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The effect of mollusc grazing on seedling recruitment in artificially created grassland gaps

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Abstract Two experiments conducted in spring and autumn 1992 examined the effect of mollusc grazing on seedling regeneration from natural grassland seedbanks by creating artificial gaps in plots in a grassland sward. Molluscs were excluded from half the gaps by application of molluscicide. Mollusc grazing in both the spring and autumn experiment significantly reduced seedling recruitment, though the intensity of grazing was greatest in autumn. Recruitment of five species was markedly influenced by molluscicide application. In spring, plots from which molluscs were excluded contained significantly more seedlings of *Chenopodium polyspermum* and *Ranunculus acris*. In the autumn, exclusion of molluscs resulted in increased populations of *R. acris, Stellaria graminea* and *Rumex acetosa. Cerastium holosteoides* populations were greatest in autumn grazed plots. Other species, notably the grasses *Holcus lanatus* and *Agrostis capillaris* and the legume *Trifolium repens* were unaffected by molluscicide application. Species diversity was significantly decreased by molluscicide application in the autumn. Gap size significantly affected the recruitment of two species. *Ranunculus acris* populations were significantly higher in small gaps in both spring and summer, while *Chenopodium* recruitment in the spring was greater in small gaps. Gap size also significantly influenced the risk of mollusc attack on *Ranunculus* as molluscs appeared to show an aggregative feeding response in the high seedling density small gaps. Selective grazing of vulnerable seedlings by molluscs may influence the eventual relative proportions of the species present and so provide a potent mechanism in shaping community composition in grasslands.

Key words Diversity · Grazing · Molluscicide · Regeneration · Seed bank

Introduction

The exclusion of molluscs from plant communities has been shown to have a marked influence on the survivorship of newly emerging seedlings (Kelly 1989; Hulme 1994; Standell and Clements 1994; Hanley et al. 1995a). Application of snail poison to chalk grassland sites affected the survival and fecundity of *Linum catharticum* (Kelly 1989). Plants in treated quadrats had higher survival rates than those planted in control plots even though the treatment was only applied for the first 5 months of a 14-month study. This observation suggests that the absence of molluscs during the seedling and juvenile stage allowed greater survivorship of individuals in treated plots. Molluscs are known to prefer seedlings to mature plants (Duthoit 1964; Byers and Bierlein 1982; Barker 1989) and as a consequence their selective influence is likely to be greatest at this stage (Crawley 1983; Fenner 1987). Hulme (1994) describes how the effect of mollusc herbivory in the field was most severe for small seedlings, while Hanley et al. (1995a) showed that mollusc grazing during the vulnerable seedling stage had marked effects upon seedling recruitment and species composition in artificially sown grassland gaps.

Seedling palatability and growth form as well as the timing of grazing may be crucial in determining seedling survivorship (Edwards and Gillman 1987; Hulme 1994; Hanley et al. 1995a,b). Edwards and Gillman (1987) describe an experiment where molluscs were allowed to graze in trays of seedlings which had germinated from soil taken from a grassland field site. Their results show that molluscs exert a selective influence upon seedlings germinating from the seedbank, which is determined by seedling palatability and morphology. The selective grazing by molluscs on highly palatable seedling species has been shown to shift the balance of competition towards more unpalatable species which would otherwise be ex-

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cluded from the vegetation of newly colonised grassland gaps (Hanley et al. 1995a). However, while several field studies highlight important aspects of mollusc/seedling interactions (Kelly 1989; Glen et al. 1991; Barker and Addison 1992; Standell and Clements 1994; Hanley et al. 1995a), none deal with the impact of mollusc grazing on more complex multi-species seedling recruitment from natural grassland seedbanks.

This paper describes two similar experiments conducted in spring and autumn 1992 that aimed to discover how natural seedling regeneration is influenced by the presence of molluscs and how factors such as seedling palatability and morphology, together with the timing of grazing and gap size, affect the recruitment of seedlings from a grassland seedbank. Gap size has been shown to be an important factor regulating seedling numbers, as different species have different optimal gap sizes for germination and onward growth (Silvertown and Smith 1989; McConnoughay and Bazzaz 1990; Williams 1992; Aquilera and Laurenroth 1993). Gap size and the effect of vertebrate herbivory have also been shown to be interrelated (Bullock et al. 1995) and it is possible that any effect that gap size has upon seedling regeneration will also influence the foraging behaviour of molluscs. Bergelson (1990) showed how aggregations of *Senecio vulgaris* were subject to more intense mollusc herbivory than *Senecio* populations growing in random distributions. Higher seedling densities, related to gap size, may lead to an aggregative response (Hassell and May 1974) by molluscs as they concentrate feeding activity in high density patches of preferred food plants.

