

Direct and indirect effects of above- and below-ground insect herbivory on plant density and performance of *Tripleurospermum perforatum* during early plant succession

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The effects of above- and below-ground insect herbivory on scentless chamomile, *Tripleurospermum perforatum* (Mérat) Wagenitz, were evaluated in a natural plant community by manipulative field experiments in 1988 and 1990. Foliar and soil insecticides were applied singly and in combination during the early colonisation of bare ground. The effects on plant density and performance were assessed and related to the occurrence of damage and of insect herbivores.

The efficacy of the insecticide treatment was evidenced by a reduction in visible damage and in the number of stems and flower heads infested. A number of insect species were found by dissection of stems and flower heads. The density of plants and their cover abundance (a reflection of the number of stems) were increased by a reduction in herbivory above or below ground, while plants in the combined insecticide treatment were taller and thinner. There was no significant interaction between the effects of the two insecticides.

The study highlights the importance of separating direct effects of herbivore reduction in a given plant species from indirect effects resulting from the modification of the competitive balance between plant species.

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Experiments on the role of insect herbivory in early plant succession, using selected insecticides to reduce above- and below-ground herbivores, have shown that certain plant species respond with a significant increase in performance (Brown and Gange 1989, Brown 1990). Annual forbs (non-graminaceous, herbaceous species) show a range of responses to insecticide application, suggestive of differential herbivore pressure on them. Individual plant performance, however, has only rarely been examined in community application of insecticides, and study has focussed on foliar feeding species (Brown et al. 1987,

Gange et al. 1989, see also review by Gange 1990). Although communities have been shown to be differentially affected by a reduction of subterranean and foliar herbivores (Brown and Gange 1989), little is known about the impact of below-ground herbivory on individual plant species. Indeed, few studies have even considered the root-feeding guilds (but see Clements et al. 1986, Goldson et al. 1987, Müller-Schärer 1991, Müller-Schärer and Schroeder 1993).

Application of insecticides to entire plant communities can influence a plant species, a) directly, by lowering the

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plant's herbivore load, and/or b) indirectly, by decreasing the herbivore pressure on neighbouring plant species and therefore potentially increasing their competitive ability. Thus, if the herbivore load varies between plant species, the insecticide may also influence individual plant species by modifying competitive interactions.

In earlier work, ruderal forb species which showed strong responses to insecticide application included the composite, *Tripleurospermum perforatum* (Brown and Gange 1989). This species was therefore considered to be an ideal 'model' for a more detailed study of the insect herbivores and the interactions between their impact and plant competition. In addition, some knowledge exists about its specialized herbivores, especially those being assessed in biological control programmes (Freese 1991, Freese and Günther 1991a, b).

The aim of the present study was to assess the impacts of insect herbivores on *T. perforatum*, using manipulative field experiments involving the judicious application of foliar and soil insecticides, applied separately and in combination. Assessment of the herbivore species composition allows the effects of insecticide application on plant performance to be related to the levels of herbivory, above and below ground. Damage-independent effects of the insecticide can then be discussed in terms of modification of the competitive balance between plant species.

Methods

Two adjacent field sites (30 m × 18 m) in the first year of colonisation of bare ground in 1988 and 1990 were prepared according to the methodology described in Brown and Gange (1989). Using a randomised block design, each of five blocks containing four 3-m × 3-m plots (separated by 2-m 'walkways') were allocated to the following four treatments: 1) control, with natural levels of insect herbivory, 2) foliar insecticide (Dimethoate-40), to reduce leaf- and flower-feeding insects, 3) soil insecticide (Dursban 5G), to reduce below-ground insect herbivory and 4) a combination of both insecticides. Details of the insecticides used, the method and rate of application and their efficacy are given in Brown and Gange (1989). The experimental sites were fenced to exclude rabbits, and mollusc herbivory was reduced by the application of slug pellets.

In 1988, the vegetation was sampled using pins (3 mm in diameter) at three-weekly intervals from mid-April to late September inclusive. The number of touches of *T. perforatum* on 50 pins (5 linear frames of 10 pins – see Brown and Gange 1989) for each plot on each sampling occasion was used to derive measures of frequency (number of pins touched), cover abundance or local shoot frequency (total number of touches of pins) and height (expressed as the weighted mean height index, based on

the number of touches at different height intervals on the pin, see Gibson et al. 1987).

