



Effect of Herbivore Density, Timing of Attack and Plant Community on Performance of Creeping Thistle *Cirsium arvense* (L.) Scop. (Asteraceae)

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Creeping thistle, *Cirsium arvense* (L.) Scop. (Asteraceae), is one of the most serious weeds in ecological compensation areas (within-field or border refugia) in Europe. Since conventional weed control measures are restricted in compensation areas, augmenting indigenous agents for biological control of the weed may be a feasible alternative. In this paper, we studied the effect of density of the shield beetle, *Cassida rubiginosa* Müller (Coleoptera, Chrysomelidae), and two vegetation types typical for ecological compensation areas, on the performance of creeping thistle plants in an open field experiment. Early-season larval feeding had no measurable effect on creeping thistle growth, while late-season feeding significantly reduced shoot growth. These findings were attributed to higher feeding rates of the herbivores at higher ambient temperatures late in the season. Defoliation had a strong effect on the above-ground performance of *C. arvense* plants, but not on the below-ground performance. In contrast, the plant community affected all below-ground performance parameters measured, but only some of the above-ground performance parameters of creeping thistle. A combination of high levels of plant competition and herbivory by *C. rubiginosa* larvae led to 50% mortality in *C. arvense* plants during the growing season. We conclude that augmentation of indigenous herbivores of *C. arvense* in combination with breaking up the root system by tillage and the establishment of a highly competitive plant community of beneficial herbs may be a feasible way to control this problematic weed in ecological compensation areas.

Keywords: biological weed control, augmentation, indigenous agents, herbivory, insect–plant interaction, defoliation, density dependence, timing of infestation, plant competition, field study, ecological compensation area, *Cassida rubiginosa*, *Cirsium arvense*

INTRODUCTION

Creeping thistle *Cirsium arvense* (L.) Scop. is considered as one of the world's worst weeds (Holm *et al.*, 1977) and the third most important weed in Europe (Schroeder *et al.*, 1993). It has become increasingly problematic in ecological compensation areas where conventional control measures are restricted (Bacher *et al.*, 1997). Thus, biological or integrated control,

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exploiting both plant competition and herbivory by specialized indigenous insects, may be an inexpensive and sustainable alternative.

Ecological compensation areas are within-field or border refugia for the enhancement of biodiversity in the agricultural landscape. They are part of integrated and organic farming systems in Europe. In Switzerland, for example, certified integrated farming demands that at least 5% of the farm land is assigned for ecological compensation (Häni *et al.*, 1998). Compensation areas are often arranged as strips of 3–5 m width between fields. There are two common types of ecological compensation area: fallow land, where the vegetation recruits exclusively from the seed bank and root fragments in the soil, and seeded herb plots, where seeds of desirable herbs are added to the field after tillage. These herb species are selected for their attractiveness to beneficial arthropods (Nentwig, 1998) and their high competitive ability, so that they displace part of the natural vegetation. Apart from the augmentation of beneficial organisms, the seeded herbs are expected to suppress problematic weeds, thus restricting spread of the latter into adjacent fields and facilitating re-cultivation of the compensation area. This would compensate farmers for the added expenses related to this compensation area type. However, it is not yet clear if problematic weeds are more restricted in seeded herb plots than in fallow land.

Making use of indigenous herbivorous insects for weed biocontrol requires the augmentation of naturally occurring populations of such herbivores to higher densities. For a successful approach, knowledge must be gained on the agent densities required to obtain the desired control level, and on the factors preventing the agents to attain such population levels. Information on the latter may lead to the development of strategies to increase population densities of the agents.

This paper investigates the effect of herbivory by a shield beetle, *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae), on the performance of creeping thistle plants growing in two different plant communities, representing the two types of ecological compensation areas discussed above. In a recent study, Ang *et al.* (1995) addressed the response of *C. arvensis* to density of *C. rubiginosa* and plant competition in a field cage experiment, using the North American strains of the weed and the beetle, both of which were accidentally introduced into North America, and found severe effects of the herbivore on almost all performance parameters measured. We adapted the experiment to European conditions where both the weed and the herbivore are indigenous, taking into account current practice in preparing and managing ecological compensation areas. In order to obtain results that can be generalized to real field situations we carried out our study as an open field experiment.