Materials and methods

Experimental treatments

The study was carried out at the Southampton University ecology meadow situated near Chilworth, Hampshire (grid reference SU 185 403). An area of 40 × 40 m was staked out and within it eight 5 × 5 m plots were randomly arranged. Four of these plots were chosen at random and were treated with molluscicides, namely Fertosan and metaldehyde slug pellets (I.C.I.). The outer (10 cm wide) perimeter of each treated plot was sprinkled with 100 g of slug pellets, acting as a barrier to prevent mollusc immigration, while 300 g of pellets were evenly applied within the plots to kill molluscs at the surface. Liquid Fertosan (62.6 g powder dissolved in 4 l of water) was watered onto the gaps during dry late evening (to avoid evaporation) in order to kill molluscs resting within the soil as well as acting as an irritant at soil level. The remaining four 25-m^2 plots were left as untreated controls. Molluscicide was applied every month to the four treated plots for the duration of the spring and autumn germination experiments. Dead or dying slugs were removed from gaps in order to prevent local nutrient enrichment.

Five 30-cm-diameter and five 15-cm-diameter circular gaps were created in each plot using turf cutters. These gap sizes are similar to naturally occurring grassland gaps such as molehills. The gaps were randomly positioned in the plots, although with the restriction that no two gaps were closer than 20 cm. When the turf was removed, all plant fragments were removed and rhizomes dug out in order to reduce vegetative regeneration. Care was taken to replace as much of the soil as possible so that the natural seedbank was not exhausted by the removal of the turf. In total there were 20 replicates of each gap size for each molluscicide treatment. Gaps dug for the spring germination experiment were prepared on 12 April 1992 and the number and identity of seedlings appearing in each gap was recorded weekly until June 1992 (without removing any). The procedure was repeated in the autumn experiment using newly cut gaps in different areas of the plots. The autumn gaps were dug on 15 September 1992 and the number and identity of seedlings recorded monthly until June 1993. Total seedling populations for each species on each sampling occasion were determined for the four molluscicide/gap size treatments. The mean number of seedlings appearing in each treatment during the course of the experiments was then calculated from the sample totals. The seedling population in the 15-cm-diameter gaps was multiplied by a factor of four to standardize the number of seedlings with those in the 30-cm-diameter gaps. The effect of molluscicide application and gap size on seedling recruitment for the most frequently occurring species was assessed by subjecting the pooled population means to two-way ANOVA. Species diversity was calculated using the Shannon-Wiener index (Southwood 1966) on the mean seedling species populations. The significance of the difference between indices was calculated using the method described by Zar (1984).

Mollusc populations

Eight frogged (i.e. partially hollowed) house-bricks (22 × 10 cm × 7 cm) were randomly arranged in each grid in order to survey the mollusc population of each grid. This method was intended to provide a rough assessment of the relative numbers and species of molluscs present resulting from seasonal changes and molluscicide application. The mollusc populations were recorded at the same time as the seedling data.

Results

Experiment 1: spring mollusc populations

The first mollusc survey was conducted 11 days before the first application of molluscicide was made. Initially mollusc populations of both sets of plots were similar and were dominated by the snail *Vallonia excentrica* (Table 1). During the course of the experiment there was a continuous decline in total mollusc number and species number within populations in both treated and untreated plots, although populations in treated plots were generally much lower. As the experiment progressed the majority of the fauna consisted of members of the Arionidae and Limacidea, *Deroceras reticulatum* being the most abundant species.

