural fields by a 5 to 10 m wide strip of undisturbed vegetation. In addition to the control, in three treatments densities of above-ground insects and below-ground insects were reduced separately and in combination. The density of above-ground insects were reduced from plots by spraying a solution of Perfekthion every 14 days (BASF, dimethoate 40%; 0.36–0.54 ml diluted in 130–170 ml water). With the development of the vegetation the concentration was increased during the ongoing season. Density of below-ground insects were reduced by watering the plots with 1 l suspension of Hortex every four weeks (Celaflor, chlorpyrifos 2%; 50 g l^{-1}). In a greenhouse experiment, no side effects were found to result from the application of the insecticides on two plant species abundant in the old-field (*Chenopodium album*, *Fallopia convolvulus*, see also Brown and Gange 1989a, Fraser and Grime 1997). Furthermore, there are no reports about direct side effects of these compounds on microflora, vertebrates and invertebrates other than arthropods (Jackson 1952, Barrett and Darnell 1967, Barrett 1968, Spokes et al. 1981, Anon. 1985, Brown and Gange 1989b, Domsch 1992, Tomlin 1994, Dell'Omo and Shore 1996, Solomon et al. 2001). The insecticides used are therefore considered appropriate for insect exclusion experiments. Controls were treated with water only. Each treatment was replicated two-fold in ten blocks (n = 80).

The vegetation was sampled in 1998 and 1999 eight times a year from April to October with the point quadrate method. Our sampling frame of 1 m^2, divided in 7×7 quadrates, was placed into the centre of the experimental plots. Each of the 49 pins ($\varnothing$ 3 mm) was placed randomly within one of these quadrates (stratified random sampling, Greigh-Smith 1983). For every plant species the number of touches of the pins with living plant material were recorded.

Data analyses

Prior to any statistical analysis, leaf decomposition rates and contents of water, nitrogen and carbon were arcsinv-transformed to reduce heterogeneity of variances and non-normality, whereas the raw data for palatability, specific leaf area and C/N-ratios were used. Since the insect exclusion experiment involved repeated measurements over time on the same plots a repeated measures ANOVA was applied to the data for each year separately. We used a general linear mixed model (Proc Mixed in SAS/STAT 8.0) and a first-order autoregressive covariance structure selected by Akaike's Information Criterion. These analyses were performed only for those plant species that occurred in more than a third of the experimental plots. The number of touches of those plant species (their cover abundance) was square-root transformed prior to analyses. Mean cover abundance of every plant species was estimated across all sampling dates of 1998 and 1999 respectively. The effect of insecticide treatment was calculated as the change in cover abundance due to the application of foliar insecticide and application of soil insecticide. Because we did not find any significant interaction between the effects of both compounds, factor means were used for calculating the effects of insect exclusion. Only very few plant species were evenly distributed across the experimental field. Most species showed a patchy distribution. Large differences between the treatment means were therefore often associated with high standard deviations and did not necessarily refer to strong effects of insect exclusion. Thus, insecticide effect was assessed as effect size d (Gurevitch and Hedges 1993). Effect size d is the difference between the means of two groups (cover abundance of plant species on plots with or without insecticide application in our study) divided by their pooled standard deviation to standardize the effect among plant species. This metric is widely used in meta-analyses and may give a more realistic measure of the insecticide effect than the simple percentage change.

The relationships between palatability, decomposition and leaf traits as well as insect imposed changes in cover abundance across plant species were assessed by the Pearson's correlation coefficient (r).

