Higher-order interaction between molluscs and sheep affecting seedling numbers in grassland

B.H. Clear Hill and J. Silvertown (*)

Ecology and Conservation Research Group, Department of Biology, Open University, Walton Hall, Milton Keynes, MK7 6AA, UK
(*) Correspondence author: Jonathan Silvertown; E-mail: J.Silvertown@open.ac.uk; Fax: +44 1908 654167

Received: 18.10.96 Accepted: 25.3.97

Abstract

Vertebrate and invertebrate herbivores are both important in mesotrophic grasslands and these two different classes of herbivore potentially interact in their effect upon plant populations. We used two field experiments to test for higher order interactions (HOIs) among sheep, slugs and seedlings, using the mechanistic definition that an HOI occurs when the presence of one species modifies the interaction between two others. In each experiment slug addition and slug-removal treatments were nested inside treatments that altered sheep grazing intensity and timing, and the emergence of seedlings from experimentally sown seeds was monitored. In Experiment 1, seedling numbers of *Cerastium fontanum* were increased by intense summer grazing by sheep in both slug-addition and slug-removal treatments, but winter grazing by sheep only increased seedling emergence if slugs were removed. In Experiment 2, winter grazing by sheep significantly reduced total seedling emergence of four species sown (*Lotus corniculatus, Plantago lanceolata, Leucanthemum vulgare, Achillea millefolium*), but the effect was only seen where slugs were removed. Though the experimental system is a relatively simple one with only four components (sheep, slugs, seedlings and the matrix vegetation), higher order interactions, a combination of direct and indirect effects and possible switching behaviour by slugs are all suggested by our results.

Keywords: Herbivory, higher order interactions, seedling emergence, sheep, slugs.

Résumé

Les herbivores, aussi bien vertébrés qu'invertébrés, ont leur importance dans les pelouses mésotrophiques et ces deux classes différentes d'herbivores interagissent potentiellement dans leurs effets sur les populations végétales. Nous avons réalisé deux expériences sur le terrain pour rechercher des interactions d'ordre supérieur (HOIs) entre les moutons, les limaces et les plantules, en utilisant la définition mécaniste selon laquelle une HOI se produit lorsque la présence de l'une des espèces modifie l'interaction entre les deux autres. Dans chaque expérience, des traitements avec addition ou suppression de limaces sont emboîtés dans des traitements altérant l'intensité et la durée du pâturage par les moutons ; l'émergence de plantules à partir de graines semées expérimentalement est surveillée. Dans l'expérience 1, les nombres de plantules de *Cerastium fontanum* augmentent avec un pâturage estival intense par les moutons, aussi bien avec addition qu'avec suppression de limaces ; mais le pâturage hivernal n'accroît l'émergence des plantules que si les limaces sont enlevées. Dans l'expérience 2, le pâturage hivernal réduit significativement l'émergence totale des plantules des quatre espèces semées (*Lotus corniculatus, Plantago lanceolata, Leucanthemum vulgare, Achillea millefolium*) mais l'effet n'est visible que là où les limaces ont été enlevées. Bien que le système expérimental soit relativement simple, avec seulement quatre composantes (moutons, limaces, plantules et matrice végétale), des interactions d'ordre supérieur, une combinaison d'effets directs et indirects, et un possible comportement d'aiguillage par les limaces sont tous suggérés par nos résultats.

INTRODUCTION

The recruitment of plants from seed is dependent upon the availability of seed from the seed rain or from a dormant seed pool, the presence of suitable germination sites and the ability of seedlings to avoid or to tolerate herbivore attack. In mesotrophic grassland vertebrate herbivores such as sheep and cattle are important in this process in two ways: as potential consumers of seedlings and as the main agents determining microsite characteristics that affect seedling recruitment, such as the height of the vegetation, the condition of the soil surface and the presence of canopy gaps (Silvertown, 1981; Silvertown & Wilkin, 1983; Silvertown & Smith, 1988; Bakker, 1989).