The effect of molluscicide application

Molluscicide application had a highly significant ($F_{1,32}$ = 39.711, $P < 0.001$) effect on the mean number of seedlings appearing in gaps during the experiment (Figs. 1a, b, and 2). This is reflected in the relative populations of the two most abundant species that appeared in the gaps. The mean seedling populations of *Chenopodium polyspermum* ($F_{1,32}$ = 58.277, $P < 0.001$) and *Ranunculus acris* ($F_{1,32}$ = 40.734, $P < 0.001$) were greatly reduced in grazed plots. *Holcus lanatus* seedlings were unaffected by grazing, as were the remaining small popula-

Table 1 Mean mollusc populations recorded in molluscicide treated and untreated grassland plots prior to and during two experiments conducted at Chilworth meadow, Hampshire

Species	INITIAL SURVEY		SPRING		AUTUMN	
	Treated	Untreated	Treated	Untreated	Treated	Untreated
Arion ater	0	2	0	0	0	0.8
Arion spp. "Durham"	0	0	0	0	0	0.3
A. fasciatus	1	0	0.1	0.5	0.2	2.4
A. hortensis	1	0	0	0	0	0.4
A. intermedius	2	0	0.2	0	0.1	1.3
A. subfucus	0	1	0	0.1	0.2	0.3
Deroceras caruanae	0	2	0.1	0.2	0	0.2
D. reticulatum	5	7	0	2.0	1.4	16.9
Limax maximus	0	0	0	0.2	0	0
Acicula fusca	6	2	0	0.1	0.4	0.1
Cepaea hortensis	0	0	0	0	0	0
Vallonia excentrica	21	25	0.3	0.8	0.3	0.3
TOTAL	36	39	0.7	4.0	2.7	23.0

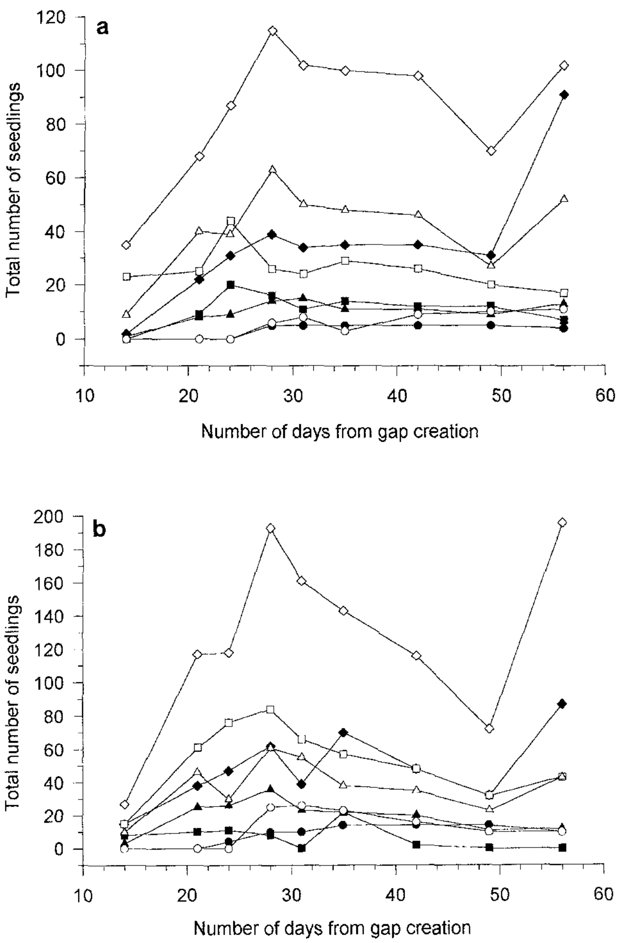

Fig. 1a,b The effect of molluscicide application on the seedling populations of *Holcus lanatus*, *Chenopodium polyspermum*, *Ranunculus acris* and total number of seedlings recorded in **a** 15-cm-diameter and **b** 30-cm-diameter grassland gaps on sampling occasions between April and June 1992. *Symbols:* ● *Holcus lanatus*, ▲ *Ranunculus acris*, ■ *Chenopodium polyspermum*, ◆ Total seedlings, Closed symbols – Grazed gaps; Open symbols –Ungrazed gaps

tions of other species present. Species composition was not significantly influenced by molluscicide application, although grazing did tend to increase diversity. Shannon-Wiener diversity indices in 15-cm-diameter gaps were 0.716 and 0.614 for grazed and ungrazed plots respectively, while in the larger gap size the index values were 0.741 (grazed) and 0.640 (ungrazed).

