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Top-down control and its effect on the biomass and composition of three grasses at high and low soil fertility in outdoor microcosms

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Abstract We used outdoor microcosms in order to freely manipulate three trophic levels (ladybird/aphid/grass) at two soil fertility levels (low and high). Two hypotheses were tested: (1) that top-down control is only a mechanistic factor at high soil fertility, and (2) that herbivory increases secondary plant succession by preferentially feeding on the fast-growing early-successional grasses. Plant biomass responded dramatically to the high soil fertility treatment, as did aphid numbers in the absence of ladybirds, and ladybird activity (ladybirds feeding on aphids). At low soil fertility, plant biomass was low, aphid numbers were small, and ladybird activity was minimal. Only at high soil fertility did top-down control cause a significant response to plant biomass and species composition. The two fast-growing, early-successional grasses (*Poa annua* and *Arrhenatherum elatius*) had a greater biomass in the presence of the ladybirds compared to when the ladybirds were absent, while the slow-growing, late-successional grass (*Festuca ovina*) suffered. The opposite was found when ladybirds were absent but aphids present. These results suggest that herbivory may increase the rate of secondary succession, but that top-down control of herbivory by carnivores may reduce the impact of herbivory in high productivity communities.

Key words Tri-trophic interactions · Top-down control · Secondary succession · Outdoor microcosms

Introduction

When Hairston et al. (1960) proposed their hypothesis (“HSS model”) of top-down control of herbivores in

answer to the question “why is the world green?” they assumed, for the purposes of their model, that vegetation was uniform and that plant species do not vary in their ability to defend themselves against herbivory. The HSS model has prompted much discussion (e.g. Murdoch 1966; Ehrlich and Birch 1967) and many tests of the hypothesis, as well as generating many alternative hypotheses. For this reason, the “HSS paper” could be considered revolutionary, according to the definition of Kuhn (1970), in causing a paradigm shift. One of the most important hypotheses to emerge has been plant defence theory (e.g. Feeny 1976; Rhoades and Cates 1976; Coley et al. 1985), where the effect of herbivory depends on the relative defensive mechanisms of the plant. The experiment described in this paper links the trophic-dynamic concept, broadly outlined in the HSS model, together with plant defence theory.

A number of researchers have shown a negative correlation between plant defence and the maximum relative growth rate of plants (Grime et al. 1968, 1997; Coley 1983; Sheldon 1987; Southwood et al. 1986). Maximum relative growth rate is also related to the successional stage of a plant within a community (early successional species are fast-growing, late successional species are slow-growing), and that relative growth rate is related to the available productivity of the environment (fast-growing species found at high resource supply rates, slow-growing species found at low resource supply rates) (Mooney 1972; Grime 1977; Bazzaz 1979; Chapin 1980; Mooney and Gulmon 1982; Bryant et al. 1983; Bryant and Chapin 1986; Coley 1988). It has been proposed, therefore, that early-successional species are less well defended against herbivores than later-successional species (Cates and Orians 1975; Feeny 1976; Rhoades and Cates 1976; Grime 1979). Furthermore, it has been suggested that the effect of herbivory may be to increase the rate of succession by preferential feeding on early-successional species (Schowalter 1981; Godfray 1985; Bryant and Chapin 1986; Walker and Chapin 1986). In general, this result has been consistent in experimental

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studies conducted with generalist herbivores (Ross et al. 1970; Hanley and Taber 1980; Hatton and Smart 1984; Walker and Chapin 1986; Berdowski and Zeilinga 1987; Bryant 1987; Veblen et al. 1991; Brown and Gange 1992; see Davidson 1993 for review).

S.D. Fretwell and L. Oksanen have proposed a hypothesis that links trophic dynamics with productivity (Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen 1990). Their theory is based on the number of levels in the food chain. S.D. Fretwell and L. Oksanen proposed that primary productivity dictates the length of the food chain (higher productivity = longer food chain). Where food chains have odd numbers of trophic levels, grazers would be predator-limited, resulting in the classic HSS prediction, i.e. landscapes with abundant, green vegetation. But when food chains have even numbers of trophic levels, plants would be grazer-limited and landscapes should appear barren (Fretwell 1977, 1987; Oksanen et al. 1981; Fraser and Grime 1997). Essentially, this is a "top-down" model except that productivity has been accorded a key role as the factor influencing trophic interactions.

