

Germination and population structure of spear thistle *Cirsium vulgare* in relation to experimentally controlled sheep grazing

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Summary. The size and number of rosettes of *Cirsium vulgare* were censused in a 4 ha sheep grazing trial on lowland calcareous grassland in paddocks receiving controlled winter, spring and summer grazing treatments. Spring grazing significantly increased thistle rosette numbers, and there were always fewer rosettes in size classes 250 mm–300 mm under the heavier grazing treatments. The emergence of seeds of *Cirsium vulgare* sown by hand into each of the grazing treatments was monitored and showed a positive effect of spring grazing. When the percent emergence of sown seeds was used as a covariate in the analysis of rosette numbers in the experimental paddocks, it was found to account for 77% of the variance in thistle numbers. It was concluded that the main effect of grazing on thistle rosette numbers is an indirect one exercised through the effects of grazing on germination conditions. Seeds of *Cirsium vulgare* were sown into artificial gaps at another grassland site, to determine the effect of gap-size upon seedling emergence. Germination was poor, but significantly more seedlings emerged in gaps 10–20 cm diameter, than in 5 cm gaps or in control plots without a gap. A computer simulation model was used to explore the relationship between gap density and thistle population dynamics. A threshold density of gaps was found to exist, below which thistle populations went extinct, and above which the thistle population grew geometrically. The degree of aggregation of dispersed seeds did not alter the threshold gap-density for plant extinction, but did affect the rate of increase of the thistle population when the threshold gap-density was exceeded. It is concluded that strategies for controlling *Cirsium vulgare* populations by grazing management will be most effective if aimed at reducing suitable sites for establishment in spring. The success of such attempts will depend upon the soil fertility of the site, and sudden outbreaks of *Cirsium vulgare* infestation can be expected if a sward gradually deteriorates through over-grazing.

Key words: *Cirsium vulgare* – Grazing – Seed germination – Epidemic model – Plant population dynamics

The grazing management of pastures can be manipulated to produce large and sometimes rapid changes in sward composition (Jones 1967; Milton 1947). When grazing is

managed without sufficient regard to its effect upon the botanical composition of the sward, increases in the abundance of troublesome weeds can result. It is well known that overgrazing can result in infestations of thistles in pastures, but little experimental, ecological evidence is available of how this comes about. Although there is a practical solution to this problem by just keeping grazing intensity low, this strategy may conflict with other management objectives such as obtaining maximum grazing for stock, or diversifying the botanical composition of the sward for conservation purposes. Often the maintenance and creation of plant species diversity in grasslands depends upon grazing pressure. An additional dimension is given to the ecology of thistles by the international importance of these spinose plants as pasture weeds in N. America and Australasia (Moore 1975; Michael 1968). Understanding the population dynamics of plants in their native region provides a basis for devising control measures where they are alien weeds.

This paper reports the effect of different regimes of sheep grazing on the population structure of spear thistle *Cirsium vulgare* L., and describes field germination experiments which strongly suggest that the influence of grazing on this structure is largely due to its effect on seedling emergence. This has important implications for understanding the population dynamics of species which require vegetation gaps for their regeneration, and more particularly for planning strategies of grazing management to control this weed. A simple computer stimulation model is used to explore the relationship between gap density and thistle population dynamics.

Site and methods

Grazing trial

The study was conducted in a sheep grazing trial at Little Wittenham Nature Reserve, Abingdon, Oxfordshire. The 4 ha site of the grazing trial has a gentle slope with a south-facing aspect and is situated on calcareous loam/calcareous clay loam. It has been under permanent grass since the 1950's, but prior to that was cultivated on several occasions. The site has received no fertilizer since 1984. The grazing trial was begun in February 1986. Grazing treatments, applied separately in fenced 0.25 ha experimental paddocks, were all combinations of: Winter grazed/not grazed, Spring grazed/not grazed and, Summer grazed to 3 cm or 6 cm

Table 1. Design of the sheep grazing experiment. Grazing periods were: Winter 1 Nov.–21 Mar., Spring 21 Mar.–21 May, Summer 21 May–1 Nov. A minus sign indicates no grazing and a plus 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

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

sward height. Two ewes per paddock were used for winter and spring grazing treatments, and in summer numbers were adjusted on a weekly basis to achieve the desired sward height. The design of the grazing trial was fully factorial with two randomized blocks of eight paddocks each (Table 1).

*Germination of *Cirsium vulgare* in the grazing trial*

Two permanent quadrats were set up in each paddock, with corners marked by buried plastic pipes. Seeds of *Cirsium vulgare* were sown individually into the quadrats with forceps which were used to lodge them in the top 3 mm of the soil surface. A total of 121 seeds per quadrat were sown at 20 mm intervals in an 11 × 11 grid. A modified point-quadrat frame was used to locate grid positions accurately before sowing and after emergence. One quadrat in each paddock was sown in November 1987 and the second quadrat per paddock was sown in March 1988. Quadrats were checked for seedling emergence at regular intervals between sowing and May 23rd 1988.

Cirsium vulgare population structure in the grazing trial

In spring 1988 the paddocks of the grazing trial contained a large number of *Cirsium vulgare* rosettes which had established in or before the previous year. This population had been subject to some management in spring 1987 when rosettes in all paddocks were decapitated. Thus none had been allowed to flower in 1987, although large numbers of plants survived the attempt to control them. In April 1988 eight belt transects were marked out in each paddock covering half the area of each, excluding a 3 m border which was not sampled. Every rosette in the transects was counted and the largest diameter measured to the nearest 10 mm.

Cirsium vulgare emergence in experimental gaps

A factorial experimental design was used to investigate the effect of gap size and small mammal seed predation upon emergence. Experimental sowings of seeds of *Cirsium vulgare* were made into artificial gaps in a mown grassland site on the campus of the Open University at Milton Keynes, Buckinghamshire. In November 1987 forty seeds per plot were sown with forceps into a 5 cm diameter circular area in the centre of each of 90 quadrats. Half the plots were caged with wire 9 mm mesh cages to exclude small mammals. In February 1988 four gap treatments (including

Table 2. 3-way ANOVA results for the emergence (arcsin transformed percent) of *Cirsium vulgare* seedlings (a) in May, sown in the grazing experiment the previous November

Source	ss	df	F	p
Block	0.002	1	0.257	0.628
Winter	0.039	1	5.545	0.051
Spring	0.043	1	6.120	0.043
Summer	0.011	1	1.493	0.261
Win × Spr	0.001	1	0.200	0.668
Win × Sum	<0.001	1	0.008	0.931
Spr × Sum	0.003	1	0.470	0.515
Win × Spr × Sum	0.003	1	0.392	0.551
Error	0.049	7		

a no-gap control) were assigned randomly to the plots, with equal replication in caged and uncaged treatments. Circular gaps, 5 cm, 10 cm and 20 cm diameter were cut to ground level in the centre of each plot. There were ten replicates per enclosure treatment (i.e. 20 in all) for gap treatments and fifteen replicates per enclosure treatment (i.e. 30 in all) for the no-gap control. Plots were regularly inspected for seedling emergence, which was recorded finally on 18 May 1988.

Computer simulation model

A simple computer model was constructed to explore the relationship between gap density and thistle population dynamics, using the simulation programme STELLA, running on an Apple Macintosh microcomputer. The model envisaged a field colonized by an 'ideal' monocarpic, perennial plant which is only able to establish from seed in gaps of a specified minimum area. This situation appears to correspond to the biology of *Cirsium vulgare* at the Little Wittenham field site. The frequency distribution of seeds-per-gap in the model was determined by a negative binomial expression which allowed seed dispersal to be varied between random ($k=1$) and highly aggregated ($k=10$). Seedling mortality within gaps was strongly density-dependent, with no more than one surviving seedling allowed per gap. Thus, the number of surviving seedlings was equal to the number of gaps receiving at least one seed. The latter was calculated as $1 - (k/(m+k))^k$, where m was the mean number of seeds per gap, and seed aggregation was determined by the value of k . Gaps were generated in a single pulse at the beginning of the year, and uncolonized gaps disappeared at the end of each year. The effect of gap density (d) and the degree of aggregation among dispersed seeds (k) on thistle dynamics was determined by observing the effect of varying these parameters on population size at $t=50$ years.

Results

*Germination of *Cirsium vulgare* in the grazing trial*

Emergence of *Cirsium vulgare* sown in November 1987 was recorded finally on 23 May 1988. Arcsin transformed values were analysed by 3-way ANOVA. Only spring grazing showed a significant effect on emergence and there were no significant treatment interactions (Table 2). Main treatment effects are shown in Fig. 1. Emergence of *Cirsium vulgare* sown in March 1987 was monitored until June 1988,

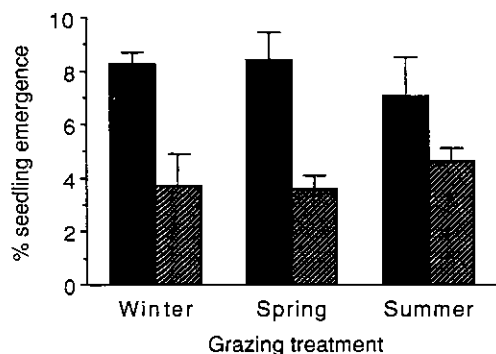


Fig. 1. Main effects of sheep grazing treatments upon emergence of *Cirsium vulgare* sown in the grazing experiment November 1987. Grazing in winter or spring or grazing to 3 cm height in summer are indicated by solid columns; No grazing in winter or no grazing spring or grazing to 6 cm height in summer are indicated by cross-hatched columns. Means and standard errors (bars) are back-transformed arcsin percentages

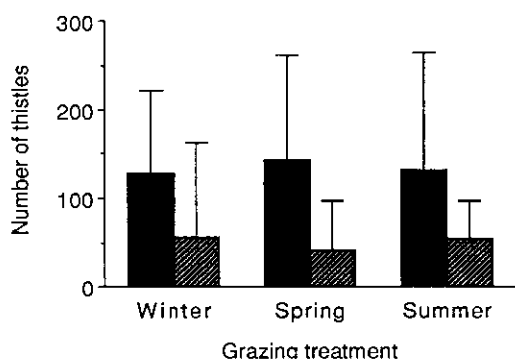


Fig. 2. Main effects of sheep grazing treatments upon the number of established *Cirsium vulgare* rosettes in the census of April 1988. Key to grazing treatments as for Fig. 1. Standard errors are indicated by bars

but in several paddocks no seedlings emerged at all, and overall there were insufficient to make statistical analysis possible.

Cirsium vulgare population structure in the grazing trial

Untransformed values for rosette numbers and for mean rosette size were analysed separately by 3-way ANOVA. Spring grazing significantly affected rosette numbers (Fig. 2, Table 3a), but when percent emergence of No-

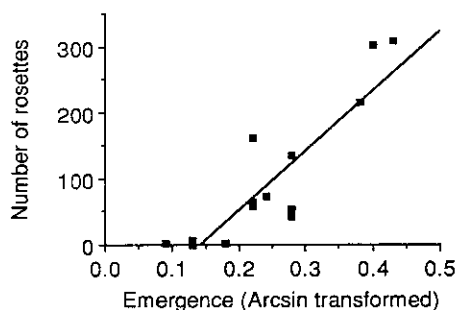


Fig. 3. The relationship between *Cirsium vulgare* rosette numbers in the sixteen paddocks of the experiment and the probability of emergence (arcsin transformed) of seeds sown into the paddocks. The regression line shown is Number of rosettes = $-127.6 + 903 \times$ Emergence, $r = 0.88$, $P < 0.01$

Table 4. 3-way ANOVA results for the size of *Cirsium vulgare* rosettes in the grazing experiment

Source	ss	df	F	p
Block	1296.0	1	0.297	0.603
Winter	6889.0	1	1.577	0.249
Spring	870.3	1	0.199	0.669
Summer	4970.3	1	0.250	0.322
Win \times Spr	1089.0	1	0.249	0.633
Win \times Sum	529.0	1	0.121	0.738
Spr \times Sum	3660.3	1	0.838	0.390
Win \times Spr \times Sum	11025.0	1	2.524	0.156
Error	30577.0	7		

vember-sown *Cirsium vulgare* in the respective paddocks was incorporated in the ANOVA as a covariate, the effect of spring grazing disappeared, and a significant block effect and a strong effect of emergence were revealed (Table 3b). The correlation of rosette numbers with emergence was significant (Fig. 3 $r = 0.88$, $n = 16$, $P < 0.01$).

ANOVA revealed no significant effects of grazing upon mean rosette size in the experiment (Table 4). Size distributions (Fig. 4) of rosettes in paddocks receiving different main treatments were compared by χ^2 . There were significant differences between the two winter treatments, between the two spring treatments and between the two summer treatments (respectively: $\chi^2 = 50.91$, $P < 0.001$; $\chi^2 = 28.79$, $P < 0.005$; $\chi^2 = 30.05$, $P < 0.005$; all d.f. = 11). The chief difference common to all these comparisons between treatments was a greater proportion of rosettes in the

Table 3. (a) 3-way ANOVA results for the number of *Cirsium vulgare* rosettes in the grazing experiment; (b) as for (a) with arcsin transformed percent emergence of seedlings in the paddocks treated as a covariate

(a)					(b)				
Source	ss	df	F	p	ss	df	F	p	
Block	21535.6	1	3.86	0.090	12798.2	1	6.46	0.044	
Emergence	—	—	—	—	27162.7	1	13.71	0.010	
Winter	20093.1	1	3.60	0.100	13.575	1	0.01	0.937	
Spring	40300.6	1	7.22	0.031	1160.6	1	0.586	0.473	
Summer	23793.1	1	4.27	0.078	5030.1	1	2.539	0.162	
Win \times Spr	333.1	1	0.06	0.814	89.6	1	0.045	0.839	
Win \times Sum	3751.6	1	0.672	0.439	3096.7	1	1.563	0.253	
Spr \times Sum	11718.1	1	2.101	0.191	4025.8	1	2.032	0.204	
Win \times Spr \times Sum	264.1	1	0.047	0.834	489.8	1	0.247	0.637	
Error	39049.9	7			11887.2	6			

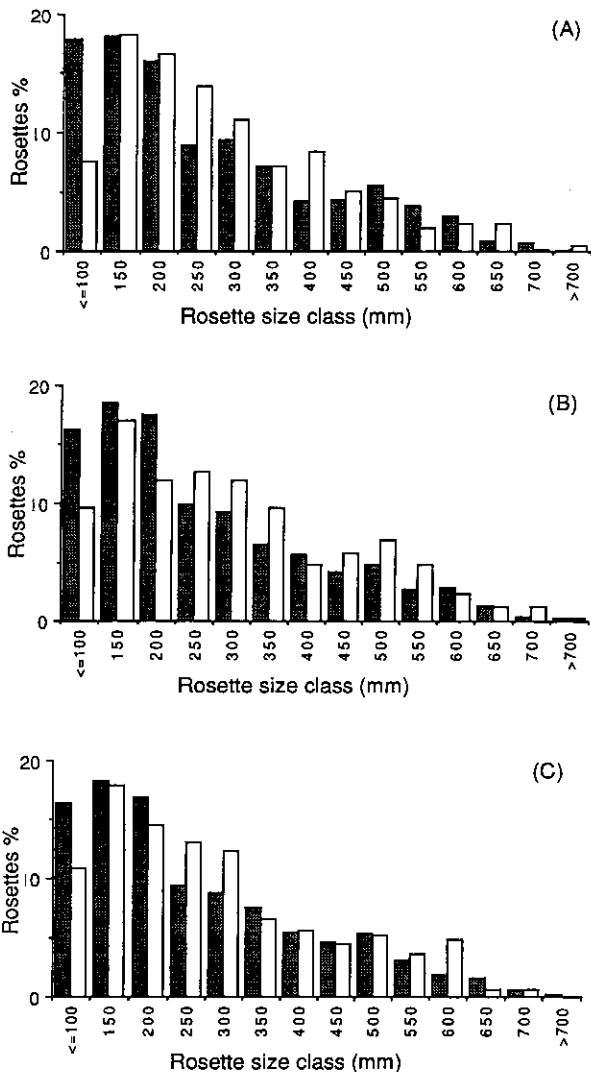


Fig. 4A–C. Mean size-frequency distributions of *Cirsium vulgare* rosettes for the three main grazing treatments. Key to grazing treatments in (A) winter, (b) spring, and (C) summer as for Figure 1

250–300 mm size classes when grazing was light in summer or absent in winter and spring (Fig. 4).

Cirsium vulgare emergence in experimental gaps

Seedlings of *Cirsium vulgare* emerged in only 42 of the 90 experimental plots, making ANOVA of the number of seedlings in treatments inappropriate. The effects of treatments on the number of plots with seedlings were analysed by G-tests of independence (Sokal and Rohlf 1981). There was no significant effect of small mammal exclosures on the number of plots in which seedlings emerged ($G=2.87$, d.f. = 1, $P > 0.05$), so results of the two exclosure treatments were pooled. There was significant heterogeneity in emergence among gap size treatments ($G=19.03$, d.f. = 3, $P < 0.001$), with significantly higher probabilities of emergence in gap sizes 10 cm or 20 cm, than in 5 cm gaps or control plots ($G=5.13$, d.f. = 1, $P < 0.05$) (Fig. 5).

Computer simulation model

The model showed that a threshold density of gaps existed, below which thistle populations went extinct, and above

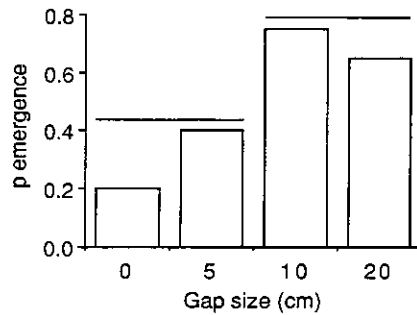


Fig. 5. Probability of seedlings of *Cirsium vulgare* emerging in artificial gaps (5 cm, 10 cm, 20 cm dia.) and control plots (0 cm). Treatments linked by a horizontal bar are not significantly different. 0 cm and 5 cm are significantly different from 10 cm and 20 cm, $P < 0.05$

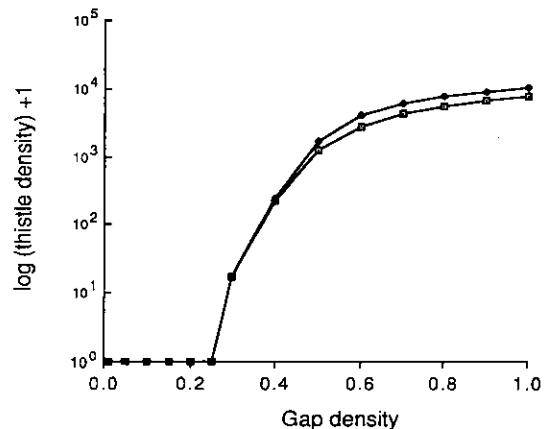


Fig. 6. The relationship between log thistle density at $t=50$ (plotted as $\log(\text{density}) + 1$ to resolve zeros) and gap density, derived from the computer simulation model, for randomly dispersed seeds ($k=10$; solid points) and seeds dispersed in clumps ($k=1$; open points)

which the thistle population grew geometrically. The degree of aggregation of dispersed seeds (set by the parameter k of the negative binomial) did not alter the threshold gap-density for plant extinction, but did affect the rate of increase of the thistle population when the threshold gap-density was exceeded (Fig. 6).

Discussion

The size of thistle populations in the paddocks of the grazing trial was significantly increased by spring grazing. The sowing experiment gives us an insight into this effect. The relationship between rosette numbers per paddock in April 1988 and emergence of *Cirsium* seeds sown in November 1987 was a strong one, although there is no necessary reason for these variables to be closely related. Emergence was itself positively affected by spring grazing, and it appears to be this relationship which caused spring grazing to have a positive effect on rosette numbers: when emergence is treated as a covariate in the ANOVA of rosette numbers, the grazing effect is replaced by a strong effect of emergence. The effect of grazing on rosette numbers was therefore an indirect one.

The influence of grazing upon emergence was not as great as that of emergence upon rosette numbers. The main grazing treatments explained 56% of the variance in emergence, half of this (28%) being due to the significant spring effect. By contrast emergence explained 77% of the variance

in rosette numbers. In other words, whatever was responsible for the unexplained variance in emergence, also influenced rosette numbers.

The existence of a close relationship between seedling emergence in April 1988 and the number of thistles established a year or more previously has two important implications. First, it implies that differences between paddocks in the conditions for *Cirsium* emergence have remained consistent over several years. There were some large differences in thistle abundance between paddocks receiving the same grazing treatment which, in other circumstances, might be put down to historical accident. The most extreme example of this was a difference in thistle numbers between the two paddocks with the treatment: no winter grazing, spring grazing, 3 cm summer grazing. One of the paddocks had a population of 6 rosettes and the other a population of 309. These numbers were paralleled by differences in emergence which were 1.6% and 17.4% respectively, suggesting that the difference in population size was due to a persistent difference in emergence conditions in the two paddocks.

The second implication of the correlation between emergence and rosette numbers is that seedling emergence is the key mortality factor (*sensu* Varley et al. 1973) in the population dynamics of the plant and that other events in the life cycle, such as seed and seedling survival, rosette growth and seed production, are demographically less important in the short term. Albeit correlative, it is unusual to obtain such clear-cut evidence of this kind for a field population of plants (Silvertown 1987).

Rosette size is an important determinant of subsequent flowering and seed production (Leeuwen 1983). Therefore differences in size of rosettes between grazing treatments could potentially affect the seed production and longer-term population dynamics of the species under different grazing regimes. Grazing treatments had a slight, though significant, effect on the size distribution of rosettes in paddocks, but these differences were not large enough to be reflected in the mean size of rosettes. This supports the conclusion that, perhaps in the long term and certainly in the short-term, the emergence success of *Cirsium* seedlings appears to be the primary determinant of rosette numbers at the study site.

These results bear comparison with those of de Jong and Klinkhamer (1988) who studied the population dynamics of *Cirsium vulgare* in a dune habitat at Meijndel in the Netherlands. They too concluded that seed losses between dispersal and seedling emergence were the key mortality factor, accounting for losses of more than 95% of seeds in each of three years. They also found a consistent and statistically significant correlation between numbers of seedlings emerging at a site and seed production there the previous year. Working in the same dune area, Leeuwen (1987) found that mean seed production per plant was closely correlated with July rainfall. Dempster & Lakhani (1979) found that seedling recruitment of *Senecio jacobaea* at a dune in E. England was also closely correlated with rainfall.

Although there are no long-term data from Little Wittenham, it seems likely in this grassland habitat that grazing would be more important and rainfall less important than it is in drought-prone sand dune habitats. Seedling emergence of *Cirsium vulgare* was influenced by vegetation cover (gaps) in our experiment in Milton Keynes and in experiments at Meijndel by Leeuwen (1987). Though Leeuwen

found increased germination of spring sown seeds in gaps, autumn sown seeds germinated better in closed vegetation than in 18 cm diameter gaps: a contrary result to our own and one difficult to explain.

Our simulation model showed that *Cirsium vulgare* populations dependent upon discrete colonization sites such as vegetation gaps may behave epidemically (Carter and Prince 1981) and that potentially, even a small difference in seedling emergence or gap density between paddocks could generate a large difference in thistle numbers. Thistles in the paddocks at the experimental site have not been allowed to flower since the grazing trial began, and so this cannot have influenced the abundances measured, however it does have implications for populations where thistles are allowed to flower. In these situations one might expect sudden outbreaks of *Cirsium vulgare* infestation as a sward gradually deteriorates through over-grazing. The results of the model and of our field experiments suggest that this could be prevented by various measures aimed at controlling the size and rates of appearance and disappearance of gaps. All of these variables depend upon grazing regime. Gap disappearance rate can also be influenced by sward composition and soil fertility which will affect the rate at which potential establishment sites are available before being filled-in by the surrounding vegetation.

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