Interacting effects of herbivory and fertility on a synthesized plant community

LAUCHLAN H. FRASER and J. PHILIP GRIME

NERC/Unit of Comparative Plant Ecology, University of Sheffield, Sheffield S10 2TN, UK

Summary

1 Outdoor microcosms were used to investigate the effects of invertebrate herbivory on plant community composition, and thereby infer possible effects on the rate of secondary succession, at differing levels of soil fertility.

2 A mixture containing 24 grassland plant species of widely different functional types was established, with 12 microcosms at each of three fertility levels. Four generalist herbivores (*Helix aspersa*, *Cepaea hortensis*, *Arianta arbustorum* and *Sitobion avenae*) were added to half of the microcosms. Above-ground biomass of each species was harvested after 2 years. Reproductive variables were also measured for one species, *Poa annua*.

3 At both moderate and high soil fertility generalist invertebrate herbivores fed selectively on early successional, fast-growing species, thus increasing the relative abundance of later successional, slow-growing species. This supports the hypothesis that herbivory increases the rate of secondary succession. Flowering and viable seed production of early successional ephemerals was also reduced by the invertebrate herbivores across a wide range of soil fertility. This would seriously reduce the ability of a species to persist in the community, thereby further hastening the rate of succession.

Keywords: grain aphid, herbivory, molluscs, outdoor microcosms, plant–animal interactions, plant defence, primary functional groups, succession

Journal of Ecology (1999) **87**, 514–525

Introduction

Investigations of herbivory conducted over the last 20 years provide a comparative framework in which to search for patterns in defence allocation and in the palatability of plant species to herbivores. Most authorities agree that in ephemeral or ruderal plant species, which occupy the first seral stage of secondary succession, there is comparatively little investment in defensive structures or in secondary chemistry (Mooney & Gulmon 1982; Bryant *et al.* 1983; Southwood *et al.* 1986; Coley 1988). Ruderals are thus relatively palatable but are presumed to escape from herbivores as a result of spatial or temporal separation (Feeny 1976; Rhoades & Cates 1976). Later successional stages are usually characterized by perennial plants with a number of traits that facilitate high rates of resource capture (Mooney 1972; Grime 1977; Bazzaz 1979; Chapin 1980; Grime *et al.* 1997). Leaf

turnover of these species is rapid and, initially, when resources are readily available, such plants may be capable of fast regrowth, or compensatory growth that allows recovery from losses due to herbivores (McNaughton 1983; Coley 1983). However, as succession proceeds resources often become limited through sequestration in biomass and litter, and thus limiting for these plants which then experience mineral nutrient stress (Odum 1969; Chapin 1980). Many late successional plant species appear to be attuned to extremely infertile soils and are intrinsically slow-growers that have comparatively long-lived leaves and other structures (Grime 1977; Mooney & Gulmon 1982; Bryant *et al.* 1983, 1989; Coley 1983; Grime *et al.* 1997). For such plants tissue loss is likely to have very serious consequences. Because they replace lost tissue slowly, and occupy habitats in which resources are scarce, we may predict that they will have experienced strong selection promoting anti-herbivore defences; these plants therefore tend to allocate a large proportion of carbon to mechanical defences, e.g. thorns (Owen-Smith & Cooper 1987) and trichomes (Levin 1973), or to secondary metabolites which are

either highly toxic or reduce the digestibility of the vegetation to herbivores (Mooney 1972; Feeny 1976; Rhoades & Cates 1976; Bryant *et al.* 1983, 1991; Bryant & Chapin 1986; Coley 1988).

These patterns have been shown to relate directly to the food preferences of herbivores: herbivores prefer early successional species to later ones (Grime *et al.* 1968, 1996; Cates & Orians 1975; Reader & Southwood 1981; Coley 1983, 1988; Godfray 1985; Bryant & Chapin 1986; Southwood *et al.* 1986). As a result, several authors have predicted that because they hasten the mortality of early successional species, herbivores will accelerate plant succession (Schowalter 1981; Godfray 1985; Bryant & Chapin 1986; Walker & Chapin 1986). While in some experimental studies such an effect has been demonstrated (Walker & Chapin 1986; Berdowski & Zeilinga 1987; Bryant 1987; Sheldon 1987; Veblen *et al.* 1991; Brown & Gange 1992), other studies found that herbivory reversed or delayed succession (Cargill & Jefferies 1984; Huntly 1987; Brown *et al.* 1988; Brown & Gange 1989, 1992; Bach 1994; reviewed by Davidson 1993). However, it should be noted that all of the cited studies in the latter category involved either specialist herbivores (*Altica subplicata*, Bach 1994) or early successional species (in recently harrowed fields, Brown *et al.* 1988; Brown & Gange 1992; productive salt marsh, Cargill & Jefferies 1984, or subalpine meadows, Huntly 1987) or both (specialist invertebrates in recently harrowed fields, Brown & Gange 1989).

It has been predicted that the effect of herbivory will depend on the productivity of the system. Coley *et al.* (1985) proposed that resource availability is important in determining both the amount and the type of defence used by plants against herbivory (Jefferies *et al.* 1994; van de Koppel *et al.* 1996). Plants growing in environments where resources (e.g. nitrogen or phosphorus) are limited have intrinsically slow growth rates and frequently produce secondary metabolites that may deter herbivores (Coley *et al.* 1985). Extremely infertile soils would support little biomass, and unpalatable, long-lived perennials should become dominant at a comparatively early stage in succession. Theoretically, such habitats would not therefore support many herbivores (i.e. herbivore activity would be minimal) and there would be little change in plant composition or biomass due to herbivory (Oksanen *et al.* 1981). In contrast, soils with a somewhat higher supply of nutrients would be expected to display the classic progression of succession and, in those habitats, generalist herbivores would be expected to increase the rate of succession. At high soil fertility fast-growing ephemerals would rapidly be displaced by fast-growing perennials and these would not be expected to be displaced by slow-growing perennials as long as a high resource supply rate was sustained. It seems likely under these conditions that any biomass lost by fast-growing per-

ennials to herbivory would be compensated by rapid regrowth and so there would be no further succession.

Plant assemblages were created from a mixture of three primary functional types (fast-growing ephemerals, fast-growing perennials and slow-growing perennials) and maintained at contrasting levels of fertility. The objectives of the experiment were as follows:

1 To test the feeding preferences of generalist invertebrate herbivores in the various assemblages. Any resulting differences in plant composition due to herbivory can be used to infer its possible effect on the rate of plant succession under various conditions.
2 To examine the effect of soil fertility on the relative abundance of the three primary functional types.
3 To monitor the fate of invertebrate herbivores in plant communities varying in productivity.

Methods and materials

DESIGN OF MICROCOSMS

Sealed outdoor microcosms were located at the University of Sheffield's Tapton experimental botanical gardens in Sheffield, UK. Each was 1.5 m high × 1.2 m long × 1 m wide, with clear Perspex doors, 1.2 × 0.75 m, fixed onto the front. To facilitate airflow from the outside environment, and to help standardize internal concentrations of oxygen and carbon dioxide, four 20-cm² vents covered by an insect-proof mesh (155 × 245 μm) were inserted in the rear wall. During July and August, the hottest and sunniest months, shade netting was used to cover the roofs and Perspex doors.