We used phylogenetically independent contrasts (Harvey and Pagel 1991) to examine possible effects of phylogeny. When available, molecular based phylogenies were used (Dodd et al. 1999). Within families molecular phylogenies were compiled from Jansen et al. (1990) and Bremer (1994) in the case of the Asteraceae and from Warwick and Black (1997) in the case of the Brassicaceae. In the cases where no molecular phylogenies were available within families we used traditional taxonomy on the level of tribes, sub-tribes, genera, sub-genera, sections, sub-sections, series and aggregates which were interpreted as phylogenetic clades (Hegi
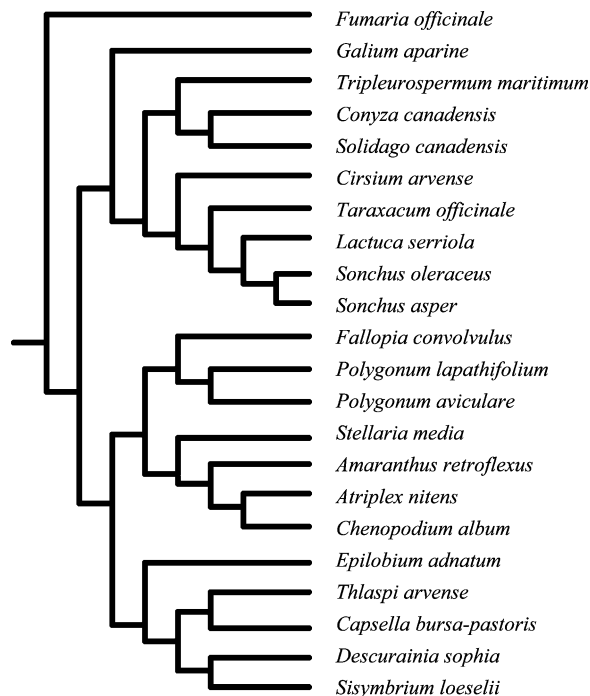

Fig. 1. Phylogeny of plant species used for the calculation of phylogenetically independent contrasts. Branch length arbitrary.

1939, Tutin et al. 1964). The resulting phylogeny is shown in Fig. 1. Contrasts were calculated with all branch length set to an equal length. Phylogenetically independent contrasts were tested using regression through the origin (Harvey and Pagel 1991, Silvertown and Dodd 1996).

Leaf traits usually show high correlations to each other. Hence simple correlation and regression techniques are not appropriate to pinpoint the relative importance of each variable on palatability and decomposition. Therefore, we applied hierarchical partitioning (Chevan and Sutherland 1991), which uses all possible regression equations to estimate the independent effect of each independent variable on the dependent variable. Furthermore this technique estimates the joint effect, that is that part of the simple correlation coefficients between the dependent and independent variables which is due to the correlations of the considered independent variable with the other independent variables.

Results

Palatability

The two herbivore species used in the palatability experiment showed conspicuous preferences for certain plant species (Appendix 1, Fig. 2). There were, how-
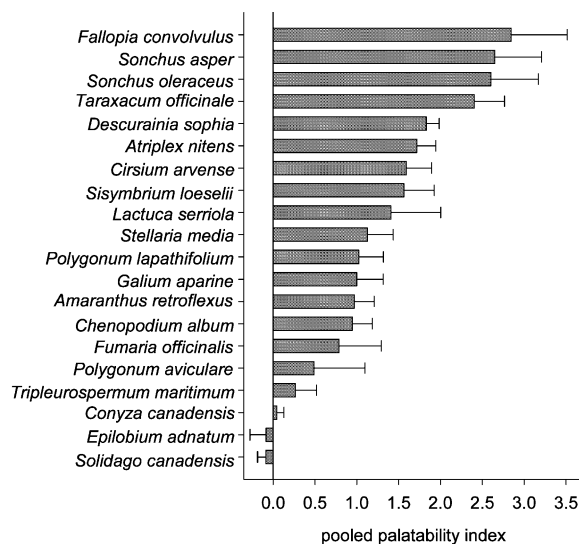
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Fig. 2. Ranked palatability across plant species which occurred during the early succession of an old field community in the eastern part of Germany. The shown estimates of palatability are the average across two herbivore species (*Acheta domesticus* and *Deroceras reticulatum)* and are expressed as consumed plant dry weight (mg) per herbivore fresh weight (g). Standard error was calculated from all replicates per species.
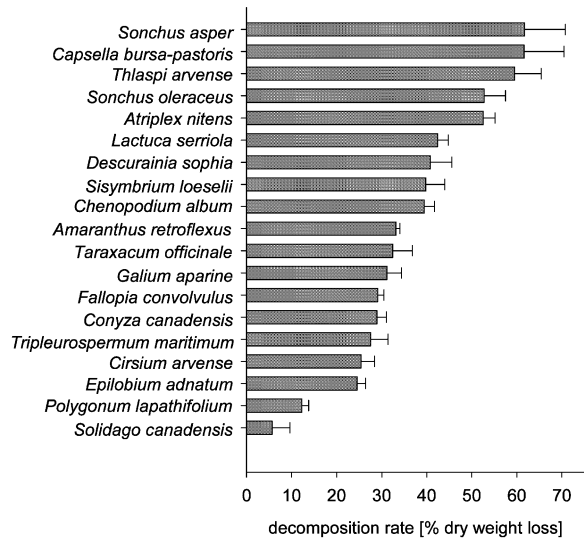