In 1990, *T. perforatum* density was determined mid-season (16 July) by randomly positioning three 0.25-m² frames in each plot and assessing the number of plants rooted within the quadrat area. The following day, 10 *T. perforatum* plants were randomly marked in each plot, dug up and carefully dissected under a microscope. The occurrence and type of herbivore damage were recorded for each shoot and for each of 10 randomly selected flower heads per plant. This allowed assessment of the number of plants damaged (showing signs of insect damage), the number of plants with the main shoot infested and the relative number of shoots and flower heads damaged by phytophagous insects. Maximum "plant height", "shoot number", "total shoot length" (the combined length of all shoots from a single plant) and the maximum "shoot diameter" were also measured (high values of the latter may reflect damage/galling to the central shoot, or vigorous growth due to reduced level of herbivory or competition). An additional 100 flower heads from each plot were randomly chosen from the dissected plants, stored in small emergence boxes and checked daily for the emergence of adult insects. By mid-August, when no further emergence took place, the flower heads were dissected, but no remaining or dead larvae or pupae were found.

Two-way analyses of variance, with blocks as the replication factor and foliar- and soil-insecticide as the treatment factors, were performed for data on frequency, cover abundance and height of *T. perforatum* in 1988, and the damage and performance variates assessed in 1990. In 1988, for each plot, the maximum seasonal value for "frequency", "cover abundance" and "height" was used in the analysis, since the magnitude of the treatment effects varied greatly over the season. Performance variates assessed in 1990 were based on plot means to avoid pseudoreplication. Analysis of covariance, with plant damage as the covariate (estimated at the individual plant level), was also performed to determine damage-independent effects of the insecticide treatments on plant performance variates. The proportion of shoots and flower heads damaged were angularly transformed, plant height (maximum shoot height), maximum shoot diameter and total shoot length were log-transformed, while the number of shoots per plant and average number of shoots per plant were square-root transformed to satisfy statistical assumptions. All statistical analyses were carried out using the general statistical program GENSTAT 5 (Payne 1987).

Results

Effects of insecticide application on frequency, cover abundance and height of T. perforatum in 1988

The application of insecticides to the plant community establishing on bare ground significantly increased maxi-

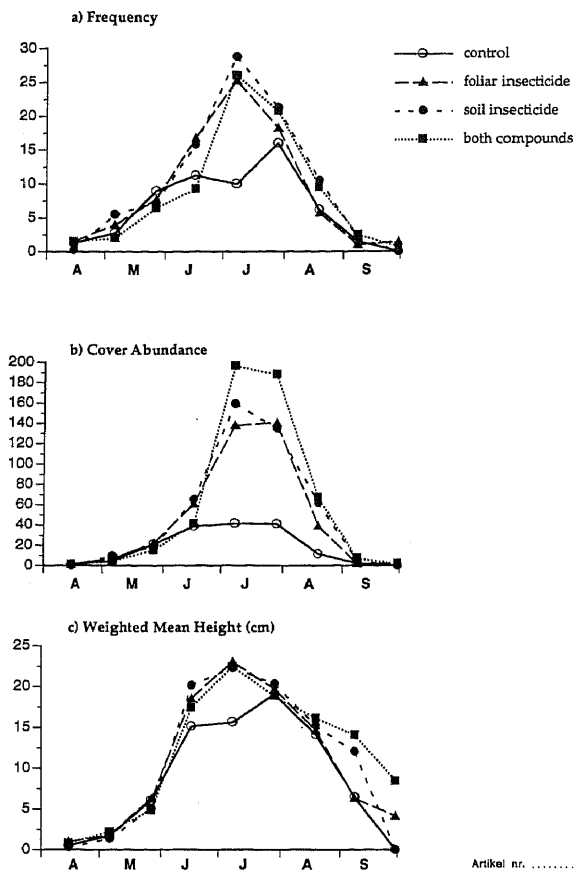


Fig. 1. Responses of *Tripleurospermum perforatum* to plant community application of foliar and soil insecticides.

num cover abundance of *T. perforatum* ($F_{\text{Foliar Ins. (1,13)}} = 7.15, P < 0.05$; $F_{\text{Soil Ins. (1,13)}} = 12.8, P < 0.01$), while the application of both insecticides increased the level above that achieved by either on their own (Fig. 1a). The combined application resulted in a 4.5-fold increase in cover abundance during the summer months, compared to untreated plots. However, the magnitude of the effect varied considerably over the growing season, mainly as a result of the low cover abundance of the species early and late in the season. No significant effects of the two insecticide treatments, however, were observed on mean height (Fig. 1b) or frequency (Fig. 1c), although the plants in the untreated plots tended to be smaller and less abundant during the summer. Indeed, based on maximum values, plants subjected to both insecticides were significantly taller, while plants treated with soil insecticide were significantly more abundant than plants in the control plots (Fisher's PLSD, $P < 0.05$).