The experiment described here used a ladybird/aphid/grass system in microcosms to explore the Fretwell and Oksanen trophic-dynamic hypothesis, in conjunction with the hypothesis that herbivory increases the rate of secondary succession. Specifically, the objectives of the experiment were:

1. To test the hypothesis that top-down control from carnivores at high soil fertility will facilitate fast-growing, early-successional plants by reducing herbivory
2. To test the hypothesis that the rate of succession will vary depending on the productivity of the environment and the involvement of carnivory in the trophic dynamics
3. To determine the effect of carnivory on the herbivore population at contrasting soil fertility levels by monitoring the growth of the herbivores in the presence and absence of carnivores
4. To determine the food preferences of herbivores in plant communities containing the three primary plant functional strategies at contrasted levels of soil fertility.

Materials and methods

Outdoor microcosms

Thirty-six outdoor microcosms were located at the University of Sheffield's Tapton Experimental Gardens in Sheffield, England and were similar to those described in Fraser (1996). Each microcosm compartment was 1.5 m high \times 0.6 m long \times 1 m wide, covered with a strong, reinforced, UVB-protected, clear polythene fabric (monarflex). Clear perspex doors were mounted onto the front of each microcosm with the dimensions of 0.6 m \times 0.75 m. Two 200-mm² vents covered by 155 \times 245 μ m mesh were placed onto each microcosm to facilitate air-flow. Climatic monitoring of the microcosms, including temperature, CO₂ concentration, and light intensity, was conducted and compared to ambient climatic conditions.

Plants and animals used in experiment

Within each of the outdoor microcosm compartments were two containers with dimensions 25 cm high \times 50 cm long \times 40 cm wide. Each container was filled with approximately 50 kg of builders' sand. The sand was analysed for heavy metals, sodium and pH to ensure that the levels were appropriate for normal plant growth (see Fraser 1996). In early May 1995, 110 seeds of each of the three plant species, *Poa annua*, *Arrhenatherum elatius* and *Festuca ovina*, for a total of 330 seeds, were sown into each container. The herbivores included in the experiment were grain aphids (*Sitobion avenae*) while the carnivores were seven-spot lady bird adults (*Coccinella septempunctata*). The aphids were collected and reared at Tapton Experimental Gardens on a mixed grass community consisting of the three grasses included in this experiment as well as *Holcus lanatus* and *Lolium perenne*. No attempt was made to rear the aphids from a single clone. The ladybirds were collected in Millers Dale and Tideswell Dale in Derbyshire, Northern England.

Experimental design

The experiment included factorial combinations of soil fertility (low and high) and trophic interactions (herbivores and carnivores absent, herbivores present and carnivores absent, herbivores and carnivores present) replicated six times involving a total of 36 microcosms. Rorison's nutrient solution (Hendry and Grime 1993) was applied in controlled quantities to the two soil fertility treatments. Once the plants had established, the herbivores were added.

Experimental procedure

After the seeds were sown and had begun to germinate (mid-May 1995), 100 ml of full Rorison's nutrient solution was added to each container once a week for 4 weeks. The percentage germination of the three grasses were very similar at approximately 75%. Water was applied when necessary. Beginning in early June 1995, the following nutrient solutions were added on a weekly basis: 1000 ml of full Rorison's nutrient solution to each container in the high soil fertility treatment, 100 ml full Rorison's nutrient solution plus 900 ml of water was added to each container in the low soil fertility treatment.

Once the plants were well established, the herbivores were added, followed one month later by the carnivores. Repeated introductions, or multiple seeding (Beyers and Odum 1993), was used to emulate nature by favouring waves of immigration. Beginning in July, 20 aphids were added at four 2-weekly intervals for a total of 80 aphids. Starting in August, 10 ladybirds were added at 4 weekly intervals for a total of 40 ladybirds. The number of aphids in each microcosm was estimated at five separate times from mid-August to mid-October at 2-week intervals by randomly selecting ten 5-cm² areas and counting the number of aphids found on the vegetation within the areas. Ladybird activity was estimated by counting the number of active ladybirds that were on the vegetation. Five ladybird counts were conducted at weekly intervals beginning in September.

The number of flower heads produced by *P. annua* in each microcosm was counted in September 1995. At the end of the growing season (November 1995) all the above-ground vegetation was harvested, sorted to species, dried at 80°C, and weighed.

Analysis

Treatment effects on above-ground vegetation

A three-way analysis of variance was used to determine the interacting effects of plant species, trophic interactions (none; herbivores; herbivores and carnivores), and soil fertility (low and high) on above-ground plant biomass. The data was tested for heteroscedasticity using Bartlett's test and was found to have normal variance. The 95% confidence limits were calculated for all

histograms that were presented to illustrate mean differences between treatments. Furthermore, Tukey's Honestly Significant Difference test was used to separate treatment means.

