Journal of Vegetation Science 3: 35-40, 1992
© IAVS; Opulus Press Uppsala.

Complex effects of grazing treatment on an annual in a species-poor grassland community

Silvertown, Jonathan[1], Watt, Trudy A.[2,3], Smith[1], Bridget & Treweek, Joanna R.[2,4]

[1]*Department of Biology, The Open University, Walton Hall, Milton Keynes, MK7 6AA, U.K.;*
[2]*Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, U.K.;*
[3]*Present address: Wye College, University of London, near Ashford, Kent TN25 5AH, U.K.;*
[4]*Present address: I.T.E. Monks Wood Experimental Station, Abbots Ripton, Huntingdon, Cambridgeshire, UK.;*
Tel. +44 908 652503; Fax +44 908 653744;E-mail: J_Silvertown@UK.AC.OPEN.ACS.VAX

Abstract. The effects of grazing upon the establishment, survival, growth and reproduction of a grassland annual *Geranium dissectum* growing in a sward dominated by grasses were examined in a replicated grazing experiment with sheep. Seeds were sown in both summer and autumn, and grazing was controlled to produce two levels of grazing in winter, two levels in spring, and two in summer, combined in a 2 × 2 × 2 factorial experimental design. Higher intensities of grazing in the period immediately before emergence benefitted plant establishment, but subsequent survival showed many interactions between factors, demonstrating that under certain conditions and at certain times grazing was detrimental. It is suggested that the frequency of *G. dissectum* in the grassland was low because the heavy grazing conditions that foster seedling emergence also jeopardize subsequent survival. This may also be why productive grassland communities in general contain few palatable dicots.

Keywords: Emergence; Establishment; *Geranium dissectum*; Reproduction; Seed; Sheep; Survival.

Nomenclature: Clapham, Tutin & Moore (1987).

Introduction

Explaining why some vegetation types are rich in species while others are species-poor is a problem central to community ecology. This question is usually approached by looking at ecological processes in species-rich communities (e.g. Hubbell & Foster 1990; Kull & Zobel 1991; Mahdi, Law & Willis 1989; Mitchley & Grubb 1986; Palmer 1991; Silvertown & Wilkin 1983). This is a logical approach, but species-rich communities are inherently difficult to study because of their complexity. A complementary approach without this difficulty is to attack the question from the other end, and to ask why certain species-poor communities do not support greater diversity. Perhaps this question is rarely posed because the answers often seem self-evident, for example low soil pH eliminates species that are physiologically intolerant, and high soil nutrient status causes competitive exclusion (Grime 1979). Both species-rich and species-poor communities have hierarchies of species abundance, the chief difference between them being due to the greater number of non-dominants in species-rich communities than in species-poor ones (Pielou 1975). Particularly in the case of communities where competitive exclusion limits diversity, we can learn something about the obstacles to species richness by looking at how non-dominant species that are present achieve coexistence with the dominants.

The present study was carried out in a grassland dominated by grasses and in which dicot herbs were rare. The dicot *Geranium dissectum* was chosen for study because it was the only annual in the community and therefore provided a model subject with which to investigate the process of establishment from seed. The maintenance of species richness in grasslands and the creation of diverse grassland communities by management both require intensive mowing or grazing (Bakker 1989; Wells 1971). These management practices disproportionately reduce the cover of dominant species, particularly grasses, and create conditions in which new seedlings can establish (Bakker, Dekker & de Vries 1980; Gibson, Watt & Brown 1987; Watt & Gibson 1988). The timing of management by grazing can greatly influence the composition of the sward (e.g. Jones 1967), depending upon how this coincides with the phenology of species present. In the present study grazing was experimentally manipulated to determine the conditions necessary for regeneration of *G. dissectum*.

Methods

The field site and grazing experiment

The present experiment was carried out within a long-term grazing experiment at Little Wittenham Nature Reserve, Abingdon, Oxfordshire, England. The grazing experiment was set up in 1986 to determine the influence of different grazing treatments on the composition of a sward dominated by *Lolium perenne*, *Agrostis stolonifera* and *Poa trivialis*, which it was desired to convert to a more species-rich community (Treweek 1990). The site is on a calcareous loam/calcareous clay loam and has been under permanent grass since the 1950's, but prior to that was cultivated on several occasions. The site was last fertilized in 1984.