Fig. 3. Ranked litter decomposition rate across plant species which occurred during the early succession of an old field community in the eastern part of Germany expressed as percentage loss of dry weight during eight weeks. Means ± standard errors.

ever, differences in the preferences between the two herbivores. *Fallopia convolvulus* was the most palatable plant to *A. domesticus*, but quite unpalatable to *D. reticulatum*. Nevertheless, some plant species were palatable to *A. domesticus* and *D. reticulatum* (*Sonchus asper*, *S. oleraceus*), while others were unpalatable to each of the two herbivores (*Epilobium adnatum*, *Solidago canadensis*, *Conyza canadense*). Thus, the preferences of the two herbivore species were correlated across plant species ($r^2 = 0.21$, $P = 0.04$).

Decomposition

Decomposition rate expressed as dry weight loss during the 8-week litter bag experiment showed considerable variation between plant species (ANOVA, $F_{18,95} = 13.1$, $P < 0.001$, Fig. 3). The highest decomposition rates were found in *Sonchus asper* and *Capsella bursa-pastoris* (about 62% loss of dry weight during 8 weeks). In contrast, for *Polygonum lapathifolium* and *Solidago canadensis* we found decomposition rates of only 12% respectively 6%. However, for most species decomposition rates ranged between 25 to 40%.

Relationships between palatability, decomposition, and leaf and litter traits

Leaf and litter traits of plant species are given in

Appendix 1. Leaves showed a 2.3 fold respectively a 1.2 fold range for nitrogen and carbon contents across species; litter showed a 2.9 and 1.5 fold range across species for carbon and nitrogen. *Solidago canadensis* showed the highest carbon and the lowest nitrogen concentration in leaves (C/N-ratio of 21.3). Due to the high nitrogen resorption in *S. canandensis* we found a very high C/N-ratio in the litter of this species. Water content ranged from 66.9 to 89.5% with the lowest value for *S. candensis*. Differences in specific leaf area were more distinct with the minimum for *Matricaria inodora* (6.87 mm²/mg) and the maximum for *Sonchus asper* (29.0 mm²/mg).

We found significant or at least marginally significant relationships between plant palatability and each leaf trait (Table 1). Palatability was positively correlated with water content, specific leaf area and nitrogen content of leaves and negatively correlated with the leaf C/N-ratio. Only carbon concentration in litter and specific leaf area showed no significant correlation with litter decomposition rate. Weight loss was positively correlated with water content of leaves and nitrogen concentration of litter. Again, a negative correlation was found between decomposition and litter C/N-ratio. When phylogenetically independent contrasts were used, the correlations between palatability and leaf traits as well as between decomposition and litter traits remained significant (Table 1). Only the correlation of palatability with the specific leaf area was not significant at $P = 0.05$.

Table 1. Hierarchical partitions of the effects of leaf respectively litter traits on palatability and decomposition. Multiple linear regression effects are given as r^2 = coefficient of determination, i = independent effect on r^2, j = joint effect on r^2. The latter measures the effect which is due to the correlation of the considered independent variable with the other independent variables. Note that $r^2 = i+j$. C/N-ratio was not included in multiple regression, therefore only r^2 for simple regression is given in this case. Since some traits were not examined in every plant species, multiple regression was performed with minimal n and r^2 may differ from simple regression. Nevertheless, asterisks indicate P-values referring to simple regression coefficients.