MATERIALS AND METHODS

Study Site

The study was conducted 20 km from Bern on an agricultural field of 37 × 13 m. The soil of the field was a slightly organic sandy loam. There was a margin of 1.5 m width around the experimental area to the adjacent crop or road, respectively. In early March 1997, the whole site was ploughed and disk harrowed and subsequently divided into 85 2 × 2 m plots. Roots of *C. arvensis* were collected on 11 March from a nearby plant population. The roots were dug from an area smaller than 150 m² in order to obtain a low genetic variability of plant material. Roots were stored at 5–8°C in the dark and in the original soil for two weeks. On 25 March, viable root pieces of 10 cm length and 6–8 mm diameter were planted at a depth of 10–12 cm in the centre of each experimental plot. Roots of similar size were often found when digging for *C. arvensis* roots on freshly tilled agricultural fields (personal observation).

Experimental Set-up and Procedure

The study was conducted in a completely randomized two-factorial design. The two factors were 'plant community' (natural vegetation vs. a mixture of seeded beneficial herbs) and 'herbivore infestation' (no, low, moderate and high infestation level). The herb seeds were

added on 27 March at a density of 12.6 kg ha⁻¹ to half of the plots chosen at random and to the field margin (for details on the composition of the seed mixture see Schwab, 1998); in the untreated plots, plants other than the planted thistles recruited from the soil only. After seeding, the whole site was raked and rolled. Of all plots with thistles emerging until early May, 24 plots with seeded herbs and 24 plots with naturally emerging vegetation, respectively, were chosen at random. The four herbivore infestation levels were assigned randomly to the plots of the two plant communities in six replicates each. Thus, there were 2 (plant communities) × 4 (herbivore infestation levels) = 8 treatments with 6 replicates of each. The four herbivore infestation levels, no, low, moderate and high, corresponded to 0, 5, 10 and 20 larvae of *C. rubiginosa* per plant for the first three instars, and 0, 3, 6 and 12 larvae for the last two instars, respectively. This reduction was introduced to account for naturally occurring field mortality in *C. rubiginosa* (Ward & Pienkowski, 1978). *C. rubiginosa* larvae used in the experiment were reared in the laboratory. The duration of herbivore infestation matched the phenology of *C. rubiginosa* in the study region closely. On 13 June, a cohort of first instar larvae was transferred to the experimental plants. Plants were checked twice a week to ensure that the assigned number of larvae were present; missing larvae were replaced and surplus larvae removed. The most frequent instar of 50 *C. rubiginosa* larvae kept on potted creeping thistle plants located on a plot-free space on the site was determined at each census and used as the instar that was transferred to the experimental plants in the plots. After the larvae of the first cohort finished their development around 17 July and started to pupate in the surrounding vegetation, a second cohort of first instar larvae was introduced on 5 August. The second cohort finished their larval development around 22 August when the experiment was terminated.

Data Collection

The length of thistle shoots was measured weekly during the experiment. The height of the surrounding vegetation and the dominant plant species (cover abundance greater than 5%) were determined for each plot in monthly intervals. Between 26 August and 2 September, all creeping thistle plants in a 50 × 50 cm square around the planted root pieces were harvested. Roots were collected to a depth of 25 cm. The plant samples were oven dried at 60°C for 24–48 h to determine their dry weight. The following parameters were measured: the shoot length, the diameter of the shoot base, the number of leaves longer than 5 cm (hereafter termed expanded leaves), the shoot weight (all these parameters were taken for the primary shoot), the total above-ground biomass (including secondary shoots), the biomass of newly grown roots, the total below-ground biomass (including the below-ground parts of shoots), and the root-to-shoot ratio was calculated.

Storage Substances

Otzen and Koridon (1970) showed that *C. arvensis* stores fructosans, and that starch is absent. The total non-structural carbohydrate (TNC) content of freeze-dried and powdered below-ground plant parts was measured photometrically after water extraction (95°C, pH 8, 20 min) and hydrolyzation (95°C, 0.1-M HCL, 10 min) with Anthrone at 623 nm (using fructose as a standard; after van Handel, 1967). The total nitrogen content of below-ground plant parts was determined with an elemental analyzer (model NA2000, Carlo Erba Instruments, Italy).