PLANTS AND ANIMALS USED IN THE EXPERIMENT

Grassland plant species found commonly growing in the Sheffield area (Table 1) were selected such that eight were fast-growing ephemerals (i.e. their primary growth strategy according to Grime *et al.* 1988 was ruderal; R), eight were fast-growing perennials (competitors; C) and eight were slow-growing perennials (stress-tolerators; S). Although some species were strictly only one of R, C or S, most were closely related 'allies' of primary strategy types. For example, although *Galium aparine* is a ruderal it has some competitive characteristics and is thus a C-R strategy type.

Our criteria for selection of herbivores were: (i) their generalist feeding behaviour; (ii) they were commonly found within the communities from which our experimental plant species had been drawn; and (iii) they were able to survive in the environments of the microcosms. We included three mollusc species (*Helix aspersa*, *Cepaea hortensis* and *Arianta arbustorum*) and one aphid species (*Sitobion avenae*). *Helix aspersa*

Table 1 Plant species included in the outdoor microcosms. Dashes indicate species where R_{max} values are not known

	Strategy*	R_{max}†	Number of seeds per container
Fast-growing ephemerals, 'Ruderals'			
Arapidopsis thaliana (At)	SR	—	125
Cerastium fontanum (Cf)	R/C-S-R	1.46	125
Chenopodium album (Ca)	R/C-R	2.12	82
Galium aparine (Ga)	C-R	1.51	22
Plantago lanceolata (Pl)	C-S-R	1.70	55
Poa annua (Pa)	R	2.70	110
Polygonum aviculare (Pav)	R	1.43	55
Stellaria media (Sm)	R	2.43	110
Fast-growing perennials, 'Competitors'			
Arrhenatherum elatius (Ae)	C	1.30	22
Holcus lanatus (Hl)	C-S-R	2.01	82
Lolium perenne (Lp)	C-R/C-S-R	1.30	22
Petasites hybridus (Ph)	C	—	110
Poa trivialis (Pt)	C-S-R/C-R	1.40	125
Rumex obtusifolius (Ro)	C-R	1.49	55
Stachys sylvatica (Ss)	C/C-R	—	55
Urtica dioica (Ud)	C	2.35	125
Slow-growing perennials, 'Stress-tolerators'			
Brachypodium pinnatum (Bp)	SC	1.03	22
Bromopsis erecta (Be)	C-S-R/S-C	—	22
Centaurea scabiosa (Cs)	S/C-S-R	—	22
Festuca ovina (Fo)	S	1.00	82
Helianthemum nummularium (Hn)	S	0.70	55
Helicotrichon pratense (Hp)	S/S-C	0.75	22
Leontodon hispidus (Lh)	S	0.89	55
Sedum acre (Sa)	S	0.71	125

*Strategies taken from Grime *et al.* (1988).
†R_{max} values from Grime & Hunt (1975).
Species abbreviations used in analyses are given in parentheses.
Nomenclature follows that of Clapham *et al.* (1962)

(L.) was collected at Tapton experimental gardens. *Cepaea hortensis* (Muller) and *Arianta arbustorum* (L.) were collected at Miller's Dale in Derbyshire, northern England, UK. *Sitobion avenae* (F.) was collected and multiplied at Tapton experimental gardens in a mixed grass community (*Poa annua, Arrhenatherum elatius, Holcus lanatus, Lolium perenne* and *Festuca ovina*). No attempt was made to maintain a single-clone population of aphids.

EXPERIMENTAL DESIGN

Four containers, 250 mm high × 500 mm long × 400 mm wide each filled with approximately 50 kg of fine sand, were placed in the centre of each microcosm. Prior to the commencement of the experiment the sand was analysed for heavy metals, sodium and pH to ensure that the levels were appropriate for normal plant growth.

The experiment included factorial combinations of herbivory (present or absent) and three levels of soil fertility (low, moderate and high), replicated six times accounting for a total of 36 microcosms. Seeds of the 24 species were sown in May 1994 and herbivores

introduced to half the microcosms throughout August and September of that year.

EXPERIMENTAL PROCEDURES

Temperature, photon flux density and CO_2 inside the microcosms were measured periodically to determine how much they differed from ambient values and whether there was variation between microcosms. The temperature inside 10 randomly selected microcosms was measured every second day at approximately midday beginning in May and ending in October. The concentration of CO_2 and light intensity at midday was measured within each microcosm once a month between May and October 1995. A portable infra-red gas analyser was used to measure the concentration of CO_2 (p.p.m.), and a portable light sensor was used to measure photon flux density (μmol m^{-2} s^{-1}) above the canopy.

Following Burke (1993), the number of seeds used per container varied according to their recorded seed weight: < 0.20 mg = 125 seeds container^{-1}; 0.21–0.50 mg = 110 seeds container^{-1}; 0.51–1.00 mg = 82 seeds container^{-1}; 1.01–2.00 mg = 55 seeds container^{-1};

> 2.01 mg = 22 seeds container^{-1} (Table 1). After the seeds were sown and had begun to germinate (early June 1994), 100 ml of full Rorison's nutrient solution (Hendry & Grime 1993) was added to each container once a week for 3 weeks, and tap water was applied when necessary to maintain soil moisture supply. Beginning in July 1994, different controlled amounts of Rorison's were applied on a weekly basis to produce the three nutrient solution fertility levels: high received 1000 ml (56 mg nitrogen and 31 mg phosphorus), moderate received 100 ml (5.6 mg nitrogen and 3.1 mg phosphorus) and low received no nutrient solution. The difference in Rorison's was compensated with tap water. No fertilizer or water was applied over the winter (December to March), but watering when required and weekly fertilization resumed in April and continued through to November 1995.

Herbivores were added once the plants were well established (August 1994). Adult molluscs were used, but the aphids were not separated according to age, or whether they were alate or apterous. Rather than add all the herbivores at once, repeated introductions were used to simulate waves of immigration (Beyers & Odum 1993). The activity of the herbivores was more likely to remain constant between fertility treatments with this procedure, which also increased the chances of herbivores encountering exploitable stages in particular plant life histories. Three individuals of each mollusc species and 20 individuals of *Sitobion avenae* were placed in the centre of each microcosm (where the four containers abut) on each of four dates in August and September (a total of 36 molluscs and 80 aphids). All the molluscs were removed at the end of the first growing season. Fifty-four freshly collected molluscs and 120 *S. avenae* were introduced to each microcosm in the second year by following the previous year's procedure on six separate dates between June and September 1995. The total number of live molluscs remaining in each microcosm was counted at the end of the experiment (November 1995). The number of *S. avenae* in each microcosm was estimated in September 1994 by randomly selecting 10 5-cm^2 patches of ground and counting the number of *S. avenae* found on the vegetation growing there. During the second growing season, the total number of *S. avenae* in each microcosm was counted on three separate occasions in June, July and August. The plant species upon which *S. avenae* was found was also recorded in order to determine directly the feeding preferences of the aphids.

One month after the sowing of seeds, a preliminary seedling count was conducted on a random selection of containers. It was ascertained that there was a relatively equal degree of germination between species and between microcosms. At the end of the second growing season (November 1995) a final harvest was made of the above-ground biomass of one randomly selected container in each microcosm, which was clip-ped, sorted to species, oven-dried at 80 °C, and weighed. We attempted to analyse below-ground biomass but not only was it impossible to separate below-ground parts to species, but the dense root mat that developed at the soil surface also made it virtually impossible to separate sand adequately from the roots.