Effects of insecticide application on plant density and plant performance variates in 1990

In 1990, the application of insecticides led to an increase in density of *T. perforatum* (number of plants per plot)

(Fig. 2a), while the average number of shoots per plant was decreased in plots treated with insecticides (Fig. 2b). The application of the soil insecticide also resulted in a decrease in total shoot length per plants (Fig. 2e). However, plant height and shoot diameter were significantly increased and decreased, respectively, only when both insecticides were applied (Fig. 2c, d). Apart from plant density, there were no significant interactions between the insecticide treatments, indicating that their effects on these performance variates may be additive.

Effects of insecticides on levels of insect herbivory of *T. perforatum*, and its impact on plant performance in 1990

The application of both foliar and soil insecticide significantly affected the number of plants damaged, the number of plants with the main shoot infested, as well as the relative number of shoots and flower heads attacked (Ta-

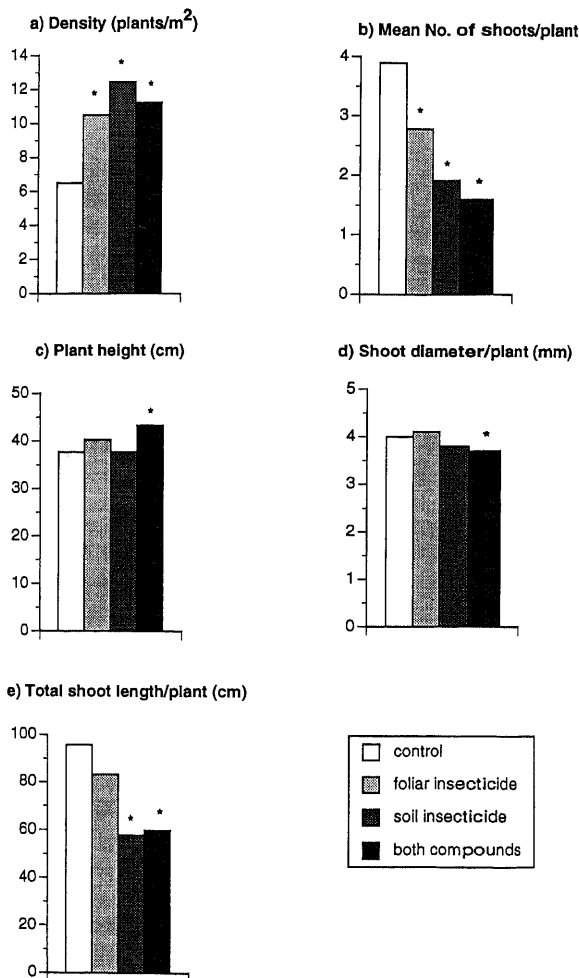


Fig. 2. Mean values of plant density and performance variates of *Tripleurospermum perforatum* exposed to different insecticide treatments during early plant succession. * = significantly different from the controls (Fisher's PLSD, $P < 0.05$)

Table 1. ANOVA on damage by insects on shoots and flower heads of *T. perforatum* following different insecticide treatments. Sums of squares (SS) and significance levels of F-ratios are given (* P < 0.05; ** P < 0.01; *** P < 0.001; see text for data transformation)

Source of variation	df	Plants damaged	Main shoot infested	% Shoots damaged	% Fl. heads damaged
Block effect	4	1.87	0.320	792	3.566
Foliar-Ins. (F)	1	3.92**	4.805***	6690*	24.837***
Soil-Ins. (S)	1	6.48**	2.645***	7367*	18.051***
F × S	1	0.18	0.845**	554	1.080
Error	12	3.37	0.880	10736	9.033

ble 1), with all these parameters being reduced when either insecticide was applied. In order to determine whether the effect of the treatment on the plant performance variates was solely a consequence of the insecticide on the level of herbivory, an analysis of covariance was performed with the observed plant damage as the covariate (Table 2). A reduction in herbivory can explain the insecticide effect on shoot length, shoot number and maximum shoot diameter, as no damage-independent effects of the insecticide treatments were observed for these plant traits. However, plant height was significantly increased by foliar insecticide treatments independently of plant damage (herbivore effect), assuming a linear effect of the covariate (Table 2).