Treatment effects on flowering

A two-way ANOVA was applied to determine the effect of soil fertility and the trophic interaction treatment on the flowering (number of flower heads) of *P. annua*. The 95% confidence intervals were calculated for each of the means. Tukey's Honestly Significant Difference test was used to separate treatment means.

Animal numbers and food preference

The growth of the aphids and the activity of the ladybirds was recorded over time. The mean number of aphids was determined at each time interval, for each plant species on which they were found, in the presence and absence of ladybirds, and at each soil fertility level. The 95% confidence limits were calculated for each mean value. The mean number of ladybirds that were found, out of the total number ($n = 40$), actively searching the grass canopy for aphids was determined at regular time intervals and for each soil fertility level. Similarly, the 95% confidence limits were calculated for each mean value.

Results

Environmental Conditions Inside Microcosms

The results of the climatic conditions inside the outdoor microcosms are presented in Fig. 1. Generally, the microcosms operated at a daytime temperature of approximately 2°C higher than ambient, but the hottest days exhibit differences of as much as 5°C. However, the microcosms were not meant to precisely emulate nature and therefore environmental variables that were different from ambient were not perceived as a problem unless they were obviously detrimental to the growth of the organisms. The CO₂ concentration varied between microcosms (Fig. 1b) depending on soil fertility level; there was approximately a 20 ppm difference between the two soil fertility treatments. The microcosms at low soil fertility had the higher CO₂ levels, while the ambient CO₂ concentration was approximately 40 ppm higher than the microcosms at the low soil fertility. The light intensity within the microcosms was lower (approximately 30%) than the direct light intensity.

Plant above-ground biomass response to fertility and the trophic interaction treatment

Soil fertility had the greatest effect on shoot biomass. Although it was difficult to discern visually, the effect of