Invertebrate herbivores, particularly slugs, have more subtle effects on recruitment that are often only apparent when these herbivores have been experimentally excluded. For example Hanley *et al.* (1995*a*) found that applying molluscicide increased the number of seedlings appearing from the seed bank in five out of six species recorded and the same authors (Hanley *et al.*, 1995*b*) showed in laboratory experiments that the grey field slug *Deroceras reticulatum* would attack and kill the seedlings of species that they reputedly avoid when the plants are larger. In field experiments Hulme (1994*a*) found that 30% of seedlings of a range of grassland species were attacked by molluscs within three days of being planted out, and in another field experiment that molluscs significantly reduced the number of grassland plants present ten months after sowing (Hulme, 1996).

In agricultural situations, damage to seeds and seedlings by slugs is known to seriously reduce establishment, especially of seedlings of species with inherently low vigour and where growth is restricted by competition from resident plants (Barker, 1989). The result of slug herbivory varies depending on plant age and physiological status as well as the amount of plant material removed (Dirzo & Harper, 1980).

Most grasslands are grazed simultaneously by vertebrates and invertebrates and the vegetation structure created by the vertebrates, particularly the height of the sward, affects the microhabitats available to the invertebrates (Morris, 1971). Because vertebrate herbivory has these manifold effects upon both plants and other herbivores there is potential for ecologically important higher-order interactions between vertebrate and invertebrate herbivory. Interactions between vertebrate and arthropod herbivores have been investigated (Gibson *et al.*, 1987), but not between vertebrates and molluscs, although herbivory by the latter may be more important than arthropod herbivory in mesotrophic grasslands (Rees & Brown, 1992; Hulme, 1994*a*, 1996).

Higher-order interactions (HOIs) are beginning to assume greater importance in ecology as experimental studies of systems with more than two components become increasingly common. The terminology of interactions is still confused, so it is necessary to state what we mean by an HOI in this study and how its presence can be detected (Billick & Case, 1994). We adopt Wootton's (1993) mechanistic definition that an HOI occurs when the presence of one species modifies the interaction between two others and we use the existence of a significant interaction term in analysis of variance as the criterion to detect such situations.

The existing evidence that vertebrate × mollusc interactions affect seedling recruitment in grasslands is scarce, circumstantial and conflicting. HANLEY *et al.* (1996) found that experimentally varying gap size, a parameter affected by vertebrate herbivory (SILVERTOWN & SMITH, 1989*a*), affected mollusc attack on seedlings of *Ranunculus acris*, although attack on other species did not depend on gap size. Gaps are essentially zones where the competitive effect of larger plants on seedlings is reduced. REES & BROWN (1992) found that competition and mollusc herbivory both had large negative effects upon fecundity in four annual crucifers, but that there was no synergism between the two effects.

The conflicting circumstantial evidence of an interaction between vertebrate and mollusc herbivory calls for field experiments that manipulate both types of herbivore directly. In this paper we report the results of such an experiment designed to test for higher order interaction between herbivory by sheep and herbivory by slugs on the recruitment of dicot seedlings. The experiments were conducted in a grassland where our previous work has shown that the sward characteristics created by different sheep grazing treatments affect the seedling emergence and establishment of dicots (SILVERTOWN & SMITH, 1989*b*; SILVERTOWN *et al.*, 1992; BULLOCK *et al.*, 1994*b*).

METHODS

Two seed sowing experiments were carried out at Little Wittenham Nature Reserve near Abingdon in Oxfordshire, England (Grid Reference: US 5681 9247) in 1992/93. The site is on a calcareous clay loam and is an outlier of the Berkshire Downs. The sward is species-poor and is dominated by *Lolium perenne* and *Agrostis stolonifera* (BULLOCK *et al.*, 1994*a*), and belongs to the MG7 mesotrophic grassland type defined by RODWELL (1992). The most abundant species of slug in the grassland at the experimental site is *Deroceras reticulatum* (Muller), the Grey Field Slug. *Arion intermedius* is also present.