The number of flowers produced by each species was recorded in October 1994, June 1995 and July 1995. *Poa annua* was the only grass to flower under all treatments, and in July 1995 three flower heads were randomly selected from each microcosm (all *P. annua* flower heads were sampled if three or less were present). *Sitobion avenae* in natural communities is known to feed preferentially on flower heads (Dixon 1985) and the effect of herbivory on *P. annua* flower heads was therefore examined. After air-drying and counting the seed number per flower head, the seeds were placed on moist filter paper in Petri dishes in a growth room at 22 °C for 2 months to determine the number of seeds that germinated per flower head.

ANALYSIS

A two-way ANOVA was applied to examine the effects of fertility and herbivory on the total biomass of the plant community. A three-way ANOVA was applied to examine the effects of the fertility treatment, the herbivory treatment, and the three primary plant functional types on above-ground biomass. The data were tested for heteroscedasticity and were found to have equal variances. The final harvest was analysed further using paired *t*-tests for each species at each soil fertility level to compare the means of the above-ground biomass in the presence and absence of herbivores.

For each fertility level, linear regression was applied to the change in above-ground biomass mediated by herbivory against R_{max} values derived from seedling growth analysis where these were available (Grime & Hunt 1975) (Table 1). R_{max} refers to the maximum relative growth rate of a plant grown under controlled optimal greenhouse conditions.

Two-way ANOVAs were applied to determine the effect of soil fertility and herbivory on flowering, seed production and seed viability of *Poa annua*. Tukey's honestly significant difference (HSD) test was used to compare treatment means.

The effect of soil fertility on the number of *Sitobion avenae* during the first growing season was tested with one-way ANOVA. A one-way ANOVA was also applied to examine the effect of soil fertility on the survivorship of the three mollusc species.

Results

ENVIRONMENTAL CONDITIONS INSIDE THE MICROCOSMS

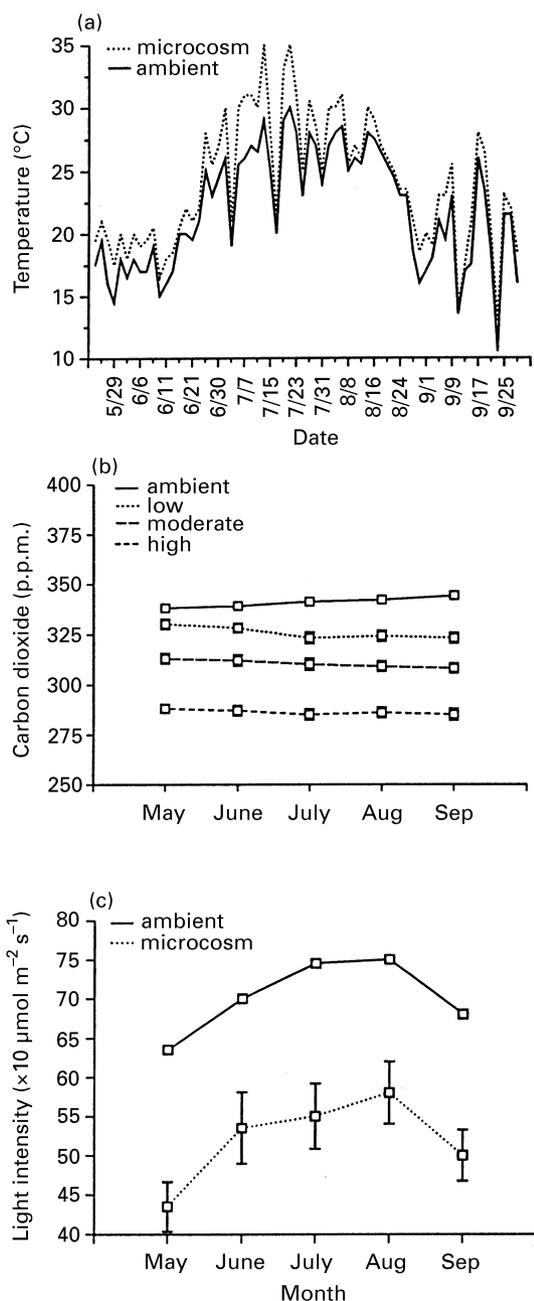The outdoor microcosms operated at a higher temperature than ambient temperatures (Fig. 1a). During

Fig. 1 Environmental conditions measured inside microcosms. (a) Temperature (°C); (b) carbon dioxide concentration (p.p.m.); (c) light intensity ($\times 10\,\mu\text{mol m}^{-2}\,\text{s}^{-1}$). Error bars represent 95% confidence limits.

the hottest periods in the summer, the microcosms reached a mean maximum of approximately 6 °C higher than ambient although, generally, the difference was 2 °C or less and no consistent variation was detected between the microcosms. The CO_2 concentration in microcosms (Fig. 1b) depended on soil fertility, with a decrease of approximately 20 p.p.m. for each increase in microcosm soil fertility. This difference was almost certainly due to higher CO_2 consumption by the greater plant biomass in the high fertility microcosms. The photon flux density within the microcosms was lower (by approximately 30%)

than the direct photon flux density (Fig. 1c), but still greatly exceeded the artificial levels normally generated in indoor growth chambers.

PLANT ABOVE-GROUND BIOMASS RESPONSE TO TREATMENTS

Herbivory and, particularly, soil fertility had significant (Table 2) and large effects on above-ground biomass after two growing seasons (Fig. 2). At high fertility plant biomass was high in both the absence and presence of herbivores (compared with the other fertility treatments), but herbivory reduced total biomass by approximately one-half. A similar relative effect of herbivores was seen at moderate fertility, although biomass was much lower. At low soil fertility, the growth of plants was very slow and herbivory had little effect.

The primary functional types responded quite differently to the herbivore and soil fertility treatments. At final harvest, both herbivory and fertility treatments had significant effects on the mean dry weights of each of the three primary functional types (Table 3). At moderate and high soil fertility, ruderals and competitors were both significantly reduced in the presence of herbivores, whereas stress-tolerators had a significantly greater biomass (Fig. 3). At low soil fertility, herbivores did not appear to have any significant influence on the biomass of any of the primary functional types.

