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# Demography of *Cirsium vulgare* in a grazing experiment

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## Summary

**1** The complete demographies of 16 populations of *Cirsium vulgare* were followed in a replicated experiment. The experiment was a factorial combination of two intensities of sheep grazing in each of three seasons – winter (grazed or ungrazed), spring (grazed or ungrazed), and summer (light or heavy grazing) – giving eight treatments in two blocks.

**2** For 6 years from 1987 to 1992 the population sizes of *C. vulgare* were monitored in each of the 16 paddocks. After 1989 grazing in spring or winter or increased grazing in summer all increased population sizes. Population sizes fluctuated widely between years.

**3** The effects of the grazing treatments and plant sizes on the transitions between nine life-history stages were determined. There were no grazing effects on seed numbers per flowerhead, postdispersal seed survival or between year seed survival in the seed bank.

**4** More-intense summer or winter grazing increased seedling emergence by increasing the proportion of microsites with no canopy or with no litter. Emergence was found to respond positively to these factors. Seedling survival was increased by winter or spring grazing and winter grazing increased the year-to-year survival of small and medium-sized rosettes. These effects probably occurred through selective grazing decreasing competition from the dominant grasses. Larger rosettes had lower mortality rates which were unaffected by the grazing treatments.

**5** There was a minimum rosette size threshold for flowering above which flowering probability increased with size. Because winter grazing increased the survival of smaller rosettes it increased the proportion of smaller rosettes in the populations and thus decreased the proportion of rosettes flowering. By the same process winter grazing decreased the average size of flowering rosettes and, because smaller rosettes produced fewer flowerheads, this treatment decreased the flowerhead number of flowering rosettes.

**6** The lepidopteran seed predator *Eucosma cana* attacked a larger proportion of heads on plants with more flowerheads. By decreasing the average number of flowerheads per flowering plant winter grazing decreased the proportion of flowerheads on a plant attacked.

**7** Matrix analysis of life tables for each paddock showed that winter and spring grazing and increased summer grazing all significantly increased the population growth rate  $\lambda$ . The population sizes of each paddock correlated significantly with the estimated  $\lambda$  values.

**8** Elasticity analysis was performed on each matrix and elasticity values within each matrix were summed to give a value for fecundity ( $e_F$ ), stasis ( $e_L$ ) and growth ( $e_G$ ). Triangular ordination of  $e_F$ ,  $e_L$  and  $e_G$  showed that  $\lambda$  became more sensitive to small changes in fecundity and less sensitive to small changes in stasis as grazing intensity increased.

**Keywords:** *Cirsium vulgare*, demography, grazing, matrix analysis, size-dependence

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## Introduction

A major objective in ecological research is to explain and to predict the distribution and abundance of organisms. There are many approaches to the problem, but population ecology may be regarded as central because it deals with the demographic parameters (birth and death rates) that directly determine abundance, and hence also the limits of distribution. Although the connection between population ecology and these core ecological issues could not be closer, there are few plant population studies detailed enough to match up to the potential of the approach. The key test of any study is whether it provides sufficient information to predict the abundance of a population at a given point in time and space. This immediately disqualifies the majority of plant demographic studies that are confined to only one or a few homogeneous sites and those where the study does not follow the whole life cycle. Of course this is not to dismiss the very valuable information provided by such studies, but only to indicate how much more we need to know.

An incomplete, but illustrative list of some studies which do pass the test include the pioneering study of *Dipsacus sylvestris* by Werner & Caswell (1977) which estimated the finite rate of population increase,  $\lambda$ , and its sensitivity in a series of different old-field populations; the study by Keddy (1981) of *Cakile edentula* along a gradient, in which the importance of dispersal along the gradient was shown by Watkinson (1985); the study of *Erophila verna* by Symonides, Silvertown & Andreasen (1987) that showed why populations of the species cycled in some areas and not others; and the study of *Sorghum intrans* by Watkinson, Lonsdale & Andrew (1989) that explained the characteristic patchiness of distribution in this species. These studies stand out because all incorporated spatial variation in demographic parameters into population dynamic models. Many, perhaps most, other plant demographic studies reveal that spatial variation in demographic parameters is ubiquitous, but only studies based on the whole life cycle can confirm the importance and role of this in plant population dynamics. Ideally what are required are demographic studies of the whole life cycle in a replicated set of field environments. This paper describes the first such study.