Sheep grazing treatments

The two experiments were carried out within the framework of an existing sheep grazing trial with a factorial, complete block design (the 'parent' experiment). The parent experiment is described in detail by BULLOCK *et al.* (1994*a*). In this study we employed only half of the treatments (all spring grazed), as shown in table I. Grazing treatments were applied in three seasons: 'winter' (1 November-21 March), 'spring' (21 March-21 May) and 'summer' (21 May-1 November). There were two levels of grazing in winter and summer. In winter, paddocks were ungrazed or grazed by two adult sheep, and in summer grazing the sward height was maintained at either 3 cm or 9 cm. This was done by weekly

TABLE I. – *The four sheep grazing treatments (letters refer to treatments selected from the design of the "parent" experiment described by* BULLOCK et al., *1994*a*).*

	Summer 3 cm	Summer 9 cm
Winter –	Trt B	Trt F
Winter +	Trt D	Trt H

measurements of the sward height followed by adjustment of the sheep stocking rate. The experiment was fully factorial with a 2 × 2 structure and 2 randomised blocks assigned over 8 (2 × 4) 50 m × 50 m paddocks.

Slug grazing treatments

Chemical methods of slug control are problematic where vertebrate herbivores and bird predators of slugs might be poisoned by molluscicides such as methiocarb lying on the soil surface. We therefore adapted a method described by FERGUSON *et al.* (1989) for estimating slug density in pasture to create field plots of low and high slug density into which seeds were sown and monitored for emergence in the field. The Defined-Area Trap (DAT) (FERGUSON *et al.*, 1989) consists of a galvanised iron ring, 150 mm deep, that was driven approximately 50 mm into the ground enclosing a sample area of 0.1 m^2. *D. reticulatum* itself cannot burrow although it does use cracks in the earth and the burrows of other animals. FERGUSON *et al.* (1989) found that slugs appeared unwilling to travel over galvanised iron. Sheep were easily able to graze inside the DATs and we saw no evidence that the traps altered grazing behaviour.

Eight traps were placed at random within the central 30 m × 30 m core area of each paddock in August 1992. Four traps were randomly assigned to the slug-addition treatment and four to the slug-removal treatment. Slugs were removed from the slug-removal traps and 1.8 g of methiocarb slug bait (Murphy's Slugit) was placed just below ground level in 50 mm lengths of 20 mm diameter plastic pipe sunk vertically into the ground at four positions in each removal trap. Previous observation had shown that *D. reticulatum* take refuge in such pipes. The traps were checked before the start of the second experiment in spring 1993 and again half way through when slugs were added or removed as necessary. All slug-addition traps contained at least two *D. reticulatum*. This gave a slug density of 20 m^{-2} which is comparable with the numbers found in assessments across the experimental area before the start of the experiment.

Seed sowing

In Experiment 1, 24 seeds of *Cerastium fontanum* were sown into each trap on 17 and 18 September 1992 at mapped positions which were monitored over the autumn and winter. Seedlings that appeared were removed once they had produced more than four true leaves. In Experiment 2, 25 seeds of each of four different dicot species were sown between 15 and 17 February 1993 in the same traps but at different positions to those used in Expt. 1. The species sown were *Lotus corniculatus, Plantago lanceolata, Leucanthemum vulgare* and *Achillea millefolium*. All seed was obtained from a commercial supplier of native plant seeds (J. Chambers, Northamptonshire, UK.). All four species were tested in the laboratory for germination prior to sowing. The germination percentages were 85% for *A. millefolium*, 78% *L. corniculatus*, 54% *P. lanceolata* and 45% *L. vulgare*. These are species suited to the soil conditions at our experimental site but which, except for *C. fontanum*, are not present there. In both experiments the traps were monitored weekly for seedlings until no new seedlings had appeared for four weeks and all surviving seedlings were beyond the cotyledon stage.