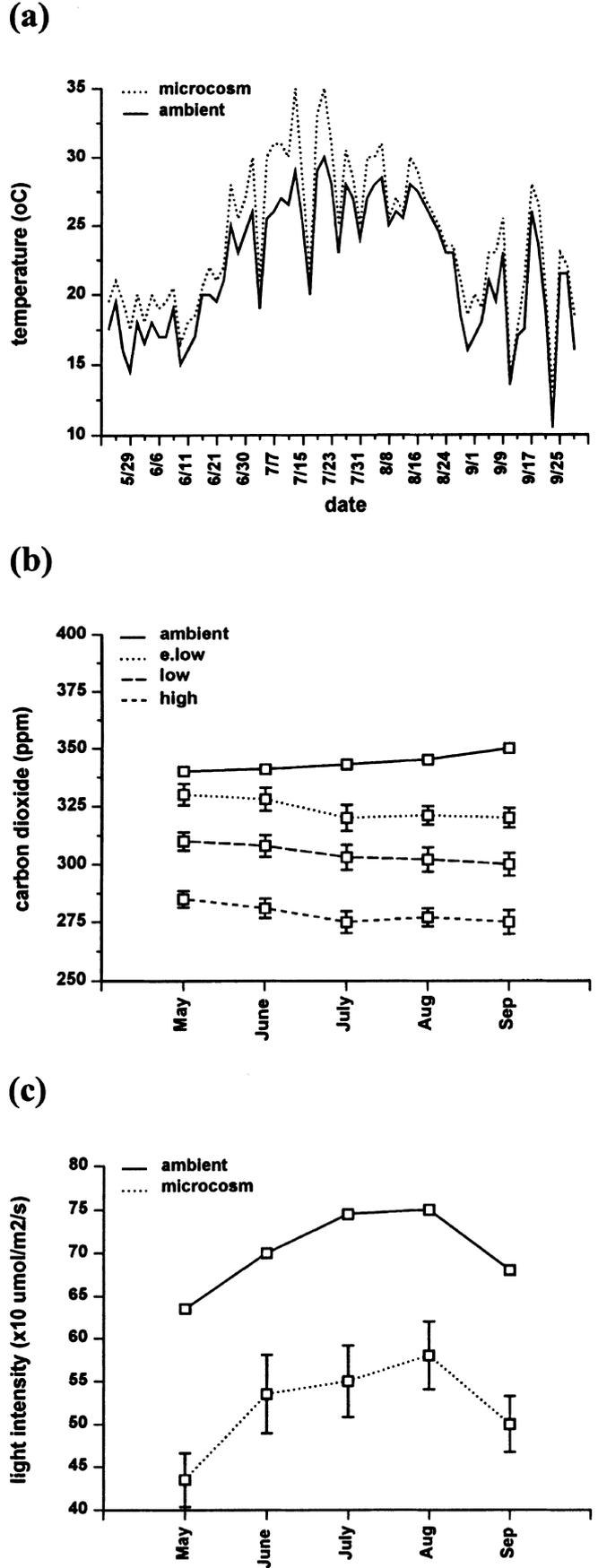


Fig. 1 Environmental conditions measured inside microcosms: **a** temperature (°C); **b** carbon dioxide concentration (ppm); **c** light intensity (x10 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Error bars represent 95% confidence limits

herbivores and carnivores was, at times, also statistically significant. However, since the experiment was only allowed to run for one growing season, the trophic interaction treatment, although significant, did not exert a large effect. Therefore, effects of treatments on secondary plant succession and community dynamics must be inferred on the basis of changes in relative abundance rather than the complete exclusion of species.

At low and high soil fertility the effect of the three trophic interaction treatments was significant. Furthermore, the differences in mean dry above-ground biomass between the three plant species (*P. annua*, *A. elatius* and *F. ovina*) were significant (Table 1). The shoot biomass of *Poa annua* was greatest where herbivores and carnivores were absent (Fig. 2). The biomass of *P. annua* grown at high soil fertility appeared higher in the presence of carnivores than in their absence. The shoot biomass of *F. ovina* was significantly higher in the presence of herbivores only at high soil fertility, but this effect was not evident when carnivores also were present. *A. elatius* had the greatest above-ground biomass in each treatment and it was not affected by the trophic interaction treatment. At both high and low soil fertility, the mean total above-ground biomass was greatest in the absence of herbivores and carnivores (Fig. 3). However, this difference was only significant at high soil fertility (Table 2).

Table 1 Results of three-way ANOVA where the independent variables are soil fertility (FERT), plant species (SP), and the trophic treatment (TROPIC), and the dependent variable is the mean above-ground plant biomass. The tables presents the sum of squares (SS), degrees of freedom (*df*), mean squares (MS), *F*-ratios, and *P*-values (*P*)

Source of variation	SS	<i>df</i>	MS	<i>F</i> -ratio	<i>P</i>
FERT	6146.496	1	6146.496	1248.751	<0.001
SP	6737.160	2	3368.580	684.376	<0.001
TROPIC	90.545	2	45.273	9.198	<0.001
FERT × SP	3349.734	2	1674.867	340.274	<0.001
FERT × TROPIC	63.636	2	31.818	6.464	0.002
SP × TROPIC	239.003	4	59.751	12.139	<0.001
FERT × SP × TROPIC	182.088	4	45.522	9.248	<0.001
TROPIC					
ERROR	974.579	198	4.922		

Table 2 Results of two-way ANOVA examining the effects of the soil fertility treatment (FERT) and the trophic interaction treatment (TROPIC) on the mean total above-ground biomass. This table presents the sum of squares (SS), degrees of freedom (*df*), mean squares (MS), *F*-ratios, and *P*-values (*P*)

Source of variation	SS	<i>df</i>	MS	<i>F</i> -ratio	<i>P</i>
FERT	19180.766	1	19180.766	856.405	<0.001
TROPIC	420.079	2	210.040	9.378	<0.001
FERT × TROPIC	315.442	2	157.721	7.042	0.002
ERROR	1478.191	66	22.397		