In Fig. 4, the mean above-ground biomass of each species per container in the presence of herbivores (y-axis) is compared to its biomass in the absence of herbivores (x-axis) at the three different soil fertility levels. The species falling below the 1:1 line therefore correspond to those exhibiting a greater relative biomass in the absence of herbivores, while those species above the line were promoted in the presence of herbivores. At moderate and high soil fertility only stress-tolerant species (i.e. *Festuca ovina, Helico-*
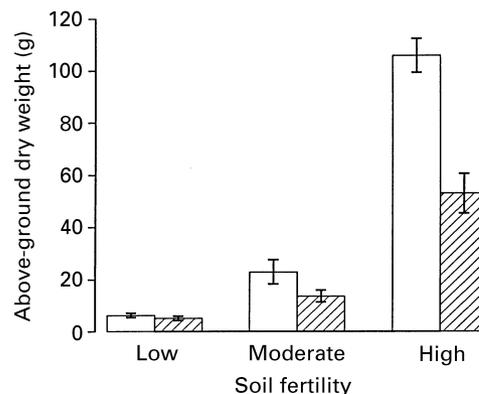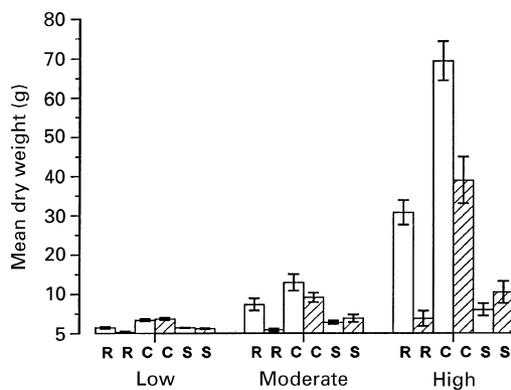

Fig. 2 Effects of fertility and herbivory on the mean shoot biomass of the total plant community grown for two seasons in outdoor microcosms. Open bars are the herbivores absent treatment, dashed bars are the herbivores present treatment. Error bars represent 95% confidence limits.

Table 2 Results of two-way ANOVA examining the effects of fertility (FERT) and herbivory (HERB) on total above-ground biomass

Source of variation	d.f.	MS	F-ratio	P
FERT	2	18621.417	963.045	< 0.001
HERB	1	3997.422	206.735	< 0.001
FERT × HERB	2	2319.639	119.965	< 0.001
ERROR	30	19.336		

Table 3 Results of three-way ANOVA examining the effects of the three primary functional types (RCS), the fertility treatments (FERT) and the herbivory treatments (HERB) on above-ground plant biomass

Source of variation	d.f.	MS	F-ratio	P
RCS	2	3568.93	465.62	< 0.001
FERT	2	6213.27	810.61	< 0.001
HERB	1	1327.99	173.26	< 0.001
RCS × FERT	4	1868.57	243.78	< 0.001
RCS × HERB	2	518.06	67.59	< 0.001
FERT × HERB	2	775.34	101.16	< 0.001
RCS × FERT × HERB	4	314.66	41.05	< 0.001
ERROR	90	7.67		

Fig. 3 Effects of soil fertility and herbivory on the mean shoot biomass (g) after two growing seasons of the three primary functional types (R = ruderals; C = competitors; S = stress-tolerators). Open bars are the herbivores absent treatment, dashed bars are the herbivores present treatment. Error bars represent 95% confidence limits.

trichon pratense, *Brachypodium pinnatum*, *Bromopsis erecta* and *Leontodon hispidus*) fell on or above the 1 : 1 line. All other species, including some stress-tolerators, fell below this line. *Holcus lanatus* had the greatest biomass in all treatments but was not significantly influenced by herbivory. Ruderals, such as *Poa annua* and *Cerastium fontanum*, suffered the greatest losses in biomass from herbivory, which is reflected in Fig. 4 by the greater distance of these points from the 1 : 1 line when the log scale is accounted for.

The regression analyses of the change in aboveground biomass mediated by herbivory against maximum relative growth rates (R_{max}) showed similar effects at each of the three soil fertility levels (Fig. 5). At moderate and high soil fertility R_{max} was significantly negatively correlated with the change in biomass due to herbivory.

FLOWERING RESPONSE TO TREATMENTS

The effects of herbivory were significant in two-way ANOVAs for each of the three dependent variables: number of *Poa annua* flower heads microcosm^{-1}, number of *P. annua* seeds flower head^{-1} and number of *P. annua* seeds (from three selected plants microcosm^{-1}) that germinated (Table 4). The effect of fertility was significant for all but the number of *P. annua* seeds that germinated (Table 4). The interaction between effects of herbivory and fertility was significant for the number of flower heads produced per microcosm. At all soil fertility levels there was a significant reduction in the number of flower heads and number of seeds per flower head in the presence of herbivores (Table 5). The number of viable seeds produced by the three flower heads was also significantly reduced in the presence of herbivores (Table 5). The combination of these effects indicated the potential for a huge decrease in components of fitness of *P. annua* due to herbivory.

HERBIVORE RESPONSE TO TREATMENTS

The numbers of *Sitobion avenae* recorded in the microcosms near the end of the first growing season were found to be significantly related to soil fertility (F-value = 108.37; d.f. = 2; P = < 0.001) (Fig. 6a).
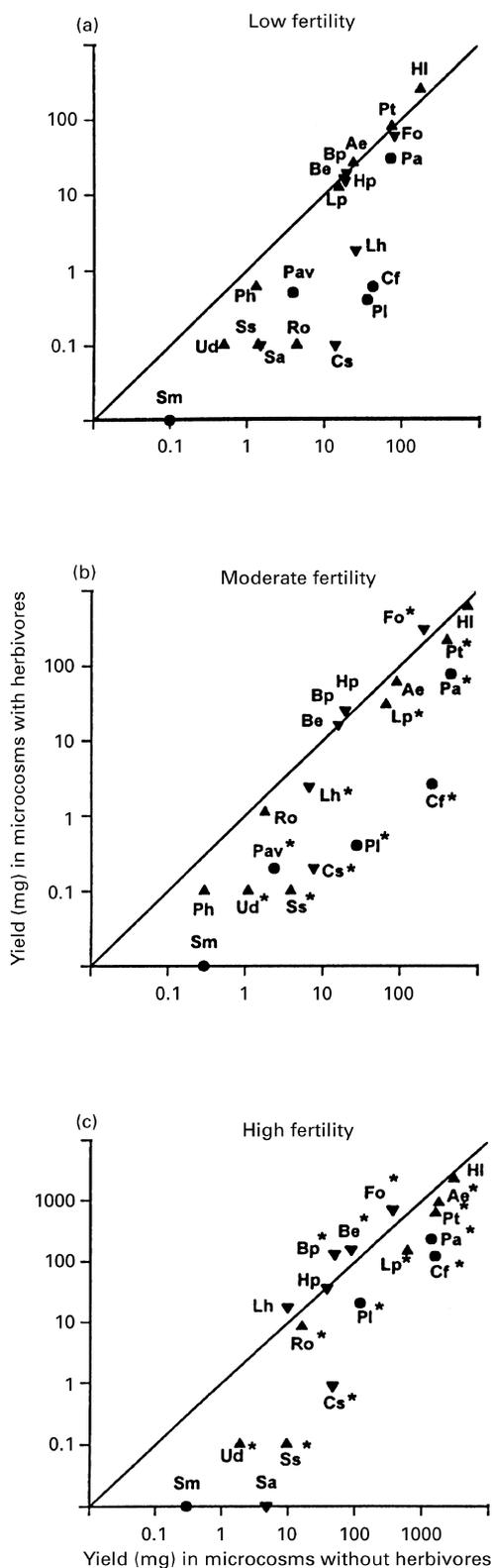
Fig. 4 Effects of herbivory on the mean shoot biomass of individuals of various species grown together for two growing seasons in outdoor microcosms at (a) low soil fertility, (b) moderate soil fertility, and (c) high soil fertility. Circles, ruderals; triangles up, competitors; triangles down, stress-tolerators. The statistical significance of changes in weight associated with herbivory is indicated as follows: *P < 0.05; **P < 0.01; ***P < 0.001. Species full names are found in Table 1. Hp and Bp in (b) overlap and therefore share the same symbol.
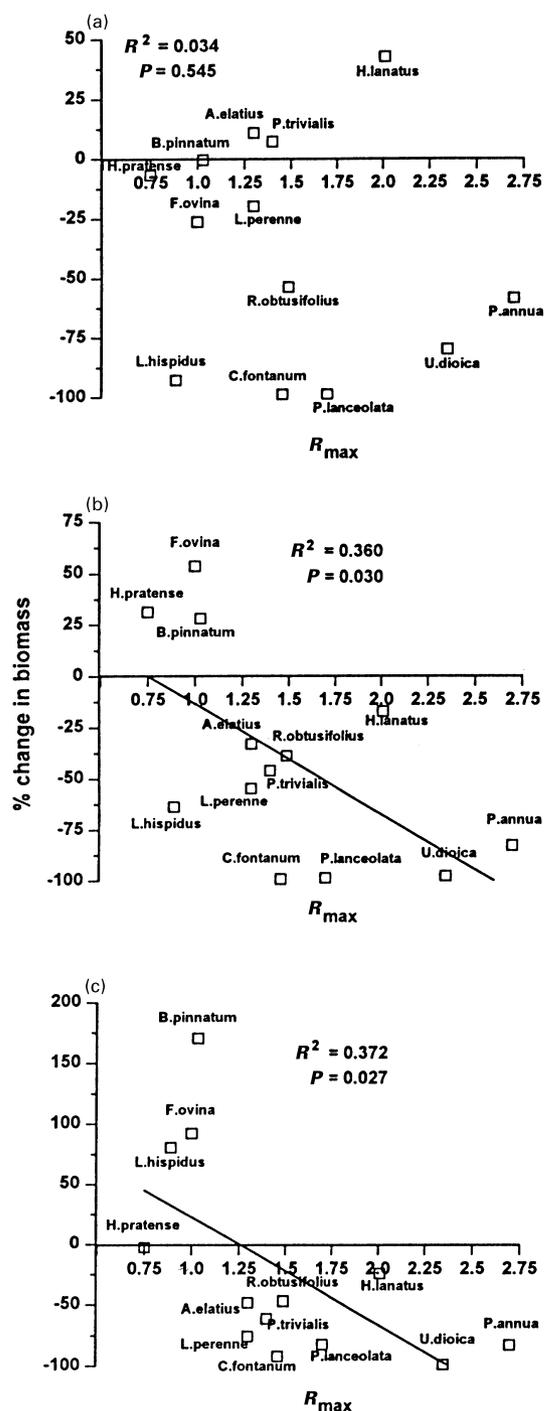