Sward characteristics at sowing positions

The microsite characteristics of each seed sowing position were recorded at the time of sowing in both experiments. This was done by recording whether a pin lowered vertically over each sowing position touched a green leaf or not (canopy closed/open) and whether the soil surface beneath the pin was bare soil or covered by stems, moss or litter. There were too few sites with an open as opposed to a closed leaf canopy to enable analysis to be performed for either experiment, so only the soil surface results are reported below.

Statistical analysis

The effect of sheep grazing and slug grazing treatments on seedling numbers was analysed by split plot ANOVA with slug treatments on the lower stratum. WOOTTON (1994) cautions that using the interaction term of an ANOVA to detect HOIs can mislead if the dependent variable is biomass or some related variable that is most appropriately characterised by a multiplicative model. This problem does not occur in our case because the dependent variable was a count.

The effects of the main sheep grazing treatments on microsite characteristics were analysed by 2-way G-tests of heterogeneity (SOKAL & ROHLF, 1995). Three-way G-tests were used to test for interaction between microsite type, slug treatment and seedling numbers pooled across grazing treatments.

RESULTS

Experiment 1

C. fontanum seedlings were first found on 6 October 1992 and monitored weekly until the end of January 1993 by which time no new seedlings had appeared for 4 weeks. On average across the whole experiment 50% of seeds sown produced seedlings (13/24 per trap). The number of seedlings was increased by hard summer (3 cm) grazing regardless of the slug treatment ($P < 0.01$) (tables II*a*, III*a*). Slugs had a strong main effect on seedling numbers ($P < 0.01$), but there were also significant two- and three-way interactions with grazing treatments (table III*a*). The three-way interaction term of the ANOVA indicates that slugs reduced seedling numbers under all grazing treatments except under 3 cm summer grazing with no winter grazing (tables II*a* & III*a*).

TABLE II. – *Mean number of seedlings emerging per treatment for* (a) Cerastium fontanum *in Experiment 1 and* (b) *all four species in Experiment 2.*

	Sheep grazing treatment			
	Summer 3 cm		Summer 9 cm	
Slug treatment	Winter +	Winter –	Winter +	Winter –
(a)				
removed	32.5	14.0	11.0	11.0
added	15.0	19.0	3.0	0.5
(b)				
removed	12.0	18.5	6.5	17
added	11.0	9.0	0.5	4.0

Experiment 2

Spring germination of the four species sown in mid February was slow, probably due to the dry weather in February and March 1993. The first seedlings to appear were

TABLE III. – *ANOVA table for seedling emergence* (a) *in Experiment 1 and* (b) *in Experiment 2. df = degrees of freedom, v.r. = variance ratio, * p < 0.05, ** p < 0.01.*

Source	df	(a) v.r.	(b) v.r.
blocks. whole stratum			
blocks	1	0.18	0.76
summer	1	33.61**	1.13
winter	1	3.21	0.84
summer. winter	1	1.60	0.08
residual	3	3.05	12.08
blocks. whole slug stratum.			
slugs	1	32.58**	28.85**
slugs. summer	1	1.22	2.28
slugs. winter	1	13.56*	5.52*
slugs. winter. summer	1	21.19**	0.25
residual	4		
TOTAL	15		

counted on 14 April 1993. By 8 June 1993 only 157 seedlings out of the 6400 seeds sown had appeared and no more appeared after this time. There were no significant differences in numbers of seedlings between the four species (table II*b*), so species were combined for analysis. ANOVA showed that the presence of slugs significantly reduced the number of seedlings and there was also a significant winter grazing *x* slug interaction (table III*b*). Winter grazing halved the number of seedlings in the slug removal treatment, but had no effect in the slug addition treatment (fig. 1). There were no significant main effects of sheep grazing treatments.