We report a demographic study of 16 populations of the spear thistle *Cirsium vulgare* growing in the compartments of a fully replicated experiment involving grazing by sheep. *C. vulgare* is a semelparous perennial that has been widely studied in areas where it is an alien pasture weed (Forcella & Wood 1986; Michaux 1989) and in dune areas in the Netherlands where it is native (van Leeuwen 1983; de Jong & Klinkhamer 1988a,b; Klinkhamer & de Jong 1988; Klinkhamer, de Jong & van der Meijden 1988). In British pastures where it is native, as well

as in pastures elsewhere, the abundance of *C. vulgare* tends to increase with grazing intensity (Klinkhamer & de Jong 1993; Forcella & Wood 1986; Silvertown & Smith 1989). A replicated experiment that systematically varies the timing and intensity of grazing between plots (paddocks) therefore provides an ideal environment in which to explore the spatial variation in demographic parameters that determine the local abundance of *C. vulgare*.

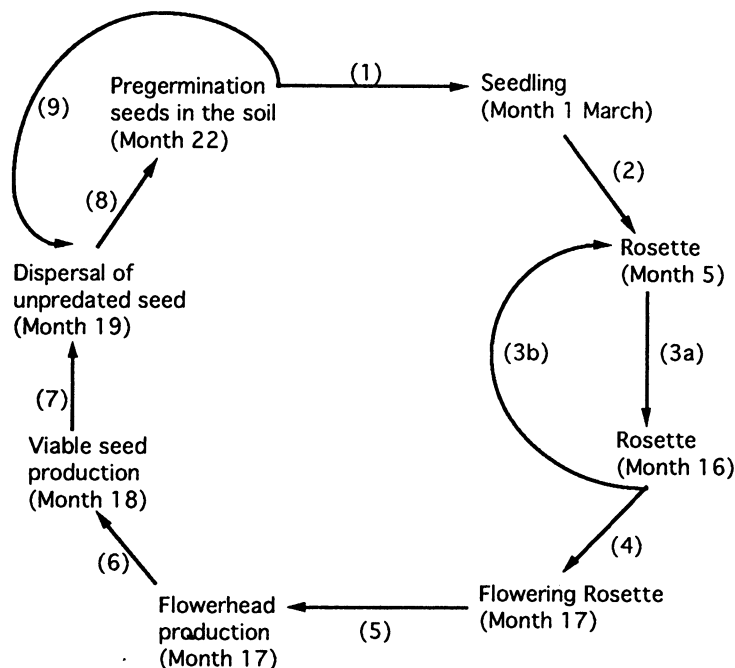
An earlier study of *C. vulgare* at our site reported a strong correlation between the observed abundance of thistle rosettes in each of the 16 paddocks and the rate of seedling emergence from seeds experimentally sown in each paddock (Silvertown & Smith 1989). Silvertown & Smith (1989) concluded from this that germination was very likely to be the most important transition in determining population size. Using annual censuses over a 6-year period and a study of all phases of the life cycle in each paddock population we are now able to compare the importance of the transitions between nine different stages of the life cycle to population size and  $\lambda$ . The life-cycle transitions studied include predispersal seed predation by larvae of the moth *Eucosma cana* and are shown in Fig. 1. Another paper uses the data reported here to model the dynamics of these populations (Gillman *et al.* 1993).

## Methods

### SITE DESCRIPTION

The grazing experiment was set up at Little Wittenham Nature Reserve in Oxfordshire, UK (National Grid reference US 5681 9247) in 1986 (Treweek 1990). The site is on an outcrop of the Berkshire Downs and the soil is a calcareous clay loam. Cultivation last occurred in the 1940s and subsequently the site was seeded with an agricultural grass mix and managed with sheep grazing and fertilizer application. When the Northmoor Trust purchased the site in 1984 all application of chemicals was ceased (Tennyson 1992). The sward is species poor and dominated by agricultural grasses (Bullock *et al.* 1994).

Grazing treatments are applied in three seasons: 'winter' (1 November – 21 March), 'spring' (21 March – 21 May) and 'summer' (21 May – 1 November). Within each season there are two levels of grazing. In winter and spring seasons paddocks are ungrazed or grazed by two Suffolk  $\times$  Mule ewes per paddock whereas in summer grazing the sward height is maintained at either 3 cm or 9 cm by weekly measurement of the sward height followed by adjustment of the stocking rate. The experiment is fully factorial with a  $2 \times 2 \times 2$  structure and two randomized blocks assigned over 16 ( $2 \times 8$ ) 50-m  $\times$  50-m paddocks (Table 1). These treatments have had small effects on the dominant grasses but many dicots have been