Fig. 5 Relationships between the percentage change in shoot biomass due to herbivory and the relative maximum growth rate (R_{max}) at (a) low soil fertility; (b) moderate soil fertility; (c) high soil fertility. See Table 1 for the known values of R_{max}.

During the second growing season, *S. avenae* was found mainly on *Poa annua*, *Holcus lanatus* and *Poa trivialis* at all soil fertility levels (Table 6). *Sitobion avenae* was found on *P. annua* even when the relative abundance of *P. annua* was low. Relative to its major contribution to the shoot biomass in all treatments, *H. lanatus* had a very low density of *S. avenae*. The

Table 4 Results of two-way ANOVA examining the effects of the fertility treatments (FERT) and the herbivory treatment (HERB) on three dependent reproduction variables

Source of variation	Number of *Poa annua* flower heads microcosm^{-1}			Number of *Poa annua* seeds flower head^{-1}			Number of *Poa annua* seeds that germinated		
	d.f.	MS	*F*-ratio	d.f.	MS	*F*-ratio	d.f.	MS	*F*-ratio
FERT	2	3256.69	29.78**	2	952.00	5.77**	2	242.19	1.49
HERB	1	6944.44	63.50**	1	8314.06	50.36**	1	10030.43	61.71**
FERT × HERB	2	1788.69	16.36**	2	159.22	0.96	2	148.88	0.92
ERROR	30	109.36		76	165.09		76	162.54	

* $P < 0.05$, ** $P < 0.01$

Table 5 Summary of *Poa annua* seed production and seed viability within treatments. Numbers presented are mean values. Within a treatment, numbers sharing the same letter are not significantly different ($P > 0.05$) using Tukey's HSD test. Fitness is calculated as the mean number of viable seeds produced per microcosm

Dependent variables	Treatment (soil fertility and herbivory; H)					
	Low −H	Low +H	Moderate −H	Moderate +H	High −H	High +H
Number of flower heads	5.17[a]	1.67[a]	60.83[c]	8.50[a]	41.83[b]	14.33[a]
Number of seeds/flower head	29.39[ab]	13.63[a]	42.25[bc]	21.57[a]	46.46[c]	20.50[a]
Number of seeds germinated/flower head	24.77[b]	7.88[a]	34.44[b]	8.36[a]	35.23[b]	9.67[a]
% germination	84.3	57.8	81.5	38.8	75.8	47.2
FITNESS	128.1	13.2	2095.0	71.1	1473.7	138.6

only other grasses exploited by *S. avenae* were *Lolium perenne*, *Arrhenatherum elatius* and *Festuca ovina*.

The effects of soil fertility on the survival of the three species of mollusc used in this experiment were statistically significant (*Arianta arbustorum*: *F*-value = 107.61; d.f. = 2; $P = < 0.001$; *Helix aspersa*: *F*-value = 27.91; d.f. = 2; $P = < 0.001$; *Cepaea hortensis*: *F*-value = 32.74; d.f. = 2; $P = < 0.001$). The plants grown at high soil fertility seemed to provide the best environment for the molluscs. Most of the molluscs in the high soil fertility microcosms survived to the end of the growing season (Fig. 6b). In contrast, less than half of the molluscs in the moderate soil fertility microcosms survived, and less than a quarter survived in the low soil fertility microcosms.

Discussion

Ecological succession was being investigated, therefore outdoor microcosms were used to provide the seasonal changes and cues required for the natural unfolding of various plant and animal life histories. However, these model communities were not intended to mirror nature (see Lawton 1996; Carpenter 1996; Fraser & Keddy 1997 for reviews and comments on the use of microcosms for ecological research). In order to examine the interactions between soil fertility, competition and the influence of invertebrate herbivory, the initial assemblage of plant species

included widely contrasted functional types that rarely occur together in nature. Moreover, the microcosms operated at slightly higher temperatures than ambient and, generally, at lower concentrations of CO_2. The CO_2 concentration varied depending on the abundance of vegetation, i.e. the greater the abundance, the lower the CO_2 levels, due to an increased rate of photosynthesis. Potentially, any factor altering the supply of carbon (or nitrogen) has the potential to modify herbivore consumption and fitness, and thus influence plant community composition indirectly (Mattson 1980; Crawley 1983). Studies have shown that individual plants grown under high concentrations of CO_2 are less palatable to herbivores as a consequence of decreased nitrogen concentration in the plant tissue (Lincoln *et al.* 1986; Lindroth *et al.* 1995). We might therefore predict that the lower concentrations of CO_2 that were measured in the outdoor microcosms might result in an increase in the palatability of the plants, although the degree to which the CO_2 concentrations were manipulated by Lincoln *et al.* (1986) and Lindroth *et al.* (1995) were much greater than those found here. Furthermore, there are no reported changes in the response of herbivores to increased concentrations of CO_2 in mixed plant communities (Arnone *et al.* 1995).