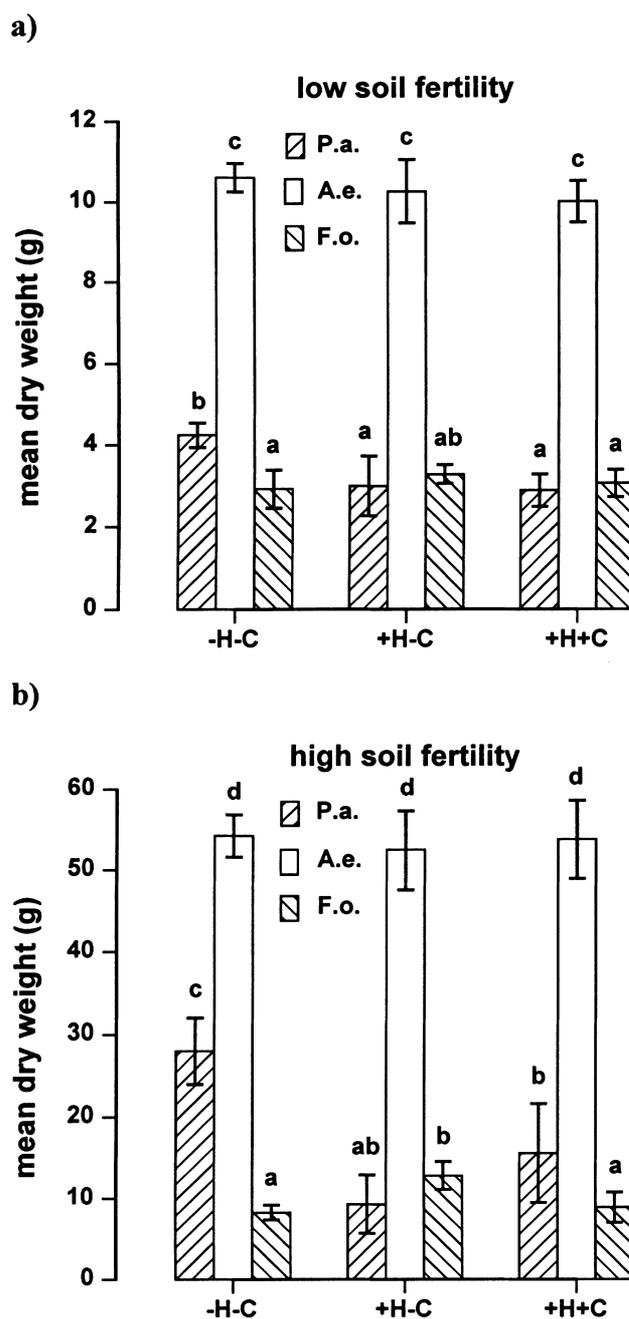


Fig. 2 The effect of the trophic interaction treatment on the shoot biomass of the three grasses at **a** low soil fertility and **b** high soil fertility. (Shaded bars *Poa annua* (ruderal), open bars *Arrhenatherum elatius* (competitor), opposite-shaded bars *Festuca ovina* (stress-tolerator). Error bars represent 95% confidence limits. Bars sharing the same letter are not significantly different using Tukey's HSD

Flowering response of *P. annua* to treatments

P. annua was the only species to flower. The effects of the fertility treatment and the trophic interaction treatment were statistically significant, both separately and in combination, on the number of flower heads produced by *P. annua* (Table 3). Fertilization increased the number of flowers produced (Fig. 4). The presence of

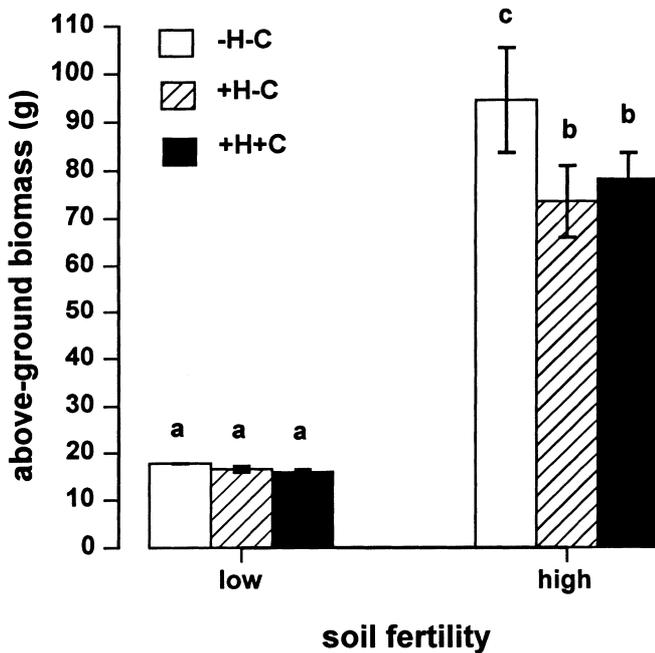


Fig. 3 The effect of the trophic interaction and fertility treatments on the total shoot biomass [*H* herbivores (- absent, + present) *C* carnivores (- absent, + present)]. Error bars represent 95% confidence limits. Bars sharing the same letter are not significantly different using Tukey's HSD