**Fig. 1** The life cycle of *Cirsium vulgare* showing the transitions investigated in this study. Seedlings emerge in early spring (1) and survivors form rosettes (2). These rosettes grow through to the summer of the following year (3a) when the survivors either flower (4) or remain vegetative. The vegetative plants may survive to the following year (3b) when they again may flower or remain vegetative. Therefore *Cirsium vulgare* does not necessarily act as a biennial. Flowering rosettes produce a number of flowerheads (5) each of which produces a number of viable seeds (6). These seeds are subject to predispersal predation (7). While they are in the soil between dispersal in late summer until germination starts in December some seeds are lost through predation and other causes (8). The surviving seeds then germinate (1) or remain as seeds and those ungerminated seeds which survive (9) supplement the seed rain in the next summer.

increased by grazing in one or more seasons (Bullock *et al.* 1994).

In the data collection and analysis it was assumed that there was no seed dispersal among the paddocks and therefore that the paddocks contained separate populations. This supposition is supported by the fact that seed dispersal is very limited in *Cirsium vulgare*. Michaux (1989) found that 91% of seeds fell within 2 m of the parent plant in a pasture population and in a sand dune population Klinkhamer, de Jong & van der Meijden (1988) found 66% falling within 2 m. The 10-m boundary around the area sampled in each paddock (see below) increased the isolation of populations.

#### POPULATION SIZES

From 1987 to 1992 the abundance of *C. vulgare* in each paddock was censused in the second week of April. In each paddock all the rosettes in seven evenly spaced 3-m-wide transects were counted. In this and all the censuses described below the 10-m strip around the perimeter of each paddock was avoided to reduce edge effects.

#### SEEDLING EMERGENCE AND SURVIVAL

From 28 to 30 November 1990, seeds (achenes) were sown individually with forceps at 5-cm intervals in permanent quadrats forming grids of 10 × 4 seeds.

Five quadrats and thus 200 seeds were sown in each paddock. The emergence (transition 1) and survival (transition 2) of seedlings were monitored every 2 weeks until 17 July 1991. By this date all the surviving plants had adult leaves and were about 5 cm in diameter and were judged to have reached the rosette stage. The total seedling emergence and the survival rate of seedlings were determined for each paddock. The seeds used in this experiment and in the seed survival study were bought from a commercial supplier and they had the same viability as seeds from the study populations (79%).

On 12 March 1991, during the peak of seedling emergence, the sward conditions where each seed

**Table 1** Design of the grazing experiment. 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 9 cm in height

Treatment	Winter	Spring
Summer 3 cm		
A	–	–
B	–	+
C	+	–
D	+	+
Summer 9 cm		
E	–	–
F	–	+
G	+	–
H	+	+

had been sown were determined. A point quadrat was placed vertically at each sowing site. The presence of a canopy was recorded if the pin touched a leaf. The conditions at the soil surface were also determined; whether the pin rested on bare soil, litter or living plant stems. At the same time 100 randomly selected sites were sampled in each paddock by the same method.

#### ROSETTE SURVIVAL, FLOWERING RATE AND FLOWER PRODUCTION

On 24–25 July 1991, 20 rosettes were located in each paddock by random quadrats and were marked. However, fewer than 20 rosettes were found in some paddocks; for instance, only five were found in 2E. The broadest diameter ('initial size') of each rosette was measured to the nearest centimetre. On 4–6 June 1992 the surviving rosettes (transition 3) were relocated and the broadest diameter ('final size') was measured. The rosettes which subsequently flowered were censused (transition 4) and numbers of flowerheads and viable buds produced were counted (transition 5).

#### SEED PRODUCTION AND VIABILITY

On 31 July 1990 all the flowering plants were mapped in each paddock. The plants were monitored regularly and their flowerheads removed when the seeds became ripe. The number of flowerheads produced by each plant and the number of flowerheads damaged by the only obvious predispersal seed predator, the tortricid moth *Eucosma cana*, were counted. Undamaged flowerheads were chosen at random in roughly equal numbers from each plant in a paddock to provide 20 flowerheads per paddock (transition 6). Twenty moth-damaged flowerheads per paddock (transition 7) were chosen in the same way and the seeds per head were counted and saved. The obviously damaged seeds were not counted or kept.