Sward characteristics at sowing positions

In Experiment 1 analysis of microsites (bare soil or other cover) showed that the hard summer grazing to 3 cm sward height significantly increased the number of bare soil sites ($G = 47.14$, $p < 0.001$). The 3-way G-test revealed no significant interaction between soil microsite type, slug grazing and seedling numbers ($G = 1.55$, $P > 0.05$), but all 2-way interactions were significant ($P < 0.01$) showing that slugs and microsite type had independent (*i.e.* additive) effects upon seedling numbers. Thirty one percent of seeds sown into bare soil appeared as seedlings, compared to 13% of seeds sown in other microsites; 18% of seeds in the slug removal treatment appeared, compared to 10% in the slug addition treatment.

In Expt. 2 G-test analysis of the sowing positions in February 1993 showed that winter grazing increased the number of bare soil microsites as opposed to other ground cover types ($G = 468.00$, $p < 0.001$). As in Expt. 1, the 3-way G-test showed no significant 3-way interaction, though microsite type and slug grazing both had significant independent effects upon seedling numbers. 4.3% percent of seeds sown into

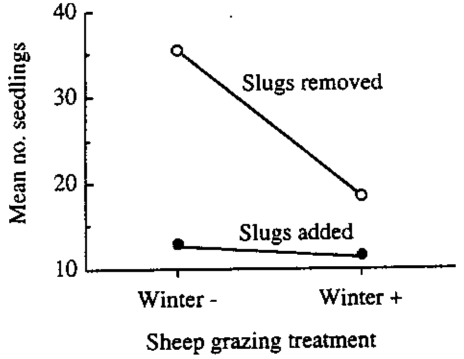

FIG. 1. – The effect of the winter sheep grazing × slug interaction on seedling numbers per treatment in Experiment 2 (summer grazing treatments pooled).

bare soil emerged, compared to 2.3% of seeds sown in other microsites; 3.4% of seeds in the slug removal treatment emerged, compared to 1.5% in the slug addition treatment.

DISCUSSION

The four components of our study system and their relationships are shown in diagrammatic form in figure 2. Both experiments reported here provide evidence for the links labelled 1 - 3 and the second experiment provides evidence for link 4; Sheep grazing decreased the proportion of soil microsites covered by vegetation (link 1), seedlings appeared more frequently in bare soil microsites than other types (link 2) and slugs reduced seedling numbers (link 3). Sheep grazing had a positive indirect effect on seedling numbers (through links 1 + 2) in Experiment 1, but in Experiment 2 winter grazing had a negative effect on seedling numbers (link 4) when slugs were absent (fig. 1).

Higher-order interactions between sheep and slug herbivory are indicated by the significant interaction terms in the ANOVAs for both experiments (table III). In Experiment 1, one particular sheep grazing treatment (winter -, summer 3 cm) eliminated the effect of slugs on seedling numbers seen in other treatments. In Experiment 2, slugs abolished the effect of winter grazing on seedling numbers (fig. 1). We suggest that the HOI in Experiment 1 could be explained by a Type III functional response (contained in link 3) to seedling density, caused by slugs switching to alternative food sources such as litter and new growth of older plants (link 5, fig. 2) where these were more available due to the absence of winter grazing by sheep. The effect of slugs switching away from seedlings in the absence of herbivory by sheep would be most positive on seedling numbers where the *previous* (*i.e.* in summer) sheep grazing treatment was most favourable to seedling emergence (*i.e.* the summer 3 cm treatment). A secondary implication of this hypothesis is that there was resource competition between sheep and slugs through links 1 + 5 (fig. 2). If this was so, the interaction would probably have been highly asymmetric.

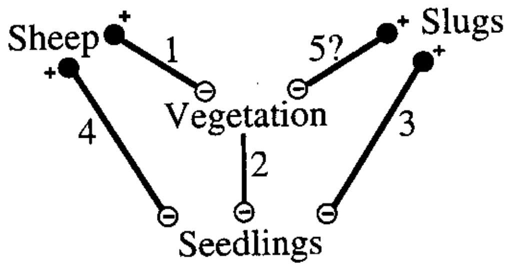

FIG. 2. – A conceptual model of the relationships between herbivores and plants in the study system. Filled circles indicate the beneficiary of an interaction, open circles the loser. Links are numbered for reference in the text.