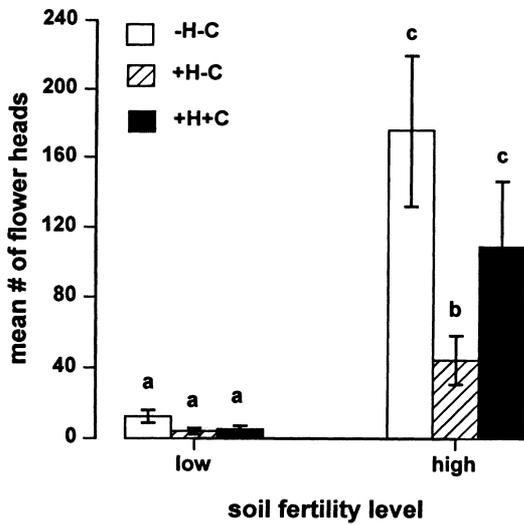


Fig. 4 The effect of the trophic interaction and fertility treatments on the mean number of flower heads produced by *Poa annua*. [*H* herbivores (- absent, + present) *C* carnivores (- absent, + present)]. Error bars represent 95% confidence limits. Bars sharing the same letter are not significantly different using Tukey's HSD

herbivores on high soil fertility treatments, however, reduced the number of flowers produced.

Herbivore and carnivore response to treatments

The numbers of *S. avenae* were related to soil fertility (Fig. 5). There was a ten-fold difference in the number of

Table 3 Results of two-way ANOVA examining the effects of the soil fertility treatment (FERT) and the trophic treatment (TROPIC) on the mean number of *Poa annua* flower heads produced. This table presents the sum of squares (SS), degrees of freedom (*df*), mean squares (MS), *F*-ratios, and *P*-values (*P*)

	SS	<i>df</i>	MS	<i>F</i> -ratio	<i>P</i>
FERT	94146.69	1	94146.69	76.41	<0.001
TROPIC	29229.39	2	14614.69	11.86	<0.001
FERT × TROPIC	22637.06	2	11318.53	9.19	0.001
ERROR	36961.83	30	1232.06		