Larval Densities in the Field

The phenology of *C. rubiginosa* was followed in the field at five sites with natural populations of the beetle from May to August. The number of *C. arvensis* shoots infested by larvae of *C. rubiginosa* and the number of larvae per shoot (all shoots included) were recorded.

TABLE 1. Repeated measures ANOVA *F* statistics for effects of plant community (Plant) and *C. rubiginosa* density (Beetle) on creeping thistle shoot height during two infestation periods

Source	SS	df	MS	<i>F</i> -Ratio	<i>P</i>
<i>First infestation period, 13.06.97–17.07.97</i>					
Plant	112.75	1	112.75	0.112	0.74
Beetle	3781.79	3	1260.6	1.249	0.305
Plant*Beetle	1391.48	3	463.83	0.460	0.712
Error	40357.31	40	1008.93		
<i>Second infestation period, 5.08.97–22.08.97</i>					
Plant	1334.68	1	1334.68	1.37	0.246
Beetle	9992.95	3	3330.98	3.46	0.025
Plant*Beetle	1988.4	3	662.8	0.69	0.565
Error	38525.48	40	963.14		

SS sum of squares; MS mean sum of squares.

Statistical Analysis

Comparisons of thistle growth were made by repeated measures analysis of variance (ANOVA) of weekly recorded shoot length data for the two infestation periods (Systat, 1997). Plant performance parameters at harvest were compared by ANOVA followed by regression analysis of thistle response to *C. rubiginosa* density (Sokal & Rohlf, 1995). If the ANOVA detected significant differences between plant communities, regression analysis was performed separately on data from each of the two plant community treatments. Otherwise, data from the plant treatments were pooled before regression. To stabilize the variances of the data, the logarithmic transformation $[\ln(y + 1)]$ was applied to weights, the square root transformation $[\sqrt{y + 0.5}]$ was applied to the counts of expanded leaves, and the arcsine transformation $[\sin^{-1}(\sqrt{y})]$ to percentages prior to ANOVA (Sokal & Rohlf, 1995). Data on shoot length and diameter were left untransformed, because transformation did not improve the homogeneity of variances and normal distribution.

RESULTS

Mortality of *C. arvensis* Root Pieces

Only 50 of the 84 planted root pieces grew shoots. Thus, we recorded a plant mortality of 40.5% prior to shooting. The mortality was equal in the natural vegetation and seeded herb mixture plots; 25 of 42 planted root pieces grew shoots in each plant community treatment.

Growth of Thistle Plants

The first cohort of larvae completed their development in 34 days, while the second cohort took only 17 days, due to higher temperatures in August. During the first infestation period no significant differences were detected in creeping thistle shoot growth (Table 1). However, during the second infestation period, significant differences between beetle treatments became evident (Table 1); the growth curves of shoots with the highest larval densities were the lowest at that time (Figure 1).

Death of Plants During the Experiment

During the experiment, 50% mortality occurred in *C. arvensis* in the seeded herb treatment at high beetle density. With the exception of a single *C. arvensis* plant, which died in one of the seeded herb plots without *C. rubiginosa* infestation, there was no other mortality. All plant deaths were recorded during the second infestation period. No live root pieces of plants that died during the experiment were found at harvest.