		specific leaf area	P*	water content	P*	nitrogen	P*	carbon	P*	C/N-ratio	P
palatability n=20	r^2	0.199	0.05	0.228	0.03	0.157	0.08	0.207	0.04	0.270	0.02
	i	0.191		0.145		0.090		0.135		–	
	j	0.008		0.083		0.067		0.073		–	
palatability (independent contrasts) n=19	r^2	0.000	>0.30	0.161	0.09	0.155	0.07	0.158	0.08	0.252	0.03
	i	0.005		0.087		0.183		0.167		–	
	j	–0.005		0.074		–0.028		–0.009		–	
decomposition n=17	r^2	0.090	0.21	0.239	0.003	0.287	0.02	0.007	>0.30	0.261	0.03
	i	0.097		0.211		0.257		0.005		–	
	j	–0.006		0.028		0.030		0.002		–	
decomposition (independent contrasts) n=16	r^2	0.073	0.29	0.295	>0.30	0.376	0.009	0.054	0.02	0.440	0.004
	i	0.046		0.157		0.253		0.018		–	
	j	0.027		0.137		0.124		0.036		–	

These results are corroborated by hierarchical partitioning (Table 1). We found high independent effects of specific leaf area, water content and carbon content of leaves for palatability and high effects of water content and leaf nitrogen for decomposition. However, when using phylogenetically independent contrasts, nitrogen remained the most important factor for both processes, followed by leaf carbon for palatability and leaf water content for decomposition. Again, specific leaf area was of minor importance for decomposition and palatability.

The measured plant traits are clearly important for decomposition as well as palatability. Hence, decomposition rate of plants was significantly correlated to palatability ($r^2 = 0.38$, P = 0.008, Fig. 4). When we analysed the data for each herbivore species separately this effect was also evident in *Acheta* ($r^2 = 0.27$, P = 0.03) but not significant in *Deroceras* ($r^2 = 0.03$, P = 0.16). The affiliation of species to families gives no hint that the correlation between decomposition and palatability is confounded by phylogeny (Fig. 4). Accordingly, the relationship between these two parameters holds also for phylogenetically independent contrasts ($r^2 = 0.40$, P = 0.007).
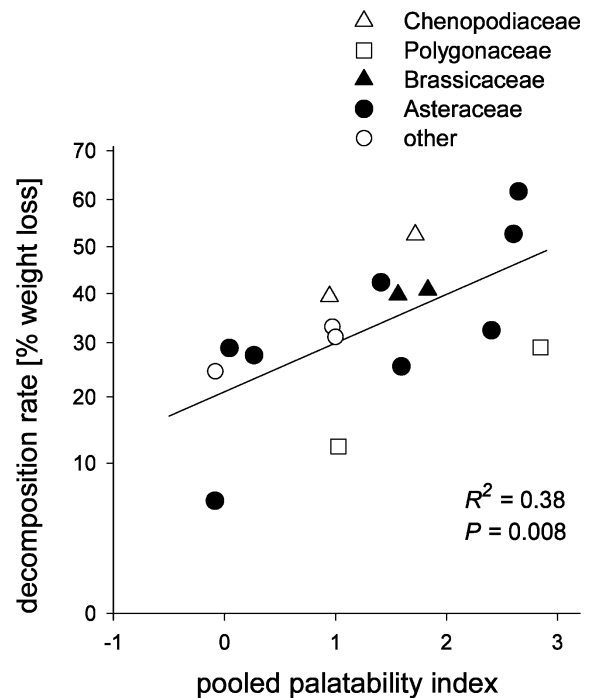

Fig. 4. Relationship between palatability of living leaves (averaged across two herbivores *Deroceras reticulatum* and *Acheta domesticus* and litter decomposition rate of plant species which occurred in successional old-field plant communities (see also Fig. 2 and Fig. 3).

Table 2. Change in cover abundance of the most frequent plant species of the experimental field (occuring in more than a third of the plots) to insectcide application. No interactions between the effects of both insecticides could be found. Therefore, percentage change refers to yearly means of the main factors. Significance levels refer to repeated measures-ANOVA and are given as n.s. for $p > 0.1$, (*) for $p < 0.1$, * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$. If no significance level is given, data did not fulfill the assumptions of ANOVA.