The purpose of the experiment was to test predictions about the impact of generalist invertebrate herbivores on plant community composition and sec-
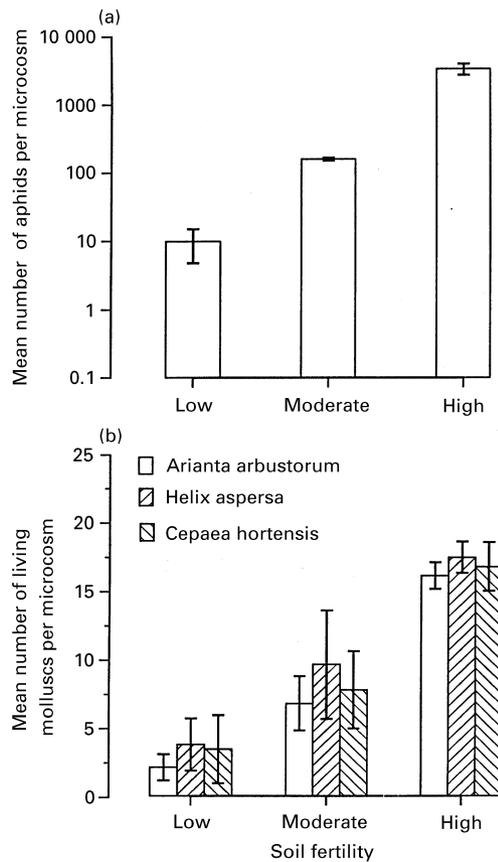
Fig. 6 Effect of soil fertility on the mean number of (a) *Sitobion avenae* after one growing season; and (b) the three mollusc species (*Arianta arbustorum*, *Helix aspersa* and *Cepaea hortensis*) after two growing seasons. Error bars represent 95% confidence limits.

analysis and interpretation allows some separation of the two processes.

Egler's (1954) model of plant succession informed the choice of experimental method used in the outdoor microcosm experiment; a plant community was assembled by sowing, at the same time, seeds of plants found in each successional stage and representing all three primary functional strategies. The inherent slow-growing nature of stress-tolerators meant they would never accumulate very large amounts of biomass in the time span of this experiment, so the direction of succession must be inferred in the results. Two conditions must be satisfied to confirm the mechanistic basis necessary for the hypothesis that generalist invertebrate herbivores increase the rate of succession.

First, the herbivores must consume the fast-growing ruderals and competitors in preference to the slow-growing stress-tolerators. Evidence supporting this condition was that *Sitobion avenae* was found only on ruderal and competitor grasses, except for a very small number found on *Festuca ovina* at high soil fertility. Feeding trials with *S. avenae* (Fraser 1996) and *Helix aspersa* (Grime *et al.* 1996) further support the hypothesis that, in general, these invertebrate herbivores prefer ruderals and competitors. Relative loss in biomass due to herbivores was also greater in ruderals and competitors, from which we can infer that the herbivores preferred these fast-growing species to the slow-growing stress-tolerators. Coley *et al.* (1985) hypothesized that fast-growing plants would be more palatable than slow-growing plants, but found no evidence (Coley 1983) to support Feeny (1976) and Rhoades & Cates's (1976) hypothesis that ephemerals have less effective defences and tend to escape predation by exploiting spatially and temporally unpredictable habitats. It is interesting to note that the generalist invertebrate herbivores studied here seemed to prefer ruderals (whose biomass suffered the greatest decrease) over competitors, confirming a significant preference seen in other palatability trials (Grime *et al.* 1968, 1996; Fraser 1996). These results suggest that ruderals are least well defended, even when compared with fast-growing perennials such as *Holcus lanatus*. Our experiment was not, however, designed to deter-

ondary succession. The influence of herbivory on the fate of individual plant species or aggregations of functional types was inferred from the relative loss, or gain, of plant biomass in the presence of invertebrate herbivores compared with the controls. However, the observed change in biomass of a plant species may not be caused simply by the direct influence of herbivory but rather through a change in interspecific competition resulting from preferential feeding by invertebrate herbivores. Both the direct and indirect influences of herbivores are important, and careful

Table 6 The mean numbers of *Sitobion avenae* recorded on the different grass species midway through the second growing season. Numbers in parentheses are 95% confidence limits

	Soil fertility		
	Low	Moderate	High
Poa annua	17.2 (3.1)	78.1 (5.2)	365.4 (67.2)
Holcus lanatus	7.1 (2.2)	56.3 (8.5)	34.0 (5.1)
Poa trivialis	4.8 (0.9)	25.0 (4.3)	82.5 (23.9)
Lolium perenne	1.1 (0.9)	22.4 (7.6)	5.4 (2.3)
Arrhenatherum elatius	0.5 (0.4)	1.5 (1.0)	19.8 (5.3)
Festuca ovina	0	0.5 (0.4)	0

mine whether ruderals may escape herbivory because of their short life cycle.

Secondly, at moderate soil fertility the biomass of slow-growing stress-tolerators in the community must be the same or greater in the presence of herbivores. Under these conditions, the indirect effects of feeding by the herbivores on fast-growing plants should reduce plant vigour and impair competitive ability (Harper 1977; Crawley 1983). Not only was the proportion of stress-tolerators increased in the presence of herbivores, but stress-tolerators also had a greater absolute above-ground biomass.

Although generalist herbivores have sometimes been shown to delay rather than accelerate succession (Davidson 1993; Jefferies *et al.* 1994), the early successional plant community in such studies is usually monocotyledonous, while the late-successional community is dicotyledonous (McNaughton 1979; Bazely & Jefferies 1986). Belsky (1986) and Owen (1990) even suggest that monocotyledons have adapted to herbivory and achieve higher fitness when grazed. Bazely & Jefferies (1986) describe an experiment in which lesser snow geese delayed succession by heavily grazing a productive salt-marsh. When the geese were excluded, the monocotyledonous *Puccinellia–Carex* community was replaced by late-successional dicotyledonous species. It is likely that both the growth form of the grazed plants as well as the recycling of nutrients caused by the intensive grazing and rapid return of faecal nitrogen to the soil allowed the fast-growing *Puccinelia–Carex* lawn to persist (Bazely & Jefferies 1986; Jefferies *et al.* 1994). Otherwise, the nutrients would be sequestered in both live vegetation and litter, resulting in available nutrients being very low and a consequent increase in the contribution of slow-growing plants.