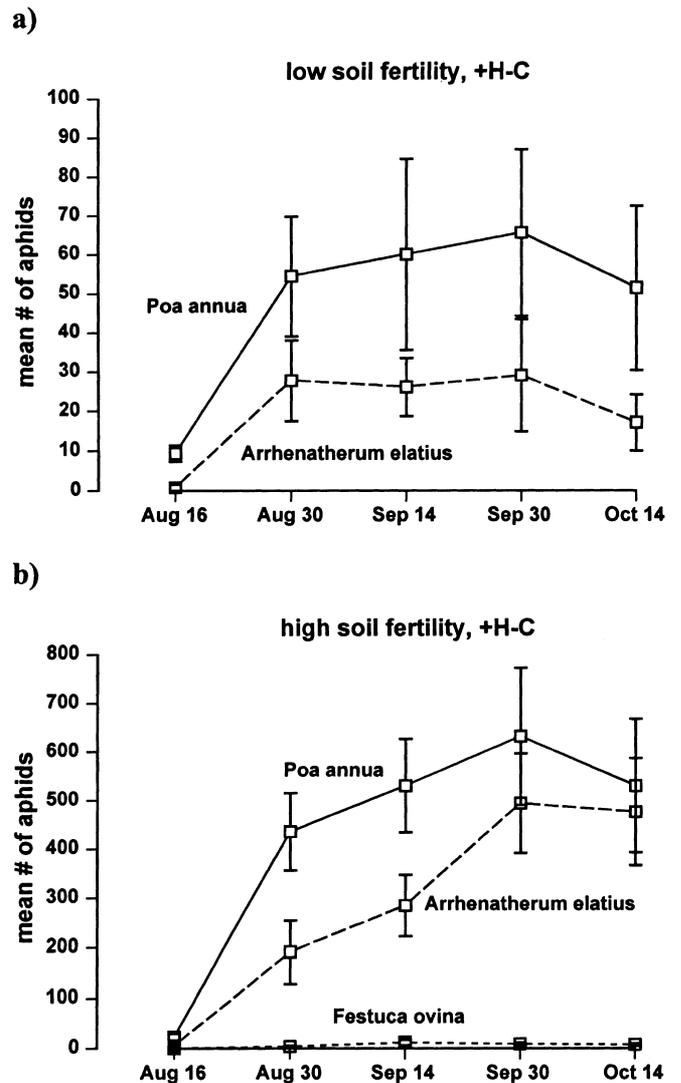
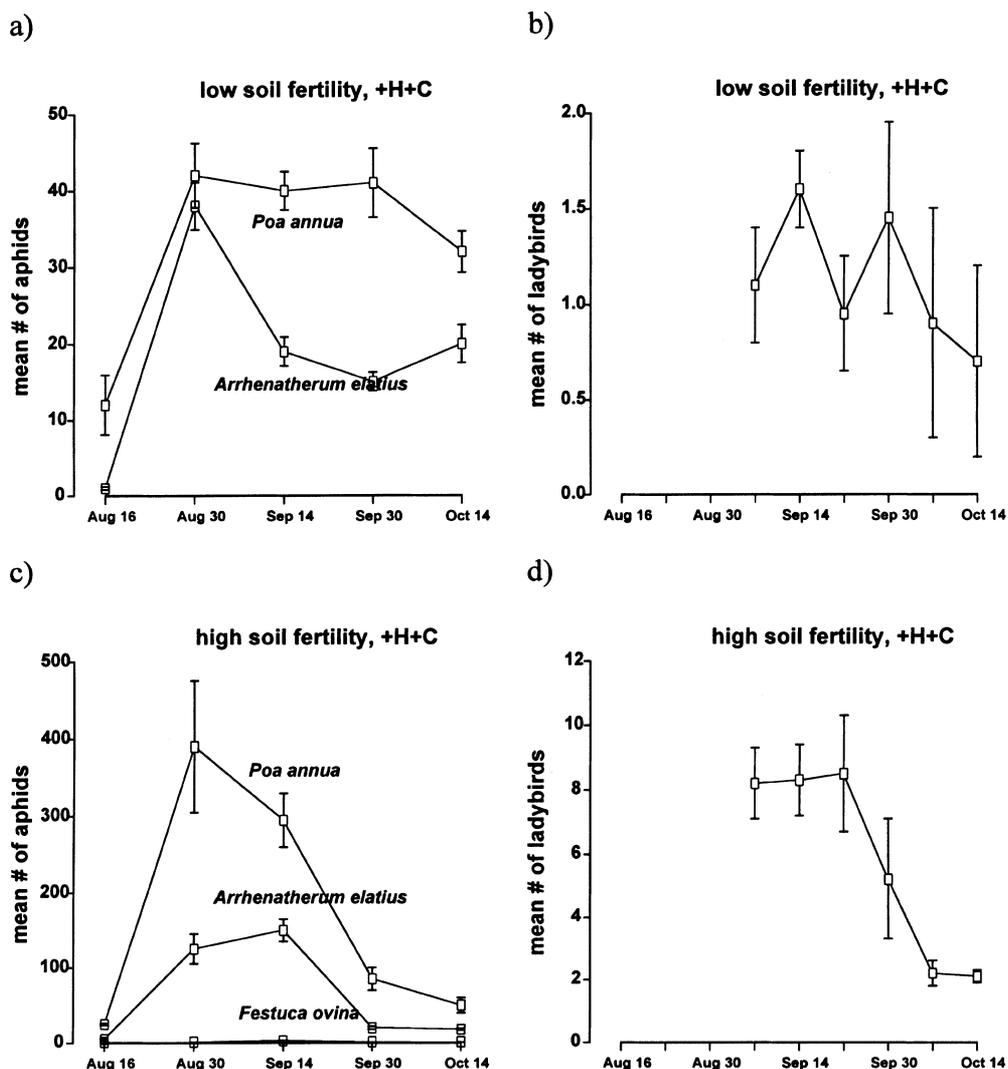


Fig. 5 Mean numbers of *Sitobion avenae* aphids on each grass species measured over time in the absence (+H-C) of carnivores (*Coccinella septempunctata*) at a low and b high soil fertility. Error bars represent 95% confidence limits

aphids found at the high soil fertility level compared to the low soil fertility level. There were always more aphids found on *P. annua* than the other two grasses. Approximately half the number of aphids found on *P. annua* were found on *A. elatius*. Few aphids were found on *F. ovina*. With the introduction of the

Fig. 6 Mean numbers of *S. avenae* on each grass species, and the mean number of *C. septempunctata* (ladybird) within the herbivore plus carnivore treatment (+H+C), measured over time at **a, b** low and **c, d** high soil fertility. Error bars represent 95% confidence limits



ladybirds, aphid numbers were reduced dramatically and continued to decline throughout the experiment (Fig. 6a, c). The activity of the ladybirds was also related to soil fertility, with the ladybirds being more numerous in the high soil fertility microcosms (Fig. 6d). Ladybird numbers peaked in late September, declining to the approximate mean value of one active ladybird per microcosm in mid-October.