species	year 1				year 2			
	foliar insecticide		soil insecticide		foliar insecticide		soil insecticide	
	change [%]	effect size d	change [%]	effect size d	change [%]	effect size d	change [%]	effect size d
Chenopodium album	7.97 n.s.	0.21	−0.6 n.s.	0.00	27.9 n.s.	0.16	191.0***	0.65
Cirsium arvense	5.6 n.s.	0.08	28.4 (*)	0.38	13.7 n.s.	0.32	44.2***	0.91
Conyza canadensis					−37.1*	−0.51	21.0 n.s.	0.21
Descurainia sophia					−8.7	−0.03	−19.4	−0.08
Epilobium adnatum					−0.2 n.s.	0.00	−79.7***	−1.81
Fallopia convolvulus	−15.3 n.s.	−0.18	−10.6 n.s.	−0.12	−12.3	−0.13	−4.0	−0.04
Galium aparine	122.0	0.47	80.6	0.36	52.2	0.42	20.8	0.19
Lactuca serriola					−49.0**	−0.60	−15.3 n.s.	−0.15
Polygonum aviculare	−14.0	−0.08	19.9	0.10	159.0	0.44	68.1	0.25
Polygonum lapathifolium	129.0	0.39	−47.3	−0.31				
Sonchus asper					−25.5 n.s.	−0.22	−76.9***	−0.93
Sonchus oleraceus					24.1	0.12	−51.1	−0.38
Stellaria media	63.2	0.34	17.1	0.11	13.2 n.s.	0.11	−72.3*	0.48
Tripleurospermum maritimum					−37.7	−0.20	165.0	0.40

Relationship between palatability and changes in cover abundance of plant species induced by herbivores

In the first year, the vegetation was dominated by monocarpic forbs (especially *Chenopodium album*). Some of these species showed strong treatment mediated percentage changes of cover abundance (e.g. *Galium aparine*, *Polygonum lapathifolium*, *Stellaria media*, Table 2). Most species were very patchly distributed across the experimental plots and means were associated with high standard errors. The percentage change of cover abundance was therefore not reflective of effect size d (Table 2). The only abundant polycarpic species in the first season was *Cirsium arvense*, which developed predominantly from root fragments and showed a marginally significant increase of cover abundance with the application of soil insecticide. In the second year, the two polycarpic clonal herbs *Cirsium arvense* and *Epilobium adnatum* dominated the community. Whereas the former species showed a substantial increase with the application of soil insecticide, the latter was strongly decreased in this treatment (Table 2). Some of the more abundant monocarpic forbs showed strong positive responses to soil insecticide, whereas less abundant species like *Lactuca serriola* and *Sonchus asper* showed negative responses. In general, the effects of foliar insecticide were less pronounced. However, the monocarpic species *Conyza canadensis* and *Lactuca serriola* were negatively affected by this treatment (Table 2).

In 1998 seven plant species and 13 species in 1999 were common enough to allow for correlation analysis of changes in cover abundance induced by herbivores versus palatability (Table 2). In none of the four correlations (two treatments in 1998 and 1999) we found any significant relationship between palatability of plants and the effect size of insecticide treatments (Fig. 5).