In nature, stress-tolerators rarely exist in habitats of high soil fertility and low disturbance. Often, there is little evidence of herbivore damage in these habitats, a condition that has been attributed to 'top-down' control by carnivores (Fretwell 1977; Oksanen *et al.* 1981; Fraser & Grime 1997, 1998; Fraser 1998). Fraser & Grime (1997, 1998) and Fraser (1998) have proposed that the reason stress-tolerators do not exist in these productive, undisturbed habitats is that they are excluded by competitors which are seemingly being indirectly protected by carnivores. If this hypothesis is correct, the situation created in the high fertility microcosms was a highly artificial one in that herbivores, uncontrolled by carnivores or parasitoids, had freedom to exploit a large mass of relatively palatable plant material. In consequence, stress-tolerators could persist, and even expand, as a result of their superior defences. In this case, succession was being forced along in circumstances in which, in nature, it would have been stalled in a state of competitive dominance until resource supply had diminished through sequestration in living and dead components.

Our results suggest that generalist invertebrate herbivores can indeed increase the rate of secondary plant succession by preferentially feeding on fast-growing ruderals and competitors rather than on slow-growing stress-tolerators. Further evidence supporting the hypothesis is that the fitness of *Poa annua*, as well as the flower production of other ruderals and competitors, was reduced in the presence of herbivores. Flower reduction by herbivory is well documented (Harper 1977; Crawley 1983; Hendrix 1988). In particular, the grass-feeding aphid, *Holcaphis holci*, can reduce the probability that a floral meristem is produced, and, at high aphid infestations, can restrict flowering altogether (Crawley 1989). Other aphids that have been found to reduce flowering and seeding include the hogweed aphid *Carvariella pastinacae* (Sheppard 1987), the aphid *Staticobium staticis* (Foster 1984), and the aphid *Uroleucon caligatum* on goldenrod (Meyer & Root 1993). The reduction in flowering would have obvious negative implications for the effectiveness of a species persisting, or expanding, in any environment. It is also quite remarkable that *Festuca ovina*, a slow-growing perennial grass, only flowered in the presence of herbivores. This clearly shows an indirect response to the suppression of the more palatable fast-growing ruderals and competitors.

Generalist feeders, as opposed to specialists, were an essential ingredient for this experiment. It was necessary to use herbivores that could feed on a broad range of foods so that the preference of the herbivores would dictate the success or failure of a plant species. Perhaps one of the reasons there has been a reluctance to accept the general hypothesis that invertebrate herbivores increase secondary succession is that specialist feeders confound the theory (Bach 1994; reviewed by Davidson 1993). This work demonstrates that the relative importance of generalist vs. specialist feeders needs to be determined.

Aphids have a high turnover rate, which means they can respond quickly to the vagaries of their environment (Dixon 1985). As their population size can be easily measured it was possible to determine the effect of soil fertility on the aphid population. Predictably, the aphids did not perform well at low soil fertility; if the aphids had not been introduced several times here it seems unlikely that they would have persisted. The increase in aphid numbers at moderate and, still further, at high soil fertility is consistent with other studies which show an increase in the rate of insect growth and reproduction with increasing host-plant fertilization (reviewed by Waring & Cobb 1992). For example, Jansson & Smilowitz (1986) found significant increases in the population growth rate of the green peach aphid *Myzus persicae* on potatoes with increasing levels of nitrogen (56, 84, 140 and 224 kg N ha^{-1}). Soil fertilization can enhance host-plant quality by increasing tissue concentrations of nitrogen, a nutrient that is frequently limiting for phytophagous insects (Mattson 1980; White 1993), or

by shifting allocation away from carbon-based secondary defences (Gershenzon 1984; Waterman & Mole 1989; Herms & Mattson 1992). There was a high mortality of molluscs in the low and moderate soil fertility treatments and those molluscs that did not die at low soil fertility appeared to be relatively inactive. In fact, mortality of the molluscs followed the soil fertility levels very closely, indicating that mollusc survival is a useful index of the nutritional quality of the vegetation.

Acknowledgements

References

Arnone, J.A. III, Zaller, J.G., Ziegler, C., Zandt, H. & Korner, C. (1995) Leaf quality and insect herbivory in model tropical plant communities after long-term exposure to elevated atmospheric CO_2. *Oecologia*, **104**, 72–78.

Bach, C.E. (1994) Effects of a specialist herbivore (*Altica subplicata*) on *Salix cordata* and sand dune succession. *Ecological Monographs*, **64**, 423–445.

Bazely, D.R. & Jefferies, R.L. (1986) Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *Journal of Ecology*, **74**, 693–706.

Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351–371.

Belsky, A.J. (1986) Does herbivory benefit plants? A review of the evidence. *American Naturalist*, **127**, 870–892.

Berdowski, J.J.M. & Zeilinga, R. (1987) Transition from heathland to grassland: damaging effects of the heather beetle. *Journal of Ecology*, **75**, 159–175.

Beyers, R.J. & Odum, H.T. (1993) *Ecological Microcosms*. Springer-Verlag, New York, NY.

Brown, V.K. & Gange, A.C. (1989) Differential effects of above-ground and below-ground insect herbivory during plant succession. *Oikos*, **54**, 67–76.

Brown, V.K. & Gange, A.C. (1992) Secondary plant succession: how is it modified by insect herbivory? *Vegetatio*, **101**, 3–13.

Brown, V.K., Jepson, M. & Gibson, C.W.D. (1988) Insect herbivory: effects on early old field succession demonstrated by chemical exclusion methods. *Oikos*, **52**, 293–302.

Bryant, J.P. (1987) Feltleaf willow–snowshoe hare interaction: plant carbon/nutrient balance and floodplain succession. *Ecology*, **68**, 1319–1327.

Bryant, J.P. & Chapin, F.S. III (1986) Browsing–woody plant interactions during boreal forest plant succession. *Forest Ecosystems in the Alaskan Taiga* (eds K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck & C.R. Dyrness), pp. 213–225. Springer, New York, NY.

Bryant, J.P., Chapin, F.S. III & Klein, D.R. (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*, **40**, 357–368.

Bryant, J.P., Kuropat, P.J., Cooper, S.M., Frisby, K. & Owen-Smith, N. (1989) Resource availability hypothesis of plant antiherbivore defence tested in a South African savanna ecosystem. *Nature*, **340**, 227–229.

Bryant, J.P., Provenza, F.K., Pastor, J., Reichardt, P.B., Clausen, T.P. & du Toit, J.T. (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics*, **22**, 431–446.

Burke, M.J.W. (1993) *Plant community responses to fertilisation, disturbance and seed inoculation in limestone grassland*. PhD Thesis, University of Sheffield, Sheffield, UK.

Cargill, S.M. & Jefferies, R.L. (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 669–686.

Carpenter, S.R. (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology*, **77**, 677–680.

Cates, R.G. & Orians, G.H. (1975) Successional status and the palatability of plants to generalized herbivores. *Ecology*, **56**, 410–418.

Chapin, F.S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.

Clapham, A.R., Tutin, T.G. & Warburg, E.F. (1962) *Flora of the British Isles*, 2nd edn. Cambridge University Press, London.

Coley, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monograms*, **53**, 209–233.

Coley, P.D. (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia*, **74**, 531–536.

Coley, P.D., Bryant, J.P. & Chapin, F.S. III (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.

Crawley, M.J. (1983) *Herbivory. The Dynamics of Animal–Plant Interactions*. Blackwell Scientific Publications, Oxford, UK.

Crawley, M.J. (1989) Insect herbivores and plant population dynamics. *Annual Review of Entomology*, **34**, 531–564.

Davidson, D.W. (1993) The effects of herbivory and granivory on terrestrial plant succession. *Oikos*, **68**, 23–35.