The effect of gap size

Gap size, like molluscicide application, had a highly significant effect on seedling regeneration. Total seedling density was greatest in 15-cm-diameter gaps ($F_{1,32}$ = 32.191, $P < 0.001$) and this was reflected in the significantly higher densities of *C. polyspermum* ($F_{1,32}$ = 40.590, $P < 0.001$) and *R. acris* ($F_{1,32}$ = 43.688, $P < 0.001$) in the smaller gaps. However, gap size appeared to exert little influence over the feeding behaviour of molluscs. In only one case, *Ranunculus* ($F_{1,32}$ = 22.734, $P < 0.001$), did molluscicide application significantly interact with gap size. *Ranunculus* seedlings were more vulnerable to predation in the smaller gap size (Tukey test, $P < 0.01$). For the remaining plant species encountered, the likelihood of predation by molluscs was not markedly influenced by the size of gap in which they germinated.

Experiment 2: autumn mollusc populations

The number of molluscs present in the autumn was generally greater than in the spring and was dominated by slugs (Table 1). Furthermore, mollusc populations in untreated plots were far greater than those in treated plots and did not markedly decrease as the experiment progressed. *Deroceras reticulatum* was the most frequently recorded species throughout the experiment, often accounting for over 80% of the total mollusc population in untreated plots.

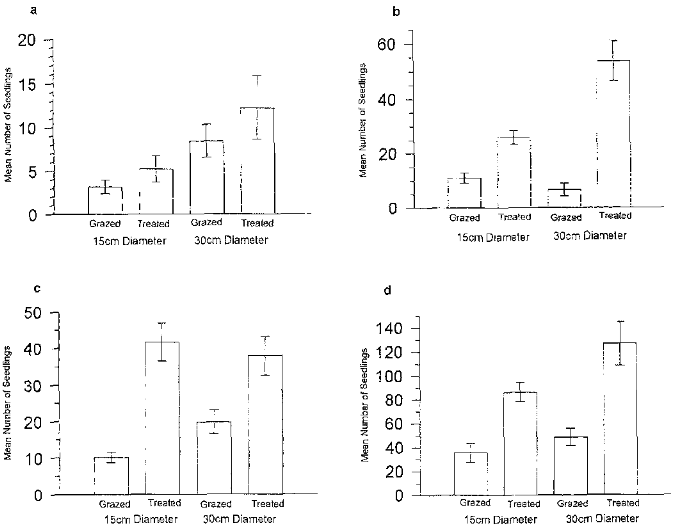

Fig. 2a–d The effect of molluscicide application and gap size on the mean number (± SE) of **a** *Holcus lanatus*, **b** *Chenopodium polyspermum*, **c** *Ranunculus acris*, and **d** total number of seedlings recorded in grassland gaps from April 1992 until June 1992

The effect of molluscicide application

The results of the autumn study, like the earlier spring investigation, show that mollusc grazing caused a highly significant ($F_{1,36}$ = 64.583, $P < 0.001$) reduction in the mean number of seedlings appearing in gaps (Figs. 3a, b and 4). *R. acris* ($F_{1,36}$ = 154.680, $P < 0.001$) and *Stellaria graminea* ($F_{1,36}$ = 39.612, $P < 0.001$) seedling populations were significantly reduced by grazing. Regeneration of *Rumex acetosa* seedlings was also significantly reduced by mollusc grazing ($F_{1,36}$ = 4.679, $P < 0.05$), although the effect was confined to 15-cm-diameter gaps. By contrast, *Cerastium holosteoides* populations were significantly greater ($F_{1,36}$ = 28.602, $P < 0.001$) in those gaps that were grazed by molluscs. *Agrostis capillaris, Holcus lanatus* and *Trifolium repens* seedlings were unaffected by the application of molluscicide, as were the small populations of other species present. The populations of grass seedlings were only recorded for the first 9 weeks of the study as it became impossible to distinguish seedlings from vegetative growth. Mollusc grazing significantly increased species diversity in both 15-cm-diameter and 30-cm-diameter gaps. Shannon-Wiener diversity indices in 15-cm-diameter gaps were 0.845 and 0.523 for grazed and ungrazed plots respectively ($P < 0.001$), while in the larger gap size, Shannon-Wiener index values were 0.732 and 0.664 in grazed and ungrazed plots respectively ($P < 0.001$).