There were three grazing periods: 'winter' (1 November - 21 March), 'spring' (21 March - 21 May) and 'summer' (21 May - 1 November) with two levels of grazing in each period. In the winter and spring periods two Suffolk × Mule lambs per paddock were either present or absent and in summer sward heights were maintained at either 3 cm or 6 cm height by weekly measurements of sward height followed by adjustment of the stocking rate. The grazing experiment was fully factorial with a 2 × 2 × 2 structure and two randomised blocks each of eight treatments assigned to 50 m × 50 m paddocks (Table 1). This experimental design was employed primarily to allow processes of vegetation change to be identified with statistical rigour, and not in an attempt to replicate management practices used elsewhere. To avoid edge effects, only the central area of 30 m × 30 m in each paddock was used for monitoring and experiments.

In autumn 1986, the frequency of all species was recorded in two 1-m^2 permanent quadrats in each paddock. *Geranium dissectum* was present in the paddocks at that time, but at too low a frequency to be recorded at this sampling intensity. In 1990, after four years of grazing management, the frequency of unsown *Geranium dissectum* was surveyed more intensively at the end of the winter grazing period. 100 1-m^2 quadrats were placed on a regular grid in the central 30 m × 30 m area of each paddock and scored for presence/absence of *G. dissectum*. Three-way analysis of variance of the counts showed a significant effect of only the winter grazing treatment upon *G. dissectum* ($F_{1,7} = 7.052$, $p < 0.05$). The mean frequencies of the species in paddocks grazed in winter, and those not grazed in winter were respectively 15.2% and 2.6%. When the survey was repeated in July 1990 during the summer grazing period, frequencies had fallen to 3.9% and 1.0% respectively. Neither this difference ($F_{1,7} = 4.408$, $p > 0.05$) nor any other was significant.

Table 1. Design of the sheep grazing experiment. A – sign indicates no grazing and a + sign indicates grazing during the relevant period. All paddocks were grazed in summer to either 3 cm or 6 cm sward height. Each of the treatments (A - H) occurred in each of two blocks.

Summer 3 cm			Summer 6 cm		
Trt	Winter	Spring	Trt	Winter	Spring
A	-	-	E	-	-
B	-	+	F	-	+
C	+	-	G	+	-
D	+	+	H	+	+

Sowing experiment

Three permanent quadrats 25 cm × 25 cm were established in the central 10 m × 10 m area in each paddock. In summer (in mid and late June) and autumn (mid September) 1987 121 seeds of *Geranium dissectum* (with a laboratory germination of 97%) were sown with forceps in the soil surface, spaced at 2 cm intervals in an 11 × 11 grid pattern. The grid allowed sowing positions to be accurately relocated, which avoided any possible confusion between sown and volunteer seedlings. In summer seeds were sown into two quadrats per paddock, but this was time-consuming and caused an unintentional delay of two weeks between each set of quadrats. Because of this delay, mid and late June quadrats were analysed separately, and in the autumn sowing only one quadrat per paddock was sown. The number of seedlings was counted at intervals: for the summer sowing in July and for both sowings in October 1987 and in March and August 1988. In August 1988 all *G. dissectum* plants were harvested at ground level and their shoot dry weight (after 7 days at 60 °C) recorded, together with the number of flowers and seed pods per plant.

Data were analysed using analysis of variance on the proportion of seeds sown which were established plants at each recording date (with angular transformation when required). The effect of grazing on seedling mortality was also examined over all recording dates using the GLM procedure in SAS (1985) with polynomial contrasts of repeated measures. The presence or absence of flowers and pods (August 1988) was analysed using χ^2 tests. The total shoot dry weight of plants per quadrat was analysed using analysis of variance on data transformed ($\log(x + 1)$) to achieve homogeneity of variance.

Results

Plant numbers

June sowings

By July both sets of June sowings had more seedlings when grazing had taken place during the previous winter; grazing during the previous spring also had a positive effect (Table 2a). For the mid-June sowing there were also significantly more seedlings when the sward was being grazed tightly in summer. However, by October only the positive effect of grazing during the previous winter remained. By the time of the March recording, there was an interaction between winter and spring grazing on the late June sown plots – higher numbers of plants were present when either there had been grazing the previous spring or during the current winter period. By August there were very low numbers of plants present, with no significant difference between the treatments.

September sowing

Plant numbers at both the October and March recordings showed a positive interaction between intensive grazing in the previous spring and summer (Table 2b). By August, the greatest number of plants was present on plots which had been grazed in winter and were being grazed intensely in summer.