Two categories of moth damage (damaged and undamaged) and 16 paddocks produces 32 categories of flowerheads. However, there were no flowering plants in four paddocks, resulting in only 24 categories. In each category the seeds from all heads were mixed and were sown 10 to a pot in John Innes seed compost. Seeds from all 24 categories were sown and the pots were arranged in the greenhouse a randomized block design with 10 blocks. Germination was monitored regularly until no further germination had occurred for several weeks (transition 6).

#### SEED SURVIVAL

Seed survival after dispersal in August–October can be divided into two categories (Fig. 1); until the germination starts in December (transition 8; pregermination period) and until the next August (transition 9; during and postgermination period survival). In the

former transition seeds either die or remain as seeds; during the latter transition seeds die, germinate or remain as seeds. Emergence was assumed to be equal to germination and was measured in transition 1. The method described here determined the fate of the remaining proportion of seeds. Quadrats (15-cm × 15-cm) were fixed in random positions in each paddock and 100 seeds were put into each. The seeds were lightly sprayed with car paint in order to allow us to differentiate them from natural seeds. The effect of spraying on viability was tested by sowing 20 seeds each in 20 pots of John Innes seed compost. Sprayed seeds were sown in half the pots and unsprayed seeds in the other pots. Emergence was monitored until two weeks after the final seedling emerged. A *t*-test showed no significant effects of spraying on the number of seedlings emerging per pot (mean = 16.6,  $t_{18} = 0.124$ ). Two quadrats per paddock were set up on 13 August 1991 and retrieved on 14 November 1991 for the transition 8 treatment and two were set up on 15 November 1990 and retrieved on 12 August 1991 for the transition 9 treatment. The quadrats for transition 9 were monitored regularly and any seedlings produced by the marked seeds counted and removed. Remaining seeds were retrieved by removing soil in the quadrats to a depth of 6 cm. These turves were air dried and sorted for the surviving seeds. Viability was determined by sowing the seeds in John Innes seed compost and measuring germination rate.

#### ANALYSIS

The rosettes censused for transition 3 were divided into three size classes after examination of the data. No first-year rosettes grew larger than 10 cm in diameter by the July after emergence and this was chosen as the upper boundary on the 'small' class. Only one rosette < 20 cm in diameter in June flowered in the same summer (see below) and so the 'medium' rosettes were between 11 and 20 cm. Rosettes larger than 20 cm in diameter were placed in the 'large' class. The grazing effects on survival (transition 3) and flowering rates (transition 4) were analysed separately for the three size classes. Apart from the single exception in the medium class, only large rosettes flowered (see below) and in order to investigate the effects of rosette size on seed production the large size class was further divided into three size subclasses of 'lower-range' (21–30 cm), 'middle-range' (31–40 cm) and 'upper-range' (> 41 cm) and used to classify the rosettes that were in the large size class in 1992. Differences among the size classes in survival, flowering rates and transition rates into other size classes and among the large size subclasses in flowerhead production were analysed by performing *G*-tests on data pooled across all paddocks.

The main and interaction effects of the grazing treatments on each transition were mostly analysed

by three-way ANOVA as determined by the experimental design. Percentage data were arcsine-transformed for analysis. However, ANOVA could not be used on certain transitions. Because eight paddocks had fewer than 20 rosettes and most of these were in the small size class, there were small sample sizes for medium and large rosette size classes in several paddocks. For these two size classes main grazing treatment effects were therefore determined by *G*-tests on data pooled over the eight paddocks of each main effect grazing contrast. The death of all rosettes in both 1E and 2E between 1991 and 1992 caused missing values for flowering rates and flowerheads per plant. There were also missing values for seeds per flowerhead, predispersal seed loss and seed viability. Because the missing values were not randomly distributed among the paddocks, *t*-tests on the main treatment effects were used to analyse grazing main effects on these variables although this meant that interaction effects could not be determined.

The effects of soil surface conditions and canopy condition at a sowing site on emergence were analysed by a three-way *G*-test on data pooled across the paddocks.

The effects of the grazing treatments on the population growth rates were determined by analysis of stage projection matrices (Caswell 1989) constructed using the data from each paddock. A year interval from June to June was used, resulting in four stages: ungerminated seeds, small rosettes, medium rosettes and large rosettes. Over the projection interval ungerminated seeds could remain ungerminated, form small rosettes or die. Small rosettes could form medium rosettes, large rosettes or die. Medium rosettes could form medium rosettes, large rosettes or could die. Large rosettes could flower and produce seeds and thus form small rosettes, could remain as large rosettes or could die. Actual data from each paddock were used to calculate the matrices except for the survival of small, medium and large rosettes and the flowering rates of large rosettes for which there were small sample sizes. For these characters either the mean over all paddocks or the mean for a grazing treatment if there was a significant grazing treatment effect were used. The mean over all pad-

docks for a transition was used when there was a missing value in a paddock.