The effect of gap size

Gap size also had a highly significant effect on seedling regeneration. After accounting for area, total seedling populations were greatest in 15-cm-diameter gaps ($F_{1,36}$ = 10.915, $P < 0.003$), although this effect was due

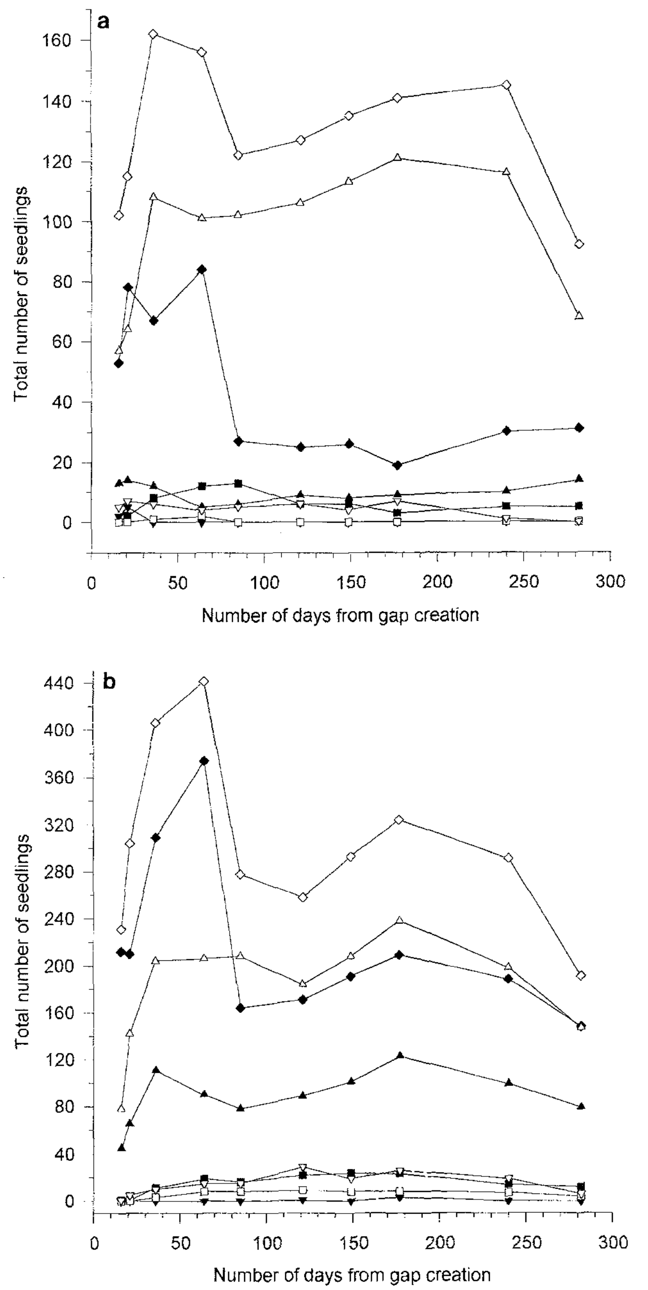

Fig. 3a,b The effect of molluscicide application on the seedling populations of *Cerastium holosteiodes*, *Ranunculus acris*, *Stellaria graminea* and total number of seedlings recorded in **a** 15-cm-diameter and **b** 30-cm-diameter grassland gaps on sampling occasions between September 1992 and June 1993. *Symbols:* ■ *Cerastium holosteoides*, ▼ *Stellaria graminea*, ▲ *Ranunculus acris*, ◆ Total seedlings, Closed symbols – Grazed gaps; Open symbols – Ungrazed gaps

largely to the presence of high *Ranunculus acris* ($F_{1,36}$ = 18.775, $P < 0.001$) populations. No other species performed better in small gaps, and indeed one species, *Rumex acetosa* ($F_{1,36}$ = 7.574, $P < 0.009$), was significantly more abundant in large gaps. There was a significant interaction between molluscicide application and gap size for the total number of seedlings ($F_{1,36}$ = 22.738, $P < 0.001$) and also for *Ranunculus acris* ($F_{1,36}$ = 50.211,