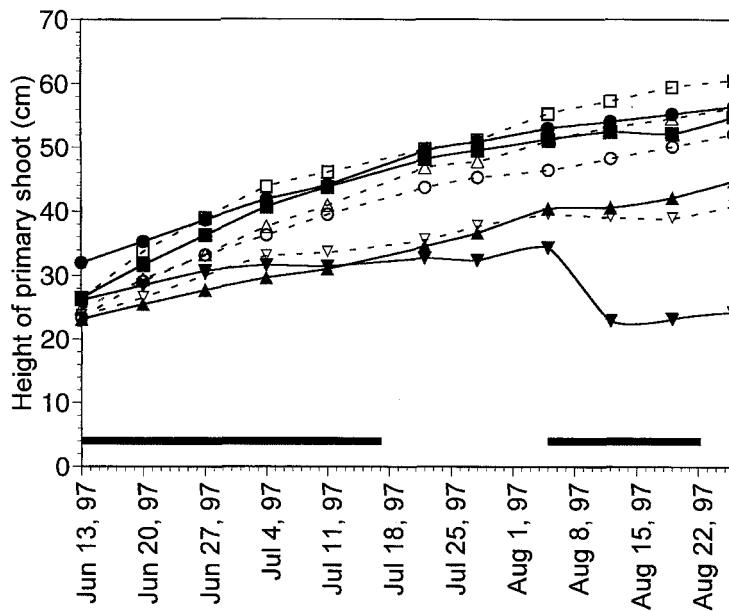


FIGURE 1. Growth of primary thistle shoots during the experiment. The bars at the bottom of the figure indicate the two *C. rubiginosa* larval infestation periods. Open symbols and dashed lines: natural vegetation; solid symbols and lines: seeded herb mixture. □ ■: control, ○ ●: low, △ ▲: moderate and ▽ ▼: high beetle density.

Vegetation Development

The major difference between the two plant communities was that the natural vegetation was dominated by ephemeral species whereas annuals and short-lived perennials were able to establish in the seeded herb community. The vegetation cover was 100% during the experiment. In May, the field was dominated by *Sinapis arvensis* L. and *Chenopodium album* L. At the beginning of the experiment in June, the vegetation of the seeded herb plots was higher than the vegetation of the natural vegetation plots (ANOVA: $F = 8.927$; $P < 0.01$). At the same time, *S. alba* L. and *Raphanus sativus* L. occurred as dominant species in single seeded herb plots and *S. arvensis*, which had dominated the field a month before, began to fade. By July, all species of the family Brassicaceae had disappeared and the field was dominated by *C. album* and *Galinsoga ciliata* (Raf.) Blake. *Trifolium pratense* L., was dominant in 62.5% of the seeded herb plots, but none of the natural vegetation plots. There were fewer dominant species in the latter type of vegetation (*U*-Test: $P < 0.01$). A total of five species (*Centaurea cyanus* L., *Borago officinalis* L., *R. sativus*, *T. pratense* and *Medicago lupulina* L.) from the seeded seed mixture were well established (ground cover $> 5\%$ in single plots). There was no difference in the vegetation height between treatments. The last measurement in August showed neither a difference in vegetation height nor in the number of dominant plant species between treatments. However, *G. ciliata*, *T. pratense* and *M. lupulina* were dominant in the seeded herb plots (the two latter are seeded herbs) whereas the natural vegetation plots were dominated by *C. album*, *Taraxacum officinale* Web. and *G. ciliata*.

Harvest

At harvest, almost all the above-ground creeping thistle parameters measured were significantly affected by beetle density (with the exception of total above-ground biomass; Figure 2), while the plant community had a significant effect only on the diameter of the shoot base, the weight of the primary shoot and the total above-ground biomass (Table 2). In