Plant mortality

When the change in plant numbers over time was compared for the mid-June sowing there was a clear difference between the shape of the decline for plots receiving or not receiving winter grazing (Fig. 1). The plots without winter grazing started with lower plant numbers in July but maintained their numbers during the winter, whereas many plants died during winter where there was grazing.

The behaviour of plants on the plots sown in late June was more complex in that there was a significant interaction between all three grazing seasons (Fig. 2a and b). Irrespective of intensity of grazing during summer (the season of sowing):

(1) plots which were grazed in neither winter nor spring had consistently low plant numbers (Fig. 2b).

(2) plots which were grazed in both winter and spring showed a steady decline in numbers from initially high levels, with the most intensively grazed plots being superior by August 1988 (Fig. 2a).

(3) plots which were grazed in spring but not in winter showed a plateau or even slight increase in numbers between October and March (Fig. 2b).

However, the response of plants on plots which were grazed in winter but not in spring depended on whether the plots were grazed intensely (to 3 cm) or laxly (to 6 cm) during the season of sowing (Fig. 2a). The former

Table 2a. Plants present as a percentage of seeds sown in June. Only significant main effects or interactions are shown or, in the absence of these, the grand mean.

			Date of recording							
			July 87		October 87		March 88		August 88	
	Sowing date		Mid	Late	Mid	Late	Mid	Late	Mid	Late
Main Effects	Summer	3 cm	39.8							
		6 cm	29.8							
		p	(0.029)							
	Winter	+	41.0	47.2	41.0	47.5				
		–	28.6	34.4	15.2	20.4				
		p	(0.017)	(0.011)	(0.002)	(0.005)				
	Spring	+	41.7	46.0						
		–	27.9	35.6						
		p	(0.006)	(0.029)						
	SE mean	(7df)	2.55	2.66	3.99	2.00				
Interactions								Winter – / +		
	Spring	–						10.3 / 33.3		
		+						30.2 / 22.7		
		p						(0.019)		
	SE mean	(7df)						4.99		
Grand mean							18.9		5.3	3.6
SE mean		(15df)					3.25		2.24	1.46

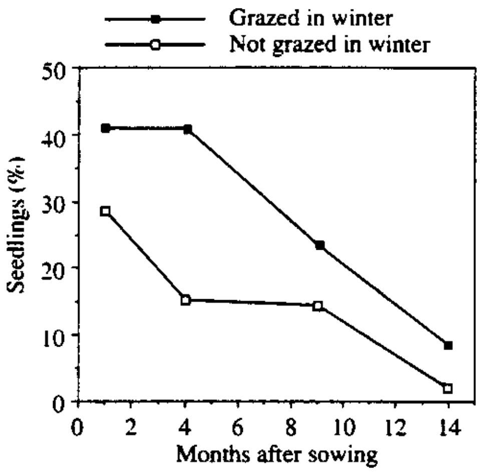

Fig. 1. Seedling mortality in the cohort sown in mid June. The difference in mortality rates between + winter grazing and - winter grazing over the winter period (Oct - March) was significant (cubic, i.e. remainder trends differ, $p = 0.043$).

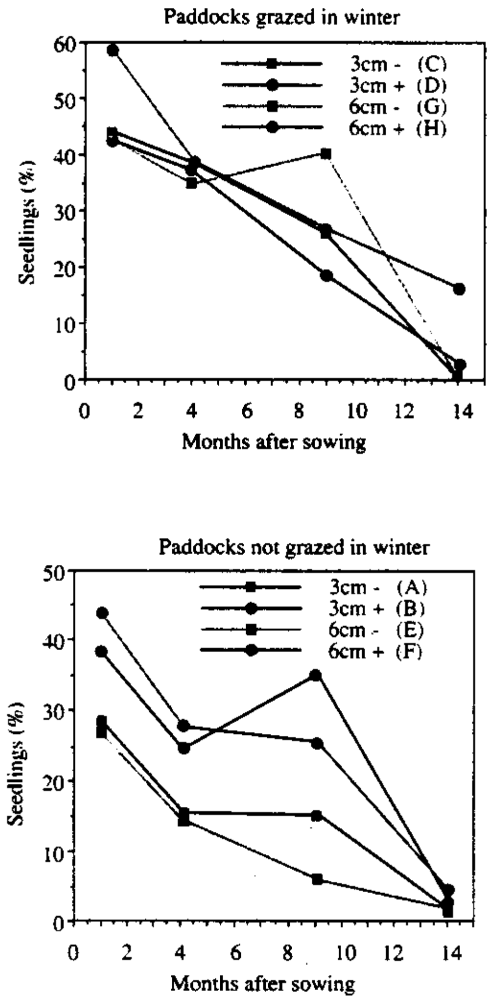

Fig. 2. Seedling mortality in the cohort sown in late June (a) with winter grazing and (b) without winter grazing. There was a Winter × Spring × Summer interaction (cubic, i.e. remainder trends differ, $p = 0.0127$).

showed the expected decline in plant numbers during the winter grazing period. In contrast, the latter plots showed a slight increase in numbers during winter grazing due to delayed germination of sown seed. There were no differences in mortality over time for the September-sown plants.