Discussion

The main purpose of this experiment was to test whether carnivores exerted a top-down control on herbivores in plant communities grown at a high soil fertility, as predicted by S.D. Fretwell and L. Oksanen (Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen 1990). If top-down control was operating, two specific results should have been observed in the presence of carnivores: (1) a reduction in the number of herbivores; and (2) an increase in plant biomass. Furthermore, according to plant defense theory, a reduction in herbivore numbers

as a result of carnivory should lead to the protection of fast-growing, early-successional plants from herbivory and the suppression of slow-growing, late-successional plants.

First of all, there is no doubt that the ladybirds reduced the total numbers of aphids at both fertility levels. As soon as the ladybirds were introduced, the aphid population was suppressed, and continued to decline over time until the last census was taken. Ladybird activity was much greater at high soil fertility as a result of a larger food supply. Host quality is a well known determinant of aphid numbers (Dixon 1985; Waring and Cobb 1992; Hartvigsen et al. 1995). Furthermore, it was generally observed that ladybird activity was greater when the temperatures were warmer. A similar result found by Sopp and Wratten (1986) showed that with increasing temperature the consumption rate of a number of carabid and staphylinid species feeding on *S. avenae* increased.

The effect that the reduction of aphid numbers had on the plant community grown at high soil fertility seems to partially support the hypothesis that herbivory

increases secondary succession. The biomass and flowering of *P. annua*, a fast-growing annual grass, was significantly reduced in the presence of herbivores at both soil fertility levels. This result was not surprising because *P. annua* was found to be very palatable to the aphid *S. avenae* (Fraser 1996). When carnivores were present the biomass and flowering of *P. annua* grown at high soil fertility was intermediate between the biomass of *P. annua* with herbivores and without herbivores. This suggests that carnivores afforded some protection to *P. annua* by reducing herbivore numbers. The same result did not occur at low soil fertility. The biomass and flowering of *P. annua* in the presence of herbivores and carnivores was the same as in the presence of herbivores alone, presumably because the carnivore activity was so low. According to S.D. Fretwell and L. Oksanen (Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen 1990), in nature a community with low production cannot support carnivores. Out of 40 ladybirds added to each of the low soil fertility microcosms, there were never more than 2 actively searching for food at any time. This suggests that the low productivity of these microcosms, as predicted, could not support carnivores. The biomass of *A. elatius*, a fast-growing perennial grass, did not respond to herbivores or carnivores, even though many aphids were found on *A. elatius*. It must be assumed that whatever photosynthates the aphids removed from *A. elatius* were compensated for by an increase in resource capture; though not over-compensated, or the biomass of *A. elatius* would be greater in the presence of the aphids. Compensatory growth is a well-documented response to damage caused by herbivores, but mainly from leaf-chewers, not leaf-suckers (McNaughton 1979, 1983; Williamson et al. 1989; Alward and Joern 1993).

The response of *F. ovina*, a slow-growing perennial grass, met the requirements of the hypothesis that herbivory increases the rate of secondary succession. The biomass of *F. ovina* grown at high soil fertility was approximately 50% greater in the presence of herbivores compared to where herbivores and carnivores were absent, a result similar to that found by Fraser (1996). Grime et al. (1997) and Fraser (1996) found through palatability tests that *F. ovina* is a relatively unpalatable grass. Therefore *F. ovina* benefits in a mixed plant community in the presence of herbivores because it experiences less shading and competition for mineral nutrients. However, the biomass of *F. ovina* in the presence of carnivores was basically equal to the biomass of *F. ovina* where herbivores and carnivores were absent. This result suggests that any advantage *F. ovina* may have had in the presence of herbivores was eliminated when carnivores were present. At low soil fertility, as expected, there was no change in biomass of *F. ovina* between the three trophic interaction treatments.

A change in the rate of secondary succession caused by herbivory and carnivory can be inferred from the data presented. As in the case of a similar microcosm experiment conducted by Fraser (1996), herbivory in-

creased the rate of succession at both fertility levels. This occurred not only by reducing the biomass of early successional species by preferential feeding but also by reducing the fitness of the fast-growing annuals by reducing flowering. When carnivores were present there was a differential response to the rate of secondary succession depending on the soil fertility level. The results presented in this paper suggest that at high soil fertility, carnivores reduced the effect of herbivores and, therefore, reduced the rate of succession to that measured in the absence of herbivores. The effect of carnivores was low at low soil fertility and, consequently, the rate of secondary succession was similar to that where only herbivores were present.

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