The transitions from (1) seed to seed, (2) seed to small rosette, (3) large rosette to small rosette and (4) large rosette to seed were calculated as follows:

- 1  $(1 - SE) \times PR \times PO$ ;
- 2  $PR \times PO \times SE \times SS$ ;
- 3  $FP \times HP \times SH \times VI \times PR \times SE \times SS$ ;
- 4  $FP \times HP \times SH \times VI \times PR \times (1 - SE)$ ,

in which *SE* represents seedling emergence proportion, *PR* pre-germination seed survival, *PO* postgermination period seed survival, *SS* seedling survival, *FP* flowering proportion of large rosettes, *HP* flowerheads per flowering plant, *SH* seeds per flowerhead and *VI* proportion of seeds viable.

The grazing effects on these four transitions were determined by ANOVA. Elasticity analysis (de Kroon, Plaisier & van Groenendaal 1986) was performed on each matrix and elasticity values within each matrix were summed to give a value for fecundity ( $e_F$ ), stasis ( $e_L$ ) and growth ( $e_G$ ) (Silvertown *et al.* 1993). Means of  $e_F$ ,  $e_L$  and  $e_G$  were calculated for each of the seven treatments A–D and F–H, and then plotted in a triangular ordination. In one of the replicates of treatment E,  $\lambda = 0$ , so we plotted the elasticities of the other replicate of this treatment.

## Results

### POPULATION SIZES

Winter grazing, spring grazing and harsher summer grazing all tended to increase thistle population sizes in all years although these effects were rarely significant in 1987, 1988 and 1989 (Table 2). However, these grazing effects were all significant in the later three years (Table 2). There were winter–spring, winter–summer, spring–summer and winter–spring–summer interactions in 1990 and a winter–summer interaction in 1991 and 1992 due to synergistic effects of the grazing treatments (results not shown). Thistle numbers fluctuated widely over the years reaching a minimum mean per paddock of 14 in 1990 and a maximum of 154 in 1992.

**Table 2** The main effects of the grazing treatments on numbers of *Cirsium vulgare* from 1987 to 1992. Interaction effects are not shown and the numbers show the mean value over the eight paddocks of that main treatment. The *F*-values of the ANOVAs are shown

Year	Winter grazing			Spring grazing			Summer grazing		
	+	–	<i>F</i>	+	–	<i>F</i>	3 cm	9 cm	<i>F</i>
1987	64.1	31.5	1.9	79.8	15.9	7.4*	65.0	30.6	2.1
1988	127.4	56.5	2.3	142.1	41.8	4.6	130.5	53.4	2.8
1989	109.6	39.8	3.1	115.5	33.9	4.2	104.9	44.5	2.3
1990	23.3	5.3	23.4**	23.9	4.6	26.8**	22.4	6.1	19.1**
1991	48.5	7.3	20.3**	41.9	13.9	9.3*	45.4	10.4	14.6**
1992	256.5	51.8	11.2*	223.0	85.3	5.1	278.6	29.6	16.6**

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Degrees of freedom are all 1,7.

**Table 3** The main effects of the grazing treatments on each transition in the life cycle of *Cirsium vulgare*. Different statistical tests were used to test significance depending on the form of the data for each transition (see text): ANOVAS giving *F*-values, *G*-tests and *t*-tests. Interaction effects from ANOVAS are not shown and the numbers show the mean value over the eight paddocks of that main treatment. The *F*-values of the ANOVAS are shown