Shoot dry weights in August

The total shoot dry weight of plants per plot was greater for spring-grazed plots in the late June sowing and for winter-grazed plots in the September sowing (Table 3).

Flower and seed pod production

By August 1988 many plots either had no plants or none with flowers or pods. The importance of intense grazing in summer in increasing the frequency of plants with flowers and with pods is shown in Table 4.

Discussion

Grazing management can influence a species in the plant community by two separate routes: (1) indirect effects due to grazing of competitors, affecting the local environment for seed germination and seedling emergence, plant survival and growth and (2) direct effects on plant survival and size by grazing of the plant itself. In plant species that are avoided by grazers there may be

Table 2b. Plants present, as a percentage of seeds sown in September [angular transformation in brackets (radians)] (only significant effects are presented).

		Date of recording					
		October 87 Spring		March 88 Spring		August 88 Spring	
		+	–	+	–	+	–
Summer	3cm	54.7	31.4 (0.281)	27.7 (0.097)	9.7 (0.144)	14.2 (0.023)	2.3
	6 cm	25.0	36.4	7.0 (0.070)	8.4 (0.186)	1.9 (0.019)	2.1 (0.021)
	p	0.036		p (0.012)		p (0.035)	
SE mean (7df)		6.68		(0.0447)		(0.0235)	

Table 3. Shoot dry weight (total per plot, g) at harvest (August 1988). log (X+1) in brackets. Only significant effects are presented.

		Mid June	Late June	September
Winter	+			25.8 (2.40)
	–			5.2 (0.88)
				p (0.031)
SE mean (7df)				(0.399)
Spring	+		20.4 (2.37)	
	–		(3.6 (0.87)	
			p (0.031)	
SE mean (7df)			(0.394)	
Grand mean		8.3 (1.21)		
SE mean (15df)		(0.321)		

Table 4. The number of quadrats in which plants produced flowers or pods by August 1988 (three dates of sowing combined). Only the main effect was significant.

	Summer Low	Summer High		Summer Low	Summer High
Flowers	12	5	Pods	15	8
No. flowers	12	19	No. Pods	9	16
	$\chi_1^2 = 4.46$	$p < 0.05$		$\chi_1^2 = 4.09$	$p < 0.05$

a simple relationship between grazing management and plant establishment. This is what was found, for example, for the thistle *Cirsium vulgare* at our study site where the influence of grazing on seedling emergence, operating via route 1, accounted for 70% of the variance in the abundance of adults (Silvertown & Smith 1989). In the present study of *Geranium dissectum* the combined influence of direct and indirect effects produce a much more complex picture indicating that plant success can depend upon both previous and current grazing treatment, upon the time of year and the stage of the plant's life cycle.

Grazing the previous winter had the most enduring positive effect on numbers of *G. dissectum* recruited from both the June sowings (Table 2a) and grazing in the spring and summer prior to sowing also benefitted establishment of seeds sown in September (Table 2b). Similar results have been found for the establishment phase of grassland perennials. For example, Foster (1964) recorded germination flushes of *Bellis perennis* immediately after cutting produced an open sward, and Putwain, Machin & Harper (1968) found a similar effect in *Rumex* spp. However, our results also show that when followed through the whole life cycle the effects of grazing were more complex. Significant interactions between grazing treatments were common, particularly for the sowings in late June (Table 2a and Fig. 2) and September (Table 2b). Intense grazing all year showed best initial establishment, steepest decline, but best survival one year later (Figs. 1, 2a). Established seedlings survived winter best when ungrazed (Figs. 1, 2b), but seedling numbers declined fast in spring as they were out-competed.

As far as plant numbers were concerned, grazing prior to seedling emergence was beneficial, but the effect of grazing after emergence depended on its past and present intensity, and this depended on season. The effects of grazing on the dry weight and reproduction of survivors was more straightforward and always positive (Tables 3, 4). Dry weight was affected by grazing treatments prior to harvest, but reproduction was influenced only by the grazing treatment current at the time of flower production when tight grazing was beneficial.