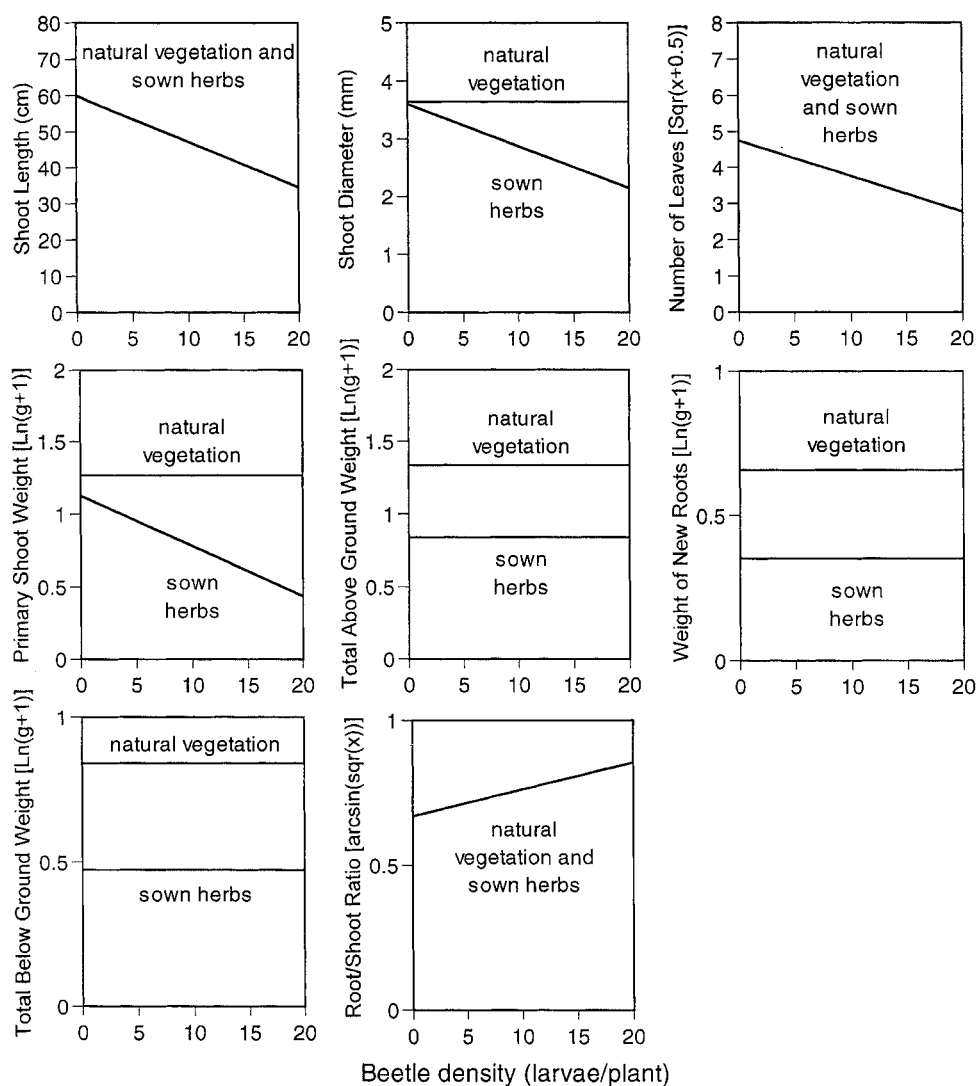


FIGURE 2. Impact of *C. rubiginosa* density and plant community on *C. arvensis*. Regressions not significant at the 5% level were displayed as means (\bar{y}). NV: natural vegetation; SH: seeded herb mixture; R^2 : coefficient of determination; P : significance level of the regression. Shoot length_{NV+SH} = $59.94 - 1.27$ Beetle density; $N = 48$, $R^2 = 0.19$, $P = 0.002$. Shoot diameter_{NV} = $4.05 - 0.24$ Beetle density; $N = 24$, $R^2 = 0.04$, $P = 0.37$, $\bar{y} = 3.65$. Shoot diameter_{SH} = $3.70 - 0.89$ Beetle density; $N = 24$, $R^2 = 0.19$, $P = 0.03$. Number of leaves_{NV+SH} = $4.76 - 0.10$ Beetle density; $N = 48$, $R^2 = 0.19$, $P = 0.007$. Primary shoot weight_{NV} = $1.55 - 0.03$ Beetle density; $N = 24$, $R^2 = 0.13$, $P = 0.09$, $\bar{y} = 1.27$. Primary shoot weight_{SH} = $1.13 - 0.03$ Beetle density; $N = 24$, $R^2 = 0.16$, $P = 0.05$. Total above-ground weight_{NV} = $1.64 - 0.04$ Beetle density; $N = 24$, $R^2 = 0.12$, $P = 0.09$, $\bar{y} = 1.33$. Total above-ground weight_{SH} = $1.12 - 0.03$ Beetle density; $N = 24$, $R^2 = 0.14$, $P = 0.07$, $\bar{y} = 0.84$. Weight of new roots_{NV} = $0.76 - 0.01$ Beetle density; $N = 24$, $R^2 = 0.04$, $P = 0.34$, $\bar{y} = 0.66$. Weight of new roots_{SH} = $0.45 - 0.01$ Beetle density; $N = 24$, $R^2 = 0.09$, $P = 0.15$, $\bar{y} = 0.35$. Total below-ground weight_{NV} = $0.96 - 0.01$ Beetle density; $N = 24$, $R^2 = 0.10$, $P = 0.30$, $\bar{y} = 0.84$. Total below-ground weight_{SH} = $0.60 - 0.01$ Beetle density; $N = 24$, $R^2 = 0.10$, $P = 0.13$, $\bar{y} = 0.47$. Root-to-shoot ratio_{NV+SH} = $0.67 + 0.09$ Beetle density; $N = 35$, $R^2 = 0.13$, $P = 0.02$.