The herbivores, and how they were affected by the insecticide treatments

Weevil larvae, most likely *Ceuthorrhynchus rugulosus* Herbst, which was found in sucking samples from *T. perforatum* in previous years (Hyman 1983), and the agromyzid fly, *Napomyca lateralis* Fallen, were the dominant species found by dissection of the stems. Both species oviposit on the leaves, mine in the stem and occasionally also attack the receptacle. *Napomyca lateralis*, which is reported to have 2–3 generations in Germany (Freese and Günther 1991a), was mainly responsible for the infestation of the young central shoot, which as a result remained less than 5 cm in length and eventually dried up. In other plant species, this type of attack has been found to remove apical dominance, subsequently stimulating the growth of side shoots (e.g. Müller-Schärer 1983, Steinger and Müller-Schärer 1992). This may well explain the increased number of shoots produced by plants in the control (herbivore) plots. The

maximum shoot diameter generally refers to the infested, stunted or dead central shoot of plants subjected to herbivory. Increased values may be a consequence of the attack resulting in a stunted growth form, sometimes resembling a gall-like enlargement.

No internal-feeding root herbivores were detected in this study, but some signs of both internal and external attack were observed. Soil samples, however, revealed large numbers of larvae of tipulid and scarabaeid species which are known to feed on seedlings of *T. perforatum* (S. Garzaroli, pers. comm.). Bacher (1994) and Hinz (1994) recently conducted field surveys in Europe for potential biological control agents against *T. perforatum* in Canada. They found two additional, most probably host plant specific root-mining weevils, *Coryssomerus capucinus* (Beck.) and *Apion confluens* Kirby, associated with the roots in most of the sites examined. However, these species were not encountered here.

The commonest species emerging from flower heads was *Apion hookeri* Kirby (Fig. 3), a monophagous weevil, which feeds exclusively on seeds of *T. perforatum* (Freese 1991). Adults feed on the host plant in early spring, before reproduction, and eggs are laid in the tubular flowers. After a developmental time of up to 7 weeks, adults emerge from the flower heads (Freese 1991). *Olibrus aeneus* Fab. (Coleoptera: Phalacridae), another species emerging from the flower heads, is oligophagous on several species of Anthemideae (Asteraceae) (Freese and Günther 1991a). The larvae are mainly phytophagous, feeding on the seeds and receptacle, but occasionally also attack larvae of other insects which inhabit flower heads. Ovipositing adults appear on the host plants in early spring and eggs are laid between the bracts and tubular flowers of young flower heads. Larvae

Table 2. ANCOVA on damage-independent effects of insecticide treatments on plant performance of *T. perforatum*. Sums of squares (SS) and significance levels of F-ratios are given (*P < 0.05; ***P < 0.001; see text for data transformation).

Source of variation	df	Plant height	Shoot number	Shoot length	Max. shoot diameter
Block	4	0.176	1.487	2.469	0.192
Foliar-Ins. (F)	1	0.675*	0.256	0.254	0.002
Soil-Ins. (S)	1	0.272	2.176	0.785	0.16
F × S	1	0.023	0.222	0.133	0.014
Error	12	0.177	5.552	7.169	0.272
Covariate (Shoot damage)	1	0.003	7.035***	7.739***	0.932***
Error	179	6.083	53.473	75.871	7.937

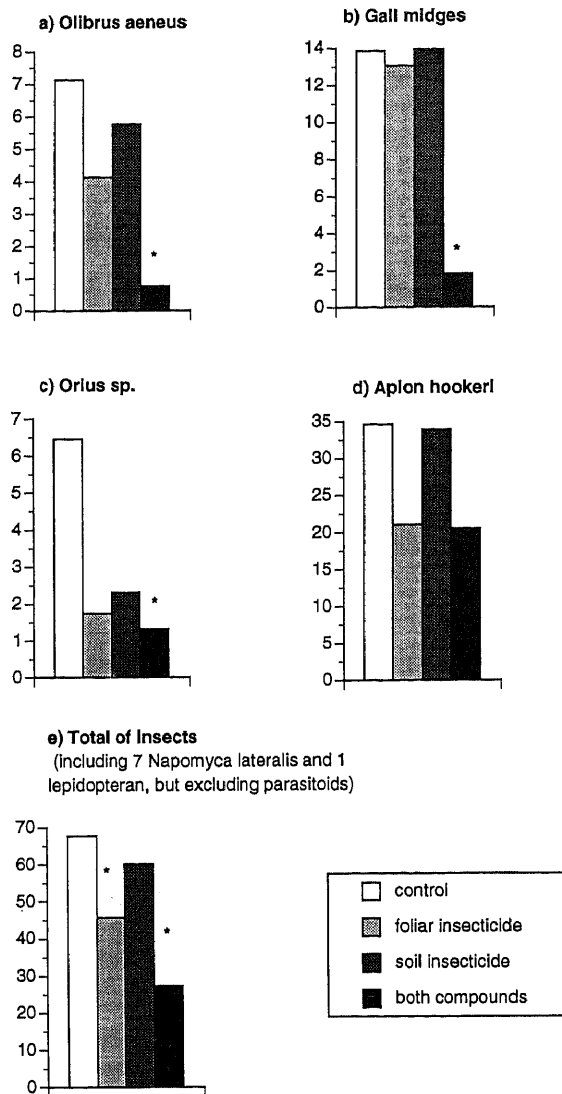


Fig. 3. Mean number of phytophagous insects emerging from 100 flower heads of *Tripleurospermum perforatum*, exposed to different insecticide treatments during early plant succession (back-transformed data). * = significantly different from the controls (Fisher's PLSD, $P < 0.05$)