Discussion

Effect of functional leaf traits on palatability and decomposition

Our study showed that within a functional group of plants (dicotyledonous herbaceous plants) of a given successional state, palatability and decomposition rate may vary considerably. Both parameters showed qualitative similar correlations with leaf and litter traits which indicate relative growth rate and competitive ability, such as nitrogen content, carbon content, water content and specific leaf area (Weiher et al. 1999). In general, fast-growing plant species tend to be more palatable due to the enhanced allocation of resources to re-growth rather than to mechanical or chemical defences, which are often carbon-based (Feeny 1976, Rhoades and Cates 1976, Southwood et al. 1986, Coley 1987). Deterrents against herbivores are also effective deterrents against decomposers (Grime et al. 1996, Wardle and Lavelle 1997, Wardle et al. 1998). According to Grime et al. (1988) all plants in our study were fast-growing competitors or ruderals. This may explain why the correlation between palatability and decomposition rate is less close in our study than in Grime et al. (1996), where a broad functional and taxonomical range of vascular plant species were used. The importance of the range of species included in a comparative study for the outcome of this study is highlighted by the
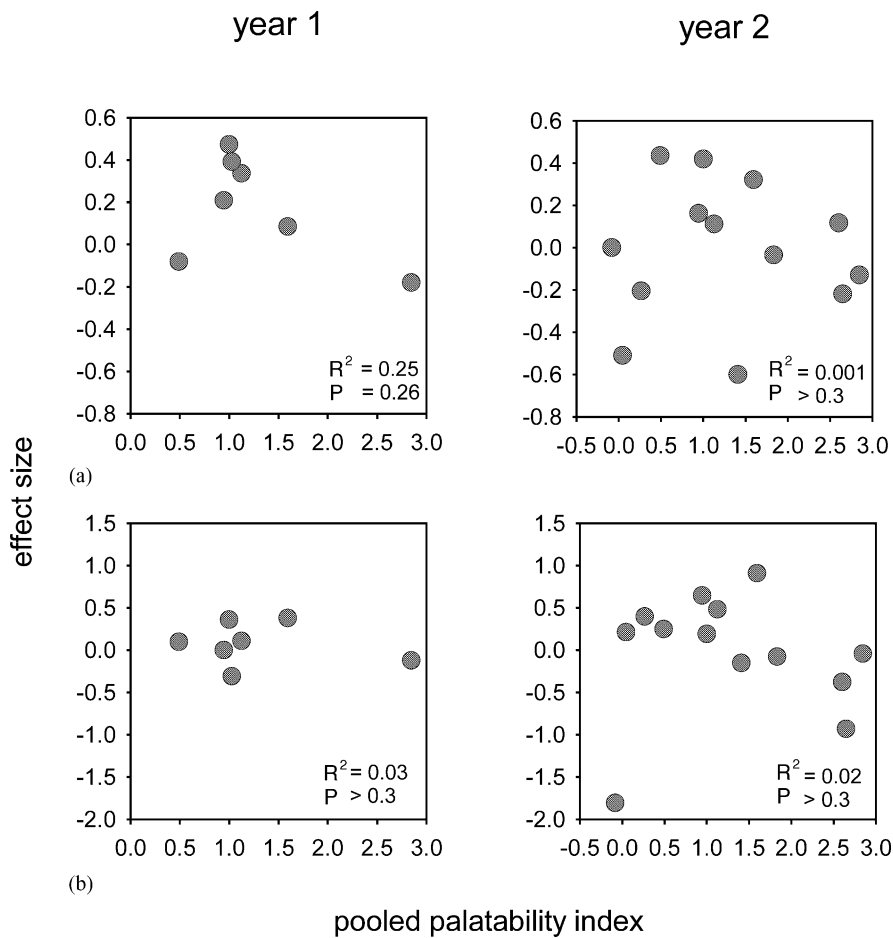
Fig. 5. Relationship between plant palatability and effect size of the change of cover abundance of plant species caused by applying (a) foliar insecticide and (b) soil insecticide during the first two years of secondary succession on an old-field. Since there are no significant relationships, no regression lines are drawn.

results of Wardle et al. (1998), who found only marginally significant or non-significant (but always positive) relationships between leaf litter decomposition rates of 16 dicotyledonous herbaceous plants species and their palatability. The results of our experiments are intermediate between the results of Grime et al. (1996) and Wardle et al. (1998). Wardle et al. (1998) did not use a pooled palatability index but performed separate analyses with the palatability indices from each of their two herbivores. However, averaging the consumption across herbivores may help to obtain a more general measure of plant palatability, which may be more indicative for the field situation with many quite different herbivores.

Functional leaf traits are correlated to litter decomposition and leaf palatability. Nitrogen content was positively correlated to both parameters, whilst carbon content was only negatively correlated to palatability. Indeed, nitrogen content of leaves shows often a negative relationship to carbon content, especially to lignin (Waring et al. 1985). So, it may be difficult to keep the effects of both parameters apart. In our study, nitrogen content was not correlated with carbon content. Thus,

plant palatability may be limited by both parameters which is also indicated by the hierarchical partitioning (Table 2). Furthermore, nitrogen content may be related to the form of carbon in leaf tissue. Plants often do not differ in leaf carbon content, but they can differ tremendously in the contents of leaf lignin, leaf phenolics, etc. In general, slow growing plants in nutrient poor habitats should have higher concentrations of carbon-based secondary compounds (Coley 1987, Davidson 1993). Obviously, variability of the carbon content in leaves of plants at a given site also modifies palatability. In our study, however, nitrogen content was found to be the most important factor for palatability as well as decomposition at least when phylogenetically independent contrasts are used.