Dixon, A.F.G. (1985) *Aphid Ecology*. Blackie, Glasgow, UK.Egler, F.E. (1954) Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. *Vegetatio*, **4**, 412–417.

Feeny, P. (1976) Plant apparency and chemical defense. *Recent Advances in Phytochemistry*, **10**, 1–40.

Foster, W.A. (1984) The distribution of the sea lavender aphid *Staticobium staticis* on a marine saltmarsh and its effects on host plant fitness. *Oikos*, **42**, 97–104.

Fraser, L.H. (1996) *Plant/animal interactions: the effects of invertebrate herbivory and productivity on plant community dynamics examined in outdoor microcosms and two north Derbyshire dales*. PhD Thesis, University of Sheffield, Sheffield, UK.

Fraser, L.H. (1998) Top-down vs. bottom-up control influenced by productivity in a North Derbyshire dale. *Oikos*, **81**, 99–108.

Fraser, L.H. & Grime, J.P. (1997) Primary productivity and trophic dynamics investigated in a North Derbyshire dale. *Oikos*, **80**, 499–508.

Fraser, L.H. & Grime, J.P. (1998) Top-down control and its effect on the biomass and composition of three grasses at high and low soil fertility in outdoor microcosms. *Oecologia*, **113**, 239–246.

Fraser, L.H. & Keddy, P. (1997) The role of experimental

microcosms in ecological research. *Trends in Ecology and Evolution*, **12**, 478–481.

Fretwell, S.D. (1977) The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine*, **20**, 169–185.

Gershenzon, J. (1984) Changes in the levels of plant secondary metabolites under water and nutrient stress. *Recent Advances in Phytochemistry*, **18**, 273–320.

Godfray, H.C.J. (1985) The absolute abundance of leaf miners on plants of different successional stages. *Oikos*, **45**, 17–25.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.

Grime, J.P. & Hunt, R. (1975) Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology*, **63**, 393–422.

Grime, J.P., Cornelissen, J.H.C., Thompson, K. & Hodgson, J.G. (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos*, **77**, 489–494.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology: a Functional Approach to Common British Species*. Unwin Hyman, London, UK.

Grime, J.P., MacPherson-Stewart, S.F. & Dearman, R.S. (1968) An investigation of leaf palatability using the snail *Cepaea nemoralis* L. *Journal of Ecology*, **56**, 405–420.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, D., Hand, W.W., Hannah, M.A., Hillier, S.H., Hodkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C. & Whitehouse, J. (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London, UK.

Hendrix, S.D. (1988) Herbivory and its impact on plant reproduction. *Plant Reproductive Ecology: Patterns and Strategies* (eds J. Lovett-Doust & L. Lovett-Doust), pp. 246–263. Oxford University Press, Oxford, UK.

Hendry, G.A.F. & Grime, J.P. (1993) *Methods in Comparative Plant Ecology – a Manual of Laboratory Methods*. Chapman & Hall, London, UK.

Herms, D.A. & Mattson, W.J. (1992) The dilemma of plants: to grow or defend. *Quarterly Review of Biology*, **67**, 283–335.

Huntly, N.J. (1987) Influence of refuging consumers (Pikas: *Ochotona princeps*) on subalpine meadow vegetation. *Ecology*, **68**, 274–283.

Jansson, R.K. & Smilowitz, Z. (1986) Influence of nitrogen on population parameters of potato insects: abundance, population growth, and within-plant distribution of the green peach aphid, *Myzus persicae* (Homoptera: aphididae). *Environmental Entomology*, **15**, 49–55.

Jefferies, R.L., Klein, D.R. & Shaver, G.R. (1994) Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos*, **71**, 193–206.

van de Koppel, J., Huisman, J., van der Wal, R. & Olff, H. (1996) Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. *Ecology*, **77**, 736–745.

Lawton, J.H. (1996) The Ecotron facility at Silwood Park: the value of 'big bottle' experiments. *Ecology*, **77**, 665–669.

Levin, D.A. (1973) The role of trichomes in plant defense. *Quarterly Review of Biology*, **48**, 3–15.

Lincoln, D.E., Couvet, D. & Sionit, N. (1986) Responses of an insect herbivore to host plants grown in carbon dioxide enriched atmospheres. *Oecologia*, **69**, 556–560.

Lindroth, R.L., Arteal, G.E. & Kinney, K.K. (1995) Responses of three saturniid species to Paper Birch grown under enriched CO_2 atmospheres. *Functional Ecology*, **9**, 306–311.

McNaughton, S.J. (1979) Grazing as an optimization process: grass–ungulate relationships in the Serengeti. *American Naturalist*, **113**, 691–703.

McNaughton, S.J. (1983) Compensatory plant growth as a response to herbivory. *Oikos*, **40**, 329–336.

Mattson, W.J. Jr (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.

Meyer, G.A. & Root, R.B. (1993) Effects of herbivorous insects and soil fertility on reproduction of goldenrod. *Ecology*, **74**, 1117–1128.

Mooney, H.A. (1972) The carbon balance of plants. *Annual Review of Ecology and Systematics*, **3**, 315–346.

Mooney, H.A. & Gulmon, S.L. (1982) Constraints on leaf structure and function in reference to herbivory. *Bioscience*, **32**, 198–206.

Odum, E.P. (1969) The strategy of ecosystem development. *Science*, **164**, 262–270.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240–261.

Owen, D.F. (1990) The language of attack and defence. *Oikos*, **57**, 133–135.

Owen-Smith, N. & Cooper, S.M. (1987) Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology*, **68**, 319–331.

Reader, P.M. & Southwood, T.R.E. (1981) The relationship between palatability to invertebrates and the successional status of a plant. *Oecologia*, **51**, 271–275.

Rhoades, D.F. & Cates, R.G. (1976) Towards a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry*, **10**, 168–213.

Schowalter, T.D. (1981) Insect herbivore relationship to the state of the host plant: biotic regulation of ecosystem nutrient cycling through ecological succession. *Oikos*, **37**, 126–130.

Sheldon, S.P. (1987) The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology*, **68**, 1920–1931.

Sheppard, A.W. (1987) *Competition between the insect herbivores of hogweed* Heracleum sphondylium. PhD Thesis, University of London, London, UK.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. (1986) Leaf palatability, life expectancy and herbivore damage. *Oecologia* (*Berlin*), **70**, 544–548.

Veblen, T.T., Hadley, K.S., Reid, M.S. & Rebertus, A.J. (1991) The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology*, **72**, 213–231.

Walker, L.R. & Chapin, F.S. III (1986) Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology*, **67**, 1508–1523.

Waring, G.L. & Cobb, N.S. (1992) The impact of plant stress on herbivore population dynamics. *Insect–Plant Interactions*, Vol. 4 (ed. E. Bernays), pp. 167–226. CRC Press, Ann Arbor, MI.

Waterman, P.G. & Mole, S. (1989) Extrinsic factors influencing production of secondary metabolites in plants. *Insect–Plant Interactions*, Vol. I (ed. E. Bernays), pp. 107–134. CRC Press, Boca Raton, FL.

White, T.R.C. (1993) *The Inadequate Environment*. Springer-Verlag, Berlin, Germany.