often move to other flower heads to complete their development and pupation takes place in the soil. Adults reappear on the flower heads in late summer (Günther 1988, Freese and Günther 1991a). These two coleopteran species were also dominant in *T. perforatum* samples from Northern and Southern Germany (Freese and Günther 1991b). Larvae of *Orius sp.* (Hemiptera: Anthororidae), which are generalists, but predominantly predatory, were also frequently found in the flower head samples, possibly emerging from eggs which were laid in or on the flower heads.

The application of foliar insecticide reduced the num-

ber of insects (excluding parasitoids) emerging from the flower heads by 33% (Fig. 3). This reduction was mainly a consequence of the significant decrease in *A. hookeri* and *O. aeneus*. In addition, the seven *N. lateralis* flies recorded from the flower head samples emerged from plants where no foliar insecticides had been applied.

However, the effect of foliar insecticide application on the emergence of adult flower feeding insects does not match the highly significant decrease in damage to flower heads in this experimental treatment (Table 1). This suggests that the foliar insecticide, although systemic, may have relatively little effect on the development of seed and receptacle feeding stages, especially the gall midges. In addition, insects such as *Apion* spp. develop quickly in the flower heads and may escape effects of the insecticides.

Discussion

Whole-plant community responses to insect herbivory have been studied in considerable detail (e.g. Brown 1990, and references therein). However, few studies have addressed responses of single species within the community (Brown et al. 1987, Gange et al. 1989), although such studies are clearly of value in interpreting community responses (Gange 1990). Furthermore, knowledge of the response of single plant species to insect herbivory within a community offers an excellent tool for managing plant communities. Specifically, the experiments show that insect herbivory plays a significant role in reducing *T. perforatum* density during early plant succession. Such plant communities are common after disturbances as in schemes such as Set-Aside in Europe. In the Canadian prairie provinces, where *T. perforatum* is a significant problem, biological control programmes have recently started against this plant species (Bacher 1994, Hinz 1994).

The higher cover abundance in 1988 following the application of insecticides, may result from either increased plant numbers or from more flowering stems per plant. The experiments in 1990 subsequently showed that application of both insecticides increased *T. perforatum* density. Individual plants, however, produced fewer shoots and were thinner and taller (Fig. 2). The finding that this latter effect (Fig. 2c) was independent of the herbivore effect (Table 2) is, at first sight, surprising. However, increased competition is normally expected to reduce plant biomass, while plant height may be increased (Tilman 1988, Weiner and Thomas 1992), as occurred here during summer. A direct effect of the insecticide on plant growth can be disregarded (Brown and Gange 1989). The results highlight the need to tease apart direct and indirect effects of insect herbivory on plant communities.

Several insect species associated with different plant organs and various plant tissue were found. Further and

more detailed studies are needed, however, to interpret the effects of the insecticides more precisely and to relate the observed damage to individual herbivore species. Specific root feeders often lay their eggs on plant leaves and early stages are therefore susceptible to foliar insecticides before they reach the roots (Müller-Schärer 1989). In this way, root herbivory may well be influenced by application of a foliar insecticide. On the other hand, the fact that the application of a soil insecticide also reduced the number of flower heads damaged (Table 1) cautions against attributing the effect of a soil insecticide only to below-ground herbivores. This is especially the case for *O. aeneus*, which pupates in the soil and showed slightly reduced numbers in the plants treated with soil insecticides. Presumably, last instar larvae were killed by the insecticide. These results clearly indicate that knowledge of the biology of the herbivore species is necessary to interpret the results of manipulative experiments such as those described here. Surprisingly, many workers pay little attention to this.

The effect of the seed feeders on seed output of *T. perforatum* was not assessed, since very few seeds were produced in 1990 due to extreme drought conditions during spring and summer. In the plots exposed to natural levels of herbivory, however, 51% of the flower heads were infested as compared to only 14% of the plants exposed to both insecticides. Under adverse climatic conditions, such losses due to herbivory may well lead to seed limited population recruitment. This is the subject of ongoing work at Silwood Park.

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