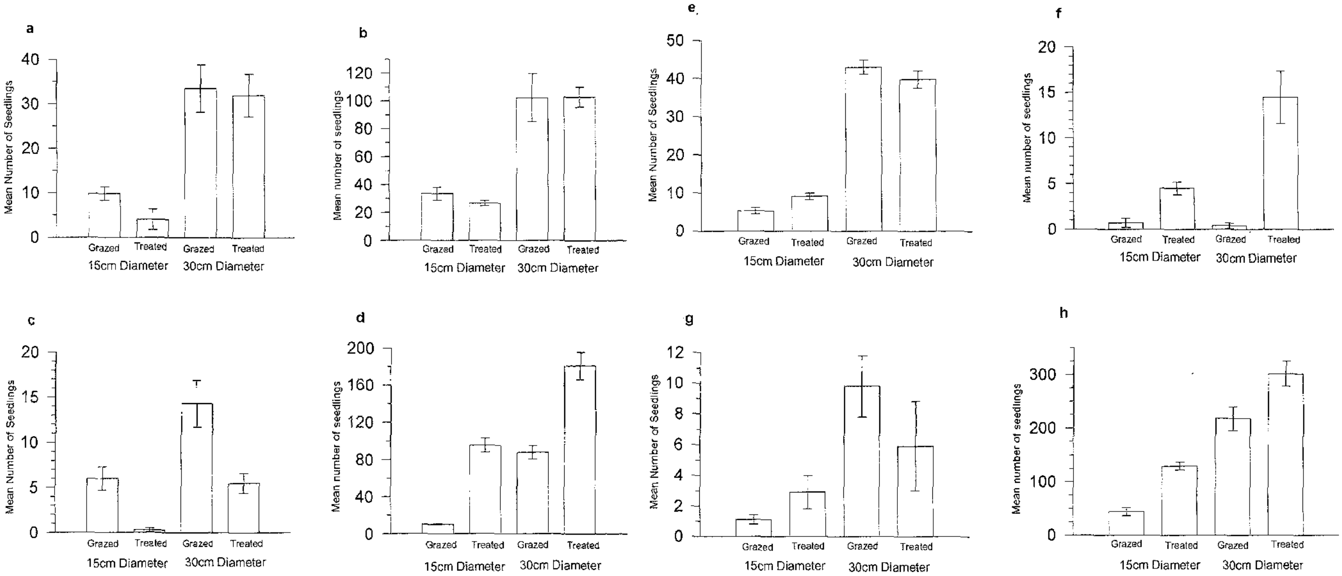

Fig. 4a–h The effect of molluscicide application and gap size on the mean number (± SE) of **a** *Agrostis capillaris*, **b** *Holcus lanatus*, **c** *Cerastium holosteoides*, **d** *Ranunculus acris*, **e** *Rumex acetosa* **f** *Stellaria graminea*, **g** *Trifolium repens* and **h** total number of seedlings recorded in grassland gaps from September 1992 until June 1993

$P < 0.001$) and *Rumex acetosa* ($F_{1,36} = 20.963$, $P < 0.001$), indicating that gap size had a significant effect on mollusc feeding behaviour in those cases. For both *Rumex* and *Ranunculus*, together with the total number of seedlings, the effect of grazing was significant more pronounced in the smaller gap size ($P < 0.01$).

Discussion

The reduction in total seedling numbers and the increase in species diversity in grazed gaps indicates that mollusc herbivory has a marked influence on seedling recruitment from the seedbank. The effect of grazing upon populations of *Ranunculus acris* and *Stellaria graminea* is similar to that described by Hanley et al. (1995a) for seedlings derived from sown seeds. The reduction of *S. graminea* populations is possibly a reflection of relatively high palatability coupled with an erect growth habit which may render certain species particularly vulnerable to mollusc attack (Edwards and Gillman 1987). Grime et al. (1968) rank *Rumex acetosa* as being of intermediate acceptability to the snail *Cepaea nemoralis*, and the grazing effect noted in the autumn experiment suggests that *R. acetosa* is vulnerable to molluscs in field conditions. There are no published data regarding the palatability of *Chenopodium polyspermum* to molluscs, although the marked reduction of this species suggests that its seedlings are highly susceptible. The presence of *Chenopodium* was somewhat unusual given that the species is regarded as a species not commonly associated with established grassland (Clapham et al. 1987) and its absence from plots during the autumn experiment and in subsequent years (Hanley 1995) suggests that its presence was transitory.

Ranunculus acris was the commonest species in both autumn and spring experiments, and the increased species diversity indices of the grazed plots was largely due to the reduced dominance of *Ranunculus*. There is evidence to suggest that germination in this species is promoted by the application of molluscicides (Hanley 1995), although the difference in populations in treated and grazed plots is much larger than that previously ascribed to germination stimulation by molluscicide application (by a factor of more than eight). Since molluscicide application is likely to influence grazing more than it does *Ranunculus* germination, it seems likely that apostatic grazing of *Ranunculus* was largely responsible for the marked effect on populations of this species.