Year	Trans.	d.f.	Winter grazing		test	Spring grazing		test	Summer grazing		test
			+	-		+	-		3 cm	9 cm	
Seedling emergence (%)	1	1,7	34.7	14.8	<i>F</i> = 23.8**	26.4	23.1	<i>F</i> = 0.7	29.9	19.7	<i>F</i> = 6.2*
Seedling survival (%)	2	1,7	43.8	16.3	<i>F</i> = 29.9***	38.3	21.8	<i>F</i> = 10.7*	30.3	29.8	<i>F</i> = 2.8
% Small rosette survival	3a	1,7	41.2	14.1	<i>F</i> = 7.3*	31.3	23.8	<i>F</i> = 0.6	34.4	21.6	<i>F</i> = 1.8
% Medium rosette survival	3b	1	78.4	50.0	<i>G</i> = 3.9*	71.4	66.7	<i>G</i> = 0.4	73.1	68.0	<i>G</i> = 1.4
% Large rosettes flowering	4	1	53.2	81.8	<i>G</i> = 5.7*	55.8	73.1	<i>G</i> = 2.1	64.4	58.3	<i>G</i> = 0.3
Flowerheads per flowering plant (1992)	5	12	21.2	35.3	<i>t</i> = 1.3	30.4	21.7	<i>t</i> = 1.2	33.1	19.4	<i>t</i> = 1.2
Flowerheads per flowering plant (1990)	5	10	11.4	27.4	<i>t</i> = 2.4*	17.7	18.8	<i>t</i> = 0.1	13.2	24.9	<i>t</i> = 1.4
Seeds per head	6	10	116	92	<i>t</i> = 2.0	105	111	<i>t</i> = 0.4	99	120	<i>t</i> = 1.8
% seeds viable	6	10	83.6	76.9	<i>t</i> = 1.3	84.8	76.7	<i>t</i> = 1.6	81.9	79.9	<i>t</i> = 0.4
% seed-heads moth attacked	7	10	64.3	74.6	<i>t</i> = 2.3*	67.3	68.8	<i>t</i> = 0.3	65.4	73.0	<i>t</i> = 1.5
Post-dispersal, pre-germination seed predation (%)	8	1,7	25.6	22.2	<i>F</i> = 0.8	24.9	22.8	<i>F</i> = 0.3	25.6	22.2	<i>F</i> = 0.8
Survival of non-germinating seeds (%)	9	1,7	7.6	7.8	<i>F</i> = 0.01	8.5	6.8	<i>F</i> = 0.5	7.0	8.4	<i>F</i> = 0.3
$\lambda$		1,7	2.53	0.81	<i>F</i> = 67.9***	2.10	1.24	<i>F</i> = 16.9**	2.11	1.23	<i>F</i> = 17.8**

\**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001.

## SEEDLING EMERGENCE AND SURVIVAL

Seedling emergence was increased both by winter grazing and by the heavier summer grazing (Table 3). Percentage seedling survival was increased by both winter and spring grazing (Table 3). ANOVA on the data of the 100-point surveys showed that both winter grazing and heavier summer grazing decreased the number of sowing sites with a canopy (Table 4). These treatments also affected the conditions at the soil surface: increasing the number of bare sites, decreasing the number of those with litter but having no effect on the number of sites covered with plant stems (Table 4).

The two characteristics of a sowing site, the soil surface conditions and the canopy conditions, had significant but independent (three-way interaction;  $G_2 = 4.6$ , NS), effects on emergence. Emergence was less under a canopy (19.7%) than with no canopy (31.5%) ( $G_3 = 294$ ,  $P < 0.001$ ). Emergence was greatest on bare soil (30.5%) medium under stems (21.2%) and least under litter (5.0%) ( $G_4 = 118$ ,  $P < 0.001$ ). It therefore seems that the grazing in winter or harder grazing in summer increased emergence by increasing the amount of bare ground.

## ROSETTE SURVIVAL AND FLOWERING RATE

The three size classes differed in survival rate between 1991 and 1992 with an increased initial size increasing the survival rate of rosettes (Fig. 2). Over the whole experiment only one large rosette died before flowering. Winter grazing increased the survival of small and medium rosettes (Table 3). Of the surviving small rosettes none remained in the small class by June 1992 but 58.1% had entered the medium class and 41.9% had become large. The surviving medium rosettes had remained medium (32.4%) or had become large (67.6%) and all the large rosettes remained large. No rosettes had regressed to smaller classes and the grazing treatments had no effect on these transition rates (Table 5).

A *G*-test on the data pooled across all paddocks showed that, with a single exception in the medium class, only rosettes in the large size class flowered and that within this class an increased final size increased the probability of flowering (Fig. 3a). Winter grazing decreased the flowering rate of large rosettes (Table 3). The reason for this can be found in the increased survival of small and medium rosettes under winter grazing (Table 3). The initial size class of a rosette in 1991 affected its final size subclass in 1992 so that small rosettes grew into mostly the lower or middle ranges, medium rosettes mostly grew into the middle range and large rosettes grew mostly into the upper range (*G*-test; Fig. 3b). Winter grazing therefore changed the distribution of sizes within the large size class by increasing the propor-