Seedling germination in Experiment 2 began in mid April by which time sheep in winter grazed treatments had been grazing for four months, so their negative effect on seedling numbers is not surprising. Slugs were apparently very active at this time too because where they were added they reduced seedling numbers to below the level where any negative effect of sheep grazing could be observed (fig. 1).

Even in a system as seemingly simple as the one described here, there are still many unknowns. We do not know whether slugs show a functional response in the field, though this would explain our results. Neither do we know whether slugs exhibit a numerical response to seedlings or other components of their food supply. However, from circumstantial evidence a numerical response seems unlikely. *D. reticulatum* has a broad diet (PALLANT, 1972) and although seedlings are very palatable they represent only a tiny proportion of the available biomass in perennial grassland. Seedling densities typically increase with vertebrate grazing pressure, so if *D. reticulatum* exhibited a numerical response to seedling density a correlation between grazing pressure and slug density might be expected. No effect of grazing on densities of *D. reticulatum* has been found in the parent experiment at Little Wittenham (J. SILVERTOWN, unpublished data) and similarly SOUTH (1989) found no evidence of *Deroceras* numbers being affected by grazing pressure in other permanent pastures, although this could have been because grazing in South's study was only intermittent and light. In contrast, READER (1992) found that more slugs were attracted to bait in grassland plots cleared of most vegetation than to bait in intact vegetation. This suggests slug abundance might be raised by severe grazing, although vertebrate grazers were not actually present in READER's study.

The plant/herbivore relationships represented in figure 2 are arguably some of the most important in mesotrophic grasslands, which are themselves very important habitats in the temperate zone. Further elucidation of the mechanisms of plant/herbivore interaction could throw light upon the role of herbivory in limiting recruitment and hence limiting plant biodiversity in species-poor grasslands such as ours. Field germination of the species in our experiments was very low by comparison with laboratory tests and although we do not know the reason for this, seed predation by rodents (HULME, 1994*b*) might be another important interaction requiring study.

ACKNOWLEDGEMENTS

We thank the Northmoor Trust and the staff of Little Wittenham Nature reserve for their considerable help and support, both financial and physical, Steve Gregory for help in the field and Mike Dodd and Richard Totts for comments on the manuscript. The work was supported by grants from the Open University Research Committee and from the AFRC under the Joint Agriculture and Environment Programme.

REFERENCES

Bakker J. P., 1989. – *Nature management by grazing and cutting*. Dr W.Junk, Hague.

Barker G. M., 1989. – Slug problems in New Zealand pastoral agriculture. *Brit. Crop Protect. Coun. Mono.*, **41**, 59-68.

Billick I. & Case T. J., 1994. – Higher order interactions in ecological communities: What are they and how can they be detected? *Ecology*, **75**, 1529-1543.

Bullock J. M., Hill B. C., Dale M. P. & Silvertown J., 1994*a*. – An Experimental Study of the Effects of Sheep Grazing on Vegetation Change in a Species-Poor Grassland and the Role of Seedlings Recruitment into Gaps. *J. Appl. Ecol.*, **31**, 493-507.

Bullock J. M., Hill B. C. & Silvertown J., 1994*b*. – Demography of *Cirsium vulgare* in a grazing experiment. *J. Ecol.*, **82**, 101-111.

Dirzo R. & Harper J. L., 1980. – Experimental studies on slug-plant interactions. II. The effect of grazing by slugs on high density monocultures of *Capsella bursa-pastoris* and *Poa annua*. *J. Ecol.*, **68**, 999-1011.

Ferguson C., Barratt B. I. P. & Jones P. A., 1989. – A new technique for estimating density of the field slug (*Deroceras reticulatum* (Muller)). *Brit. Crop Protect. Coun. Mono.*, **41**, 331-336.