Plants show a broad spectrum of trade-offs which generate correlations between leaf traits. Therefore, some simple parameters may be good estimators for general functional and ecological syndromes of traits (Wardle et al. 1998, Weiher et al. 1999). Specific leaf area and water content of living leaves are correlated to relative growth rate and the rate of photosynthesis (see references in Weiher et al. 1999). On the other hand,

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growth rate is a surrogate for competitive ability (Keddy et al. 1994), seedling establishment (Grime and Hunt 1975, Poorter and Remkes 1990, Van der Werf et al. 1993) and ecological plasticity (Weiher et al. 1999). Further, Grime et al. (1988), MacGillivray and Grime (1995), Ryser (1996) and Poorter and Garnier (1999) found a close relationship between specific leaf area, and leaf water content and characters, which indicate stress tolerance in plants.

In a phylogenetically controlled analysis the majority of relationships between palatability, decomposition, and leaf and litter traits remained significant. Only the correlation between palatability and the specific leaf area failed to pass significance (Table 2). Apparently morphological traits show more phylogenetic conservatism compared to chemical characters of leaf tissue (Prinzing et al. 2001). Furthermore, specific leaf area confounds the effects of tissue density and leaf thickness and may show a high variability between replicates (Wilson et al. 1999). Thus leaf dry matter is regarded as a more reliable surrogate for relative growth rate (Weiher et al. 1999).

By comparing the preferences of invertebrate generalists for 15 perennial herbs, Hendriks et al. (1999) found significant correlations between palatability and leaf defence traits. Whilst these correlations did not hold after phylogenetic correction, one relationship emerged only when analysing phylogentically independent contrasts. These findings are different from our study, where a phylogenetically controlled analysis did not yield other results than the comparative method. In part this may due to the fact, that in the phylogeny used by Hendriks et al. (1999) many plant species are linked by polytomies. This decreases the number of contrasts and weakens the power of the statistical test. Furthermore, all plants were grown under standardized, resource-rich conditions. Hence growth and herbivore-defence investment may differ from the natural situation. Thus, the hypothesis of a 'context dependent defence' (Hendriks et al. 1999) should be considered in further studies.

Plant palatability and insect herbivory induced changes of community composition

Independent of the underlying mechanisms, these relationships between palatability, decomposition and functional leaf traits may have an impact on nutrient cycle and productivity of plant communities. If herbivory causes a shift toward less unpalatable plant species (Grime 1979, Coley 1980) which also produce a slowly decomposing litter, herbivores should also influence nutrient cycles (Pastor and Cohen 1997, Bardgett et al. 1998, Cornelissen et al. 1999). We could not find any relationship between insect herbivory-induced changes in cover abundance in the field and plant palatability.

Thus, shifts in dominance hierarchy due to insect herbivory which we found during our experiments, are not the result of differences in the palatability between species. This is in contrast to results obtained from studies with vertebrate herbivores. Diaz (2000) showed that the exclusion of rabbits led to an increase of plant species preferred by rabbits. This has also been shown for large vertebrate grazers (Pastor and Naiman 1992, Brathen and Oksanen 2001). Wardle et al. (2002) found a significant positive correlation between litter decomposition rates of understorey and canopy tree species in natural forest throughout New Zealand and the extent to which vegetation density was reduced by browsing deer and goats. However, plants can compensate for herbivory by regrowth. We showed that preferred plants are characterized by traits which are indicative for high relative growth rates. Thus, preferred species may compensate fast for tissue loss. On the other hand, Belovsky and Slade (2000) showed that preferential feeding of grasshoppers on nutrient poor plants speeds up nitrogen cycle and increases plant production by increasing the abundance of species with higher nitrogen requirements. Nevertheless, our results support the view that changes in plant communities due to insect herbivory are the result of shifts in competition regimes and not the result of consumed plant biomass (Rees and Brown 1992). Carson and Root (2000) showed, that insect herbivory in an old field dominated by *Solidago altissima* increased the abundance of understory forbs indirectly by augmenting light availability. Thus, the regulation of plant communities by herbivory is the result of interacting effects of herbivore preference, resource availability and plant competition regime.