*Note that regression analysis was performed on transformed data. Details on transformations are given in the text.

TABLE 2. ANOVA *F* statistics for effects of plant community (Plant) and *C. rubiginosa* density (Beetle) on parameters of *C. arvensis*

(a) Above-ground plant growth

Source	Length of primary shoot		Base diameter of primary shoot		Number of leaves		Weight of primary shoot		Total above-ground biomass	
	<i>F</i> -Ratio	<i>P</i>	<i>F</i> -Ratio	<i>P</i>	<i>F</i> -Ratio	<i>P</i>	<i>F</i> -Ratio	<i>P</i>	<i>F</i> -Ratio	<i>P</i>
Plant	1.596	0.214	7.055	0.011	2.398	0.129	5.796	0.021	6.334	0.016
Beetle	3.673	0.020	2.768	0.054	3.133	0.036	2.518	0.072	2.244	0.098
Plant*Beetle	0.595	0.622	0.748	0.530	0.870	0.465	0.673	0.574	0.508	0.679

(b) Below-ground plant growth

Source	Biomass of new roots		Total below-ground biomass		Root-to-shoot ratio	
	<i>F</i> -Ratio	<i>P</i>	<i>F</i> -Ratio	<i>P</i>	<i>F</i> -Ratio	<i>P</i>
Plant	7.940	0.007	9.890	0.003	0.079	0.781
Beetle	2.217	0.101	1.849	0.154	1.489	0.235
Plant*Beetle	0.097	0.961	0.485	0.695	0.357	0.784

(c) Root nitrogen content

Source	% Nitrogen in new root parts		% Nitrogen in all below-ground parts	
	<i>F</i> -Ratio	<i>P</i>	<i>F</i> -Ratio	<i>P</i>
Plant	2.886	0.099	2.000	0.166
Beetle	0.073	0.974	0.284	0.837
Plant*Beetle	0.234	0.872	0.287	0.834

(d) Root fructosan content

Source	% Fructosans in new root parts		% Fructosans in all below-ground parts	
	<i>F</i> -Ratio	<i>P</i>	<i>F</i> -Ratio	<i>P</i>
Plant	0.134	0.716	1.381	0.247
Beetle	0.443	0.724	0.036	0.991
Plant*Beetle	1.631	0.199	0.876	0.462

detail, *C. rubiginosa* infestation significantly reduced the growth of the primary shoot (Figure 2), while plant community had no significant effect (Table 2). Plant community had a significant effect on the shoot base diameter of the primary shoot (Table 2, Figure 2), while the effect of larval density was significant only in the seeded herb plots (Figure 2). The number of expanded leaves was significantly affected by beetle density (Table 2, Figure 2), but not by the plant community (Table 2). Similarly to the diameter of the shoot base, plant community had a significant effect on the weight of the primary shoot (Table 2, Figure 2), while the effect of larval density was significant only in the seeded herb plots (Figure 2). The total above-ground thistle biomass was significantly reduced in the seeded herb plots, but was not affected by beetle density (Table 2, Figure 2).