Gibson C. W. D., Brown V. K. & Jepsen M., 1987. – Relationships between the effects of insect herbivory and sheep grazing on seasonal changes in an early successional plant community. *Oecologia*, **71**, 245-253.

Hanley M. E., Fenner M. & Edwards P. J., 1995*a*. – The effect of seedling age on the likelihood of herbivory by the slug *Deroceras reticulatum*. *Func. Ecol.*, **9**, 754-759.

Hanley M. E., Fenner M. & Edwards P. J., 1995*b*. – An experimental field-study of the effects of mollusk grazing on seedling recruitment and survival in grassland. *J. Ecol.*, **83**, 621-627.

Hanley M. E., Fenner M. & Edwards P. J., 1996. – The effect of mollusc grazing on seedling recruitment in artificially created grassland gaps. *Oecologia*, **106**, 240-246.

Hulme P. E., 1994*a*. – Seedling herbivory in grassland - relative impact of vertebrate and invertebrate herbivores. *J. Ecol.*, **82**, 873-880.

Hulme P. E., 1994*b*. – Post-dispersal seed predation in grassland: Its magnitude and sources of variation. *J. Ecol.*, **82**, 645-652.

Hulme P. E., 1996. – Herbivores and the performance of grassland plants - a comparison of arthropod, mollusk and rodent herbivory. *J. Ecol.*, **84**, 43-51.

Morris M. G., 1971. – The management of grassland for the conservation of invertebrate animals. *In*: Duffey E. & Watt A. S., eds., *The scientific management of animal and plant communities for conservation*. Blackwell Scientific Publications, Oxford.

Pallant D., 1972. – The food of the grey field slug, *Agriolimax reticulatus* (Müller), on grassland. *J. Anim. Ecol.*, **41**, 761-769.

Reader R. J., 1992. – Herbivory as a confounding factor in an experiment measuring competition among plants. *Ecology*, **73**, 373-376.

Rees M. & Brown V. K., 1992. – Interactions between invertebrate herbivores and plant competition. *J. Ecol.*, **80**, 353-360.

Rodwell J. S., Ed., 1992. – *British plant communities, volume 3. Grasslands and montane communities*. Cambridge University Press, Cambridge.

Silvertown J., 1981. – Micro-spatial heterogeneity and seedling demography in species rich grassland. *New Phytol.*, **88**, 117-125.

Silvertown J. & Smith B., 1988. – Gaps in the canopy: the missing dimension in vegetation dynamics. *Vegetatio*, **77**, 56-60.
Silvertown J. & Smith B., 1989*a*. – Germination and population structure of spear thistle *Cirsium vulgare* in relation to sheep grazing management of pasture. *Oecologia*, **81**, 369-373.
Silvertown J. & Smith B., 1989*b*. – Mapping the microenvironment for seed germination in the field. *Ann. Bot.*, **63**, 163-167.
Silvertown J. & Wilkin F. R., 1983. – An experimental test of the role of micro-spatial heterogeneity in the co-existence of congeneric plants. *Biol. J. Linn. Soc.*, **19**, 1-8.
Silvertown J., Watt T. A., Smith B. & Treweek J. R., 1992. – Complex effects of grazing treatment on the establishment, growth, survival & reproduction of an annual in a species-poor grassland community. *J. Veg. Sci.*, **3**, 35-40.
Sokal R. R. & Rohlf F. J., 1995. – *Biometry.* W.H.Freeman, San Francisco.
South A., 1989. – The effect of weather and other factors on numbers of slugs on permanent pasture. *Brit. Crop Protect. Coun. Mono.*, **41**, 355-360.
Wootton J. T., 1993. – Indirect effects and habitat use in an intertidal community: interaction chains and interaction modification. *Amer. Natur.*, **141**, 71-89.
Wootton J. T., 1994. – Putting the pieces together: Testing the independence of interactions among organisms. *Ecology*, **75**, 1544-1551.