In our study, plant palatability is not related to insect herbivory induced changes of plant community structure. In fact, the greatest changes in plant dominance were related to the reduction of below-ground insects, whereas palatability tests were done with plant leaves. As shown by Karban and Baldwin (1997) and Craine et al. (2002), and below-and above-ground parts of plants often share similar morphological and chemical traits. In a recent review, Blossey and Hunt-Joshi (2003) point to a significant lack of knowledge about the role of root herbivores in natural systems. As palatability and decomposition are correlated to leaf and litter traits, the impact of insects on ecosystem processes will not follow simple linear patterns. Hence we have to conclude that variations in palatability across species is not a good predictor for shifts in the composition of our successional plant community and associated shifts in ecosystem processes.

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Appendix 1. Leaf and litter traits of 22 plant species which are common in successional old-field plant communities of Central Europe. Palatability is given as mg consumed plant dry matter per g herbivore fresh weight. – = not determined. SLA = specific leaf area. SE = standard error.

species	leaf					litter			palatability *Acheta*		palatability *Deroceras*	
	water content [%]	SLA [mm²/mg]	N [%]	C [%]	C/N	N [%]	C [%]	C/N	mean	±SE	mean	±SE
Amaranthus retroflexus	79.6	12.8	3.44	37.7	11.0	1.48	33.8	22.8	1.28	0.27	0.66	0.49
Atriplex nitens	79.2	14.9	4.75	41.3	8.7	1.45	35.8	24.7	2.59	0.43	0.84	0.15
Capsella bursa-pastoris	–	22.1	3.89	37.0	9.5	1.54	49.1	31.9	–	–	–	–
Chenopodium album	78.0	13.2	3.78	37.6	9.9	1.42	42.8	30.1	1.47	0.44	0.42	0.20
Cirsium arvense	82.4	9.39	2.92	38.8	13.3	1.63	36.9	22.6	1.70	0.57	1.49	0.23
Conyza canadensis	74.9	18.1	3.28	43.6	13.3	1.35	38.2	28.3	1.30	0.12	−1.21	0.12
Descurainia sophia	73.7	14.0	4.26	41.9	9.8	1.21	39.2	32.4	2.17	0.20	1.49	0.2
Epilobium adnatum	75.2	16.8	2.48	42.2	17.0	1.70	33.2	19.5	0.22	0.32	−0.39	0.21
Fallopia convolvulus	79.8	14.7	3.63	38.0	10.5	1.24	34.5	27.8	5.16	1.19	0.53	0.42
Fumaria officinale	84.3	11.1	3.22	39.8	12.4	–	–	–	1.10	0.91	0.48	0.19
Galium aparine	73.8	10.7	2.51	39.2	15.6	1.91	39.9	20.9	2.17	0.47	−0.17	1.04
Lactuca serriola	83.1	18.3	2.80	41.4	14.8	1.71	39.8	23.3	2.12	1.14	0.70	0.39
Tripleurosp. maritimum	81.9	6.87	2.22	43.0	19.4	1.37	43.2	31.5	0.17	0.46	0.36	0.07
Polygonum aviculare	73.9	17.4	3.91	41.9	10.7	1.51	39.5	26.2	1.22	0.62	0.84	0.32
Polygonum lapathifolium	78.2	19.7	3.31	40.5	12.2	1.41	37.3	26.5	2.12	0.47	1.52	0.34
Sisymbrium loeselii	80.2	23.5	3.59	40.2	11.2	1.24	32.7	26.4	1.74	0.63	1.39	0.35
Solidago canadensis	66.9	13.3	2.06	43.8	21.3	0.67	42.9	64.0	−0.02	0.11	−0.15	0.43
Sonchus asper	85.8	29.0	3.29	40.0	12.2	1.84	38.5	20.9	3.59	1.06	1.71	0.36
Sonchus oleraceus	86.2	19.8	3.43	42.6	12.4	1.70	41.6	24.5	4.28	1.08	0.92	0.35
Stellaria media	89.5	7.15	4.11	37.6	9.1	–	–	–	1.63	0.38	0.62	0.61
Taraxacum officinale	79.0	25.4	2.77	35.5	12.8	0.96	36.8	38.3	3.46	0.68	1.35	0.25
Thlaspi arvense	–	9.39	3.42	36.5	10.7	1.55	33.6	21.7	–	–	–	–