In contrast, while some of the below-ground performance parameters measured were significantly affected by the plant community, feeding by *C. rubiginosa* larvae at the experimental densities had no effect on below-ground plant performance. The biomass of newly-grown roots and the total below-ground biomass were significantly reduced in the seeded herb plots, independent of beetle density (Figure 2). Because insect defoliation affected above-ground performance more than below-ground performance, the root-to-shoot ratio increased with increasing herbivore density, independent of plant community (Table 2, Figure 2). The concentration of storage substances in root parts was not affected by either factor.

Larval Densities in the Field

Larvae of *C. rubiginosa* were first found in May at the sites visited. Populations reached their highest densities in June and July, and declined in August (Figure 3(a)). The highest

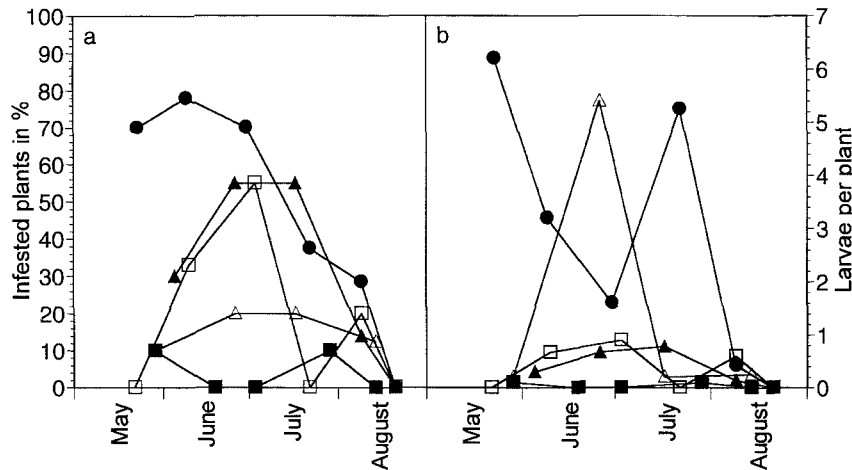


FIGURE 3. Mean *C. rubiginosa* larval densities at five sites with natural *C. arvensis* populations. The habitat types were: ● ecological compensation area; □■ ruderal site close to agricultural field; △ ruderal site; ▲ forest clearing.

larval densities were found at an ecological compensation site with more than 70% of thistle shoots infested (Figure 3(a)) and all shoots infested with an average of about two to five larvae (Figure 3(b)). However, the mean number of larvae per shoot at the other sites was less than one (except at one ruderal site at 26 June; Figure 3(b)). The highest number of fourth and fifth instar larvae found on a single thistle shoot was 9. Earlier instars occurred in densities of up to 20–30 individuals per shoot.

DISCUSSION

Mortality of Planted *C. arvensis* Root Pieces

The mortality of 40.5% of the planted root pieces was surprisingly high. For example, in a laboratory study on *C. arvensis* all root pieces of 3.5 mm diameter and longer than 2.4 cm grew shoots, and the number of shoots emerging from root pieces 2.5–10 cm long was equal or greater than the number of root pieces planted at a depth of 10 cm (Hamdoun, 1972). It appears from our study that mortality is much greater in the field than in the laboratory. Breaking up the root system of *C. arvensis*, for example by tillage, may not only limit its regrowth potential by partitioning the storage organs (Hamdoun, 1972; Dock-Gustavsson, 1997), but may also lead to high root mortality. Therefore, fragmentation of roots may substantially weaken the vigour of *C. arvensis*, and thus may facilitate subsequent control measures as a part of an integrated weed management programme against creeping thistle.

Effect of Timing of Herbivory

Growth of *C. arvensis* was more affected by the second cohort of larvae feeding late in the growing season than by the first cohort. This was probably due to the higher feeding intensity associated with the faster development of the second cohort at higher ambient temperatures in late summer. Thus, it would seem that insect densities required to effect plant growth are not the same throughout the season; higher beetle densities would be required early in the season. Moreover, all plant deaths were recorded during the second infestation period only. These findings emphasize the importance of the timing of herbivore attack; both the attacked plant stage and the seasonal performance of the agents determine successful control. The latter parameter is, however, rarely explicitly addressed in studies on

herbivore impact on plants. Weather conditions not only greatly influence plant growth and the plant's ability to compensate for herbivory (see for example Ang *et al.*, 1995, for *C. arvensis*), but also the performance of herbivores, and thus their feeding intensity and population dynamics (in particular in ectothermous herbivores), which subsequently determines their impact on the host plants.