By contrast with the majority of the more commonly occurring species, representation of *Cerastium holosteoides* was greater in (autumn) grazed gaps than it was in ungrazed plots. There are no published data regarding the acceptability of this species to molluscs, although unlike all the other common species encountered in the plots, *Cerastium* seedlings are protected by leaf hairs from an early age. This protection may have conferred on the species some degree of unpalatability to molluscs and as a result, allowed it to survive in grazed plots. The relative reduction of the species in ungrazed plots is likely to have been a result of competition from more vigorous species, a situation similar to that noted for *Senecio jacobaea* by Hanley et al. 1995a). Grasses, most commonly *Holcus lanatus* and *Agrostis capillaris*, were unaffected by grazing throughout the study. Grazing trials with the snail *Cepaea nemoralis* indicate that both *Agrostis* and *Holcus* are unpalatable to molluscs (Grime et al. 1968). Members of the Gramineae may be protected from herbivory by the presence of silica within leaf tissue (Wadham and Wynn-Parry 1981; Cottam 1985).

Mollusc numbers were much greater throughout the autumn study than during the spring. As a result, molluscs may exert a greater influence over seedling survivorship in the autumn, as described by Hulme (1994). The period through late autumn to early spring is the time of maximum activity for many molluscs, especially *Deroceras reticulatum* (Barnes and Weil 1944) and accounts for the larger slug numbers that were recorded. The effect of mollusc herbivory on *Rumex acetosa* seedlings was significant only during the autumn study, and then only in 15-cm-diameter gaps, possibly reflecting the greater mollusc populations in the autumn. Most *R. acetosa* germination occurred towards the end of the spring experiment at a time when molluscs were not common in the grazed plots. Although the general trend for grazing to increase diversity was common to both spring and autumn studies, it was only in the case of the latter experiment that a significant grazing effect occurred. This may have been due to the increased mollusc population recorded in the autumn, although the autumn study ran for a longer period (over 8 months). Species such as *Cerastium holosteoides* which were not removed by molluscs, may have been in a better position to capitalise on the removal of *Ranunculus acris* seedlings in the autumn experiment because they had longer in which to do it.

While gap size had highly significant effects on the regeneration of several species, the interaction of gap size with mollusc feeding behaviour was less pronounced. *Ranunculus acris* seedlings were grazed upon more in 15-cm-diameter gaps than they were in the larger gaps and the same pattern of herbivory was true for *Rumex acetosa* seedlings in the autumn. Gap size is known to be an important factor affecting seedling regeneration (Watt 1987; McConnoughay and Bazzaz 1987; Silvertown and Smith 1989; Williams 1992) and it appears that regeneration of *Ranunculus acris* was facilitated by smaller gap size. The pattern of herbivory on *Ranunculus* was possibly a reflection of the higher density of seedlings in the small gaps and an aggregative feeding response of molluscs similar to that proposed by Root (1973) and Hassell and May (1974). The fact that herbivory to all seedlings in the autumn study was more pronounced in smaller gaps is probably due to the large contribution *Ranunculus* made to the total seedling population (up to 71% of the total seedling population in 15-cm-diameter, ungrazed gaps). The disproportionate effect of gap size upon the grazing of *Rumex acetosa* seedlings in the autumn may simply have been a consequence of the increased grazing activity in smaller gaps.

This study has shown that the selective effect molluscs have upon individual plant species can shift the relative proportions of species in a community in favour of those which are resistant to mollusc herbivory. The marked reduction in *Ranunculus acris* populations in grazed plots may have facilitated the enhanced performance of *Cerastium holosteoides*. Furthermore, both *Agrostis capillaris* and *Holcus lanatus* seedlings, having been unaffected by grazing, may ultimately have benefited from reduced competition in grazed plots. Results reported by Hanley et al. (1995a) suggest that the apparent resistance to mollusc herbivory by *Agrostis capillaris* enables the species to increase its contribution to the vegetation in grazed communities. The two experiments reported here show that mollusc feeding behaviour is influenced by interactions between seedling characteristics, season and gap size. These interactions in turn influence the balance of competition between seedling species emerging in grassland gaps and may ultimately have a important role in determining the species composition of the mature sward.