To complete its life cycle in this community *Geranium dissectum* must negotiate a complex of obstacles to survival, growth and reproduction which appear jointly to limit its abundance. Although the composition of this plant community was a simple one, the processes operating on this minor species were not. This suggests that other minor species may be excluded or kept at very low frequency because the conditions of heavy grazing that are needed to permit seedling establishment also prohibit successful completion of the life cycle. Why *Geranium dissectum* should be successful in these conditions is not clear. In less productive communities seedling establishment by other dicots may be possible in conditions of less severe grazing which do permit successful completion of the life cycle. This may be why less productive communities are more diverse. A test of this hypothesis requires a study of the effect of grazing on vegetation gaps, which is underway in the grazing experiment.

Acknowledgements. We thank the Northmoor Trust for the provision of the site, fencing and sheep, John Sargent and staff for stock management and John Walters for field and technical assistance. We acknowledge funding from NERC (JS & BS) and SERC (TAW & JRT).

References

Anon. 1985. *SAS User's Guide: Statistics. Version 5 Edition.* SAS Institute Inc.. Cary. NC. USA.

Bakker, J. P. 1989. *Nature management by grazing and cutting.* Junk. The Hague.

Bakker. J. P.. Dekker. M. & de Vries. Y. 1980. The effect of different management practices on a grassland community and the resulting fate of seedlings. *Acta Bot. Neerl.* 29: 469-482.

Clapham, A. R.. Tutin. T. G. & Moore. D. M. 1987. *Flora of the British Isles.* 3rd ed. Cambridge University Press. Cambridge.

Foster. J. 1964. *Studies on the population dynamics of the daisy Bellis perennis L.* Ph. D. thesis. University of Wales. Bangor.

Gibson. C. W. D.. Watt. T. A. & Brown. V. K. 1987. The use of sheep grazing to recreate species-rich grassland from abandoned arable land. *Biol. Conserv.* 42: 165-183.

Grime, J. P. 1979. *Plant strategies and vegetation processes.* Wiley, Chichester.

Hubbell. S. P. & Foster. R. B. 1990. The fate of juvenile trees in a neotropical forest: implications for the natural maintenance of tropical tree diversity. In: Bawa, K. S. & Hadley, M. (eds.) *Reproductive ecology of tropical forest plants.* pp. 325-349. UNESCO/IUBS.

Jones. Ll. I. 1967. *Studies on hill land in Wales.* Technical Bulletin of the Welsh Plant Breeding Station No. 2.

Kull. K. & Zobel, M. 1991. High species richness in an Estonian wooded meadow. *J. Veg. Sci.* 2: 715-718.

Mahdi, A.. Law, R. & Willis, A. J. 1989. Large niche overlaps among coexisting plant species in a limestone grassland community. *J. Ecol.* 77: 386-400.

Mitchley, J. & Grubb. P. J. 1986. Control of relative abundance of perennials in chalk grassland in southern England. I. Constancy of rank order and results of pot- and field-experiments on the role of interference. *J. Ecol.* 74: 1139-1166.

Palmer. M.W. 1991. Patterns of species richness among North Carolina hardwood forests: tests of two hypotheses. *J. Veg. Sci.* 2: 361-366.

Pielou, E. C. 1975. *Ecological diversity.* Wiley. New York.

Putwain. P. D.. Machin. D. & Harper. J. L. 1968. Studies in the dynamics of plant populations. II. Components and regulation of a natural population of *Rumex acetosella* L. *J. Ecol.* 56: 421-431.

Silvertown, J. & Smith, B. 1989. Germination and population structure of spear thistle *Cirsium vulgare* in relation to sheep grazing management of pasture. *Oecologia* 81: 369-373.

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.

Treweek. J. R. 1990. *The ecology of sheep grazing: Its use in nature conservation management of lowland neutral grassland.* Unpubl. Ph.D. thesis. University of Oxford.

Watt, T. A. & Gibson, C. W. D. 1988. The effects of sheep grazing on seedling establishment and survival in grassland. *Vegetatio* 78: 91-98.

Wells. T. C. E. 1971. A comparison of the effects of sheep grazing and mechanical cutting on the structure and botanical composition of chalk grassland. In: Duffey. E. A. & Watt. A. S. (eds.) *The scientific management of animal and plant communities for conservation*, pp. 497-515. Blackwell. Oxford.

Received 27 November 1990:
Revision received 7 July 1991:
Accepted 15 October 1991.