Differential Effect of Herbivory and Plant Community on Plant Performance

Similar to Ang *et al.* (1995), we found an increasing effect of *C. rubiginosa* larvae on above-ground plant performance of *C. arvensis* as herbivore densities increased. The failure to detect significant herbivory effects in the total above-ground biomass is most likely due to the fact that secondary shoots received no *C. rubiginosa* larvae unless the primary shoot died. Crawley (1983, 1997) suggests that generally stress on the shoot reduces root growth. However, we did not find any effect of beetle defoliation on below-ground plant performance. In contrast, Ang *et al.* (1995) observed severe effects of *C. rubiginosa* density on root dry weight and length. We suppose that in their experiment the initially introduced adult beetles produced offspring on the plants they were confined to, so that actual beetle densities were higher than the given numbers per plant, creating a higher herbivore pressure on thistle plants than in our study. Moreover, thistle plants in the work of Ang *et al.* (1995) originated from smaller root pieces (diameter 3–4 mm, length 3–4 cm) and thus had a substantially smaller regenerative capacity (Hamdoun, 1972; Dock-Gustavsson, 1997). It therefore seems that defoliation primarily affects above-ground plant performance in *C. arvensis*, and below-ground performance is only negatively affected at high intensities of herbivory relative to the regenerative capacity of the plants.

The plant community had significant effects on biomass production both above- and below-ground. Creeping thistle performance was always reduced in the seeded herb plots. Since there were no differences in ground cover or vegetation height between the natural vegetation plots and the seeded herb plots (except at the set-up of the experiment), this effect was most probably due to the intrinsic superior competitive ability of the seeded herb species. Thus, vegetation management by seeding desirable plants can contribute to the suppression of problematic weeds such as *C. arvensis* in ecological compensation areas.

Neither herbivory nor plant community had an effect on concentrations of fructosans and nitrogen in root parts. This is in accordance with the work of Ang *et al.* (1995). McAllister and Haderlie (1985) concluded from their study on seasonal variations in *C. arvensis* root carbohydrate reserves, that carbohydrate production in excess of that which can be stored in existing root tissue would be utilized by new root growth. Müller-Ferch and Mouci (1995) investigated the effect of mowing on nitrogen and carbohydrate storage on seven common agricultural weed species (*Taraxacum officinale*, *Achillea millefolium* L., *Symphytum officinale* L., *Anthriscus sylvestris* (L.) Hoffm., *Trifolium pratense*, *T. repens* L., *Ranunculus repens* L.) throughout the growing season. They found short-term effects of mowing on carbohydrate concentration in storage organs in the former five species, but no long-term effects in any weed. No effect on nitrogen levels was detected in any species. Thus, it appears that removal of above-ground plant material rarely has long-term effects on the concentration of storage substances.

The effect of herbivory on performance of *C. arvensis* was more pronounced in the seeded herbs plant community than in the natural vegetation. A combination of high levels of plant competition and herbivory yielded the strongest negative effect on creeping thistle performance. These findings emphasize the importance of multiple stresses for successful weed control.

Our study was conducted under realistic field conditions matching closely the phenology of the weed and the herbivore in their natural habitat. We carried out the experiment on plants originating from root pieces of a size class representative for the weed on freshly tilled agricultural land. This situation applies, for example, to the preparation of ecological

compensation areas. These experimental conditions are prerequisites for a sound estimation of agent densities required to suppress *C. arvense* in ecological compensation areas.

Densities of up to 20 *C. rubiginosa* larvae per thistle shoot can be maintained under field conditions, and even occur in the field. Thus, augmentation of indigenous herbivores of *C. arvense* in combination with breaking up the root system by tillage and the establishment of a highly competitive plant community of beneficial plant species may be a feasible way to control this problematic weed in ecological compensation areas.

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