**Table 4** The main effects of grazing treatments on the sward characteristics measured in the 100 point survey. Two characteristics were measured: presence or absence of a canopy and nature of the soil surface from one of three types. Interaction effects are not shown and the numbers show the mean value over the eight paddocks of that main treatment. The *F*-values of the ANOVAS are shown

Characteristic	Winter grazing			Spring grazing			Summer grazing		
	+	-	<i>F</i>	+	-	<i>F</i>	3 cm	9 cm	<i>F</i>
% with canopy	75.3	93.9	24.5**	85.4	83.8	0.2	78.8	90.4	9.5*
Soil surface									
% Bare	36.6	14.8	205***	28.8	22.6	0.4	37.4	18.9	98***
% Stem	56.6	52.5	0.7	50.3	58.8	3.1	59.2	49.9	3.8
% Litter	6.8	32.7	64***	20.9	18.6	0.01	3.4	31.2	50***

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Degrees of freedom are all 1,7.

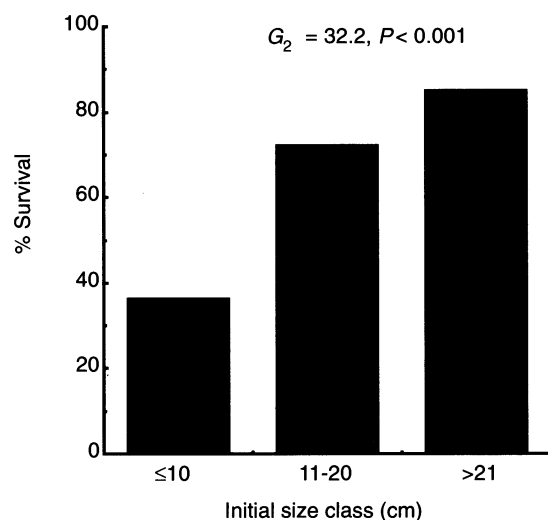
tion of lower-range rosettes (*G*-test; Fig. 3c) and thus decreasing the flowering rate of large rosettes.

#### FLOWER AND SEED PRODUCTION

Despite a strong trend for a negative effect of winter grazing there were no significant effects of the grazing treatments on the mean number of flowerheads produced per flowering plant (Table 3). The relationship between the final size and flowerhead number for those plants that flowered (Fig. 4) was studied using the pooled data. Following Klinkhamer *et al.* (1992), the logged data were analysed by regression which showed a significant linear relationship ( $F = 96.98$ ,  $n = 43$ ,  $P < 0.001$ ). The data collected in 1990 on flowerhead number were also analysed and showed similar trends to the 1992 data and the trend for winter grazing to decrease flowerhead numbers was significant in this year (Table 3). This consistency indicates that this is a real grazing effect and that it is valid to assume that the grazing effects on the other aspects of seed production determined in 1990 and discussed below also occurred in 1992. This effect was a continuance of the effect of winter grazing on rosette survival discussed above. By increasing the proportion of small surviving rosettes

and thus decreasing the mean size of flowering rosettes, winter grazing decreased the mean number of flowerheads per plant.

The number of seeds per flowerhead and the percentage viability of seeds were unaffected by the grazing treatments (Table 3). The number of flower heads per plant did not affect the number of seeds per flowerhead (linear regression;  $F = 1.34$ ,  $n = 53$ , NS). Moth attack decreased the mean number of seeds in a head from 106.2 to 32.4 (paired *t*-test,  $t_{43} = 9.76$ ,  $P < 0.001$ ). The percentage of heads damaged by the seed predator was decreased by winter grazing (*t*-test on arcsine-transformed proportions; Table 3). However, there was a complex relationship between the percentage of heads damaged and the number of heads per plant (Fig. 5). With low numbers of heads per plant, percentage damaged ranged between 0 and 100. However, where there were high numbers of heads on a plant percentage damage was always high. Linear regression was not appropriate for testing this complex relationship so an Olmstead and Tukey corner test for association (Sokal & Rohlf 1981, p. 608) was used. This determines whether there is a significant pattern in the distribution of points in a bivariate scattergram in relation to the medians of the two variables (see Fig. 5). This gave a quadrat sum of 16.5 which was significant at  $P < 0.005$ . The significance came about because the points on the right side of the head number median were clustered above the percentage damage median.