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References

Aquilera MO, Laurenroth WK (1993) Seedling establishment in adult neighbourhoods – intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. J Ecol 81: 253–261

Barker GM (1989) Slug problems in New Zealand pastoral agriculture. In: Henderson IF (ed) Slugs and snails in world agriculture (Monograph no. 41). British Crop Protection Council, Thornton Heath, pp 59–68

Barker GM, Addison PJ (1992) Pest status of slugs (Stylommatophora: Mollusca) in two New Zealand pastures. Crop Prot 11: 439–442

Barnes HF, Weil JW (1944) I. Slugs in gardens; their numbers, activities and distributions. J Anim Ecol 13: 140–175

Bergelson J (1990) Spatial patterning in plants. Opposing effects of herbivory and competition. J Ecol 78: 937–948

Bullock JM, Clear-Hill B, Silvertown J, Sutton M (1995) Gap colonization as source of grassland community change: effects of gap size and grazing on the role and mode of colonization by different species. Oikos 72: 273–282

Byers RA, Bierlein DL (1982) Feeding preferences of three slug species in the laboratory. Melscheimer Entomol Ser 32: 5–11

Clapham AR, Tutin TG, Moore DM (1987) Flora of the British Isles, 3rd edn. Cambridge University Press, Cambridge

Cottam DA (1985) Frequency dependent grazing by slugs and grasshoppers. J Ecol 73: 925–933

Crawley MJ (1983) Herbivory: the dynamics of plant-herbivore interactions. Blackwell, Oxford

Duthoit CMG (1964) Slugs and food preferences. Plant Pathol 13: 73–78

Edwards PJ, Gillman MP (1987) Herbivores and plant succession. In: Gray AJ, Crawley MJ, Edwards PJ (eds) Colonization, succession and stability (Symposia of the British Ecological Society 26). Blackwell, Oxford, pp 295–314

Fenner M (1987) Seedlings. In: Rorison IH, Grime JP, Hunt R, Hendry GAF, Lewis DH (eds) Frontiers of comparative plant ecology (New Phytologist 106 Supplement). Academic Press, London, pp 35–47

Glen DM, Cuerdon R, Butler RC (1991) Impact of the field slug *Deroceras reticulatum* on establishment of ryegrass and white clover in mixed swards. Ann Appl Biol 119: 155–162

Grime JP, McPherson-Stewart SF, Dearman RS (1968) An investigation of leaf palatability using the snail *Cepaea nemoralis*. J Ecol 56: 405–420

Hanley ME (1995) The Influence of molluscan herbivory on seedling regeneration in grassland. Ph.D. Thesis, University of Southampton

Hanley ME, Fenner M, Edwards PJ (1995a) An experimental field study of the effects of mollusc grazing on seedling recruitment and survival in grassland. J Ecol 83: 621–627

Hanley ME, Fenner M, Edwards PJ (1995b) The effect of seedling age on the likelihood of herbivory by the slug *Deroceras reticulatum*. Funct Ecol 9: 754–759

Hassell MP, May RM (1974) Aggregation of predators and insect parasites and its effects on stability. J Anim Ecol 43: 567–594

Hulme PE (1994) Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. J Ecol 82: 873–880

Kelly D (1989) Demography of short-lived plants in chalk grassland. II. Control of mortality and fecundity. J Ecol 77: 770–784

McConnoughay KDM, Bazzaz FA (1990) Interactions among colonizing annuals: is there an effect of gap size? Ecology 71: 1941–1951

Root RB (1973) Organization of plant-arthropod associations in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecol Monogr 43: 95–124

Silvertown J, Smith B (1989) Germination and population structure of spear thistle, *Cirsium vulgare*, in relation to experimentally controlled sheep grazing. Oecologia 81: 369–373

Southwood TRE (1966) Ecological methods. Chapman and Hall, London

Standell C, Clements RO (1994) Influence of grass seed rate, herbicide (bentazone), molluscicide (methiocarb) and insecticide (triaphos) on white clover (*Trifolium repens*) establishment, herbage yield and sward botanical composition. Crop Prot 13: 429–432

Wadham MD, Wynn-Parry D (1981) The silicon content of *Oryza sativa* L. and its effect on the grazing behaviour of *Agriolimax reticulatus* Müller. Ann Appl Bot 48: 399–402

Watt TA (1987) Establishment of *Senecio jacobaea*. L. from seed in grassland and in boxed swards. Weed Res 27: 267–274

Williams RJ (1992) Gap dynamics in subalpine heathland and grassland vegetation in south eastern Australia. J Ecol 80: 343–352

Zar JH (1984) Biostatistical analysis. Prentice-Hall, New Jersey