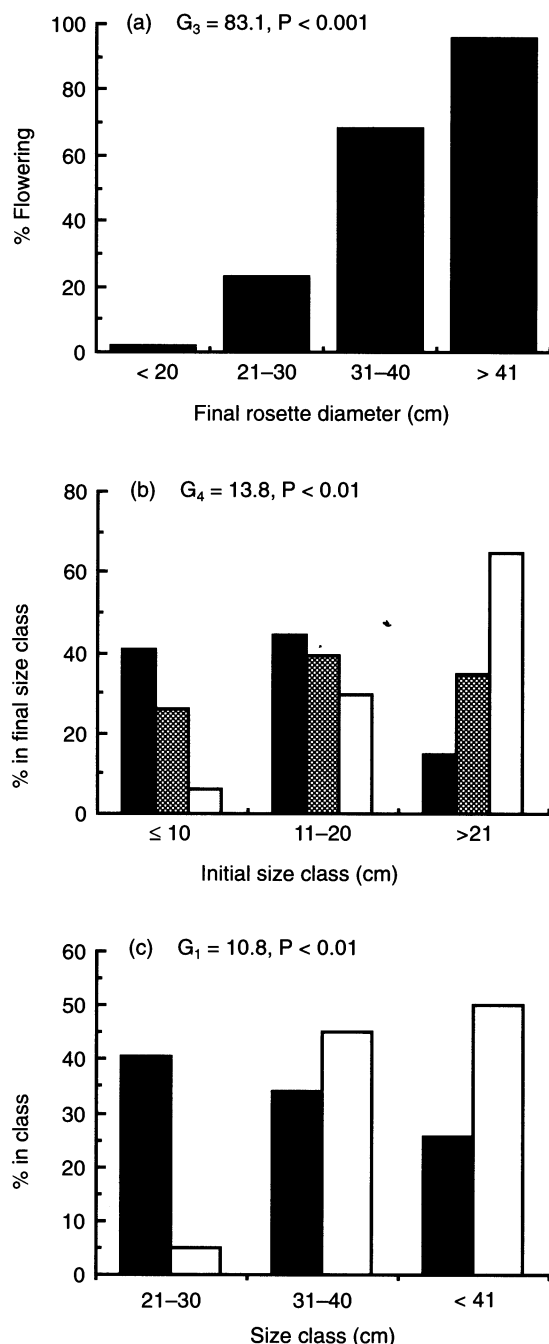
**Fig. 2** The effect of rosette diameter class in July 1991 on percentage survival until June 1992. The results of a *G*-test are shown.

**Table 5** Results of *G*-tests on the effects of the grazing treatments on the transitions between rosette size classes from 1991 to 1992. This tests whether the main grazing treatment affected the proportion of surviving small rosettes becoming medium rosettes as opposed to large rosettes, or the proportion of surviving medium rosettes becoming medium rosettes as opposed to large rosettes

Initial size class	<i>G</i> -values for effects of grazing in each season		
	Winter	Spring	Summer
Small	0.79	0.12	0.53
Medium	0.12	1.71	2.13

None of the *G*-tests were significant, d.f. = 1.





**Fig. 3** The relationship between grazing, rosette size and flowering. (a) The effect of rosette diameter class in June 1992 on percentage flowering in that year as analysed by a  $G$ -test. (b) The effect of the initial size class of rosettes on the frequency distribution of final sizes of those rosettes that reached the large size class. There are three final size subclasses within the large size class: lower-range, 21–30 cm (■); middle-range, 31–40 cm (▨); and upper-range > 41 cm (□). (c) The effect of winter grazing on the subclass size frequency distribution of surviving rosettes within the large size class. The results of a  $G$ -test is shown. ■ = Grazed, □ = Ungrazed.

#### SEED SURVIVAL

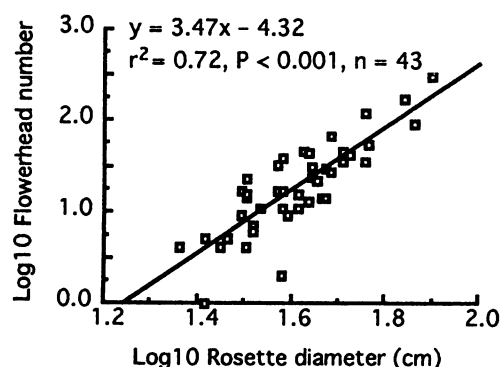
Of the 200 seeds put out in each paddock for the estimation of transition 8 (postdispersal, pregermination survival) an average of 66.8 whole (not obviously damaged) seeds were retrieved. On average 57.5% of

these remaining seeds were viable which is less than the 80% viability of the original 200 seeds. This change in percentage viability was probably due to a preference of seed predators for viable seeds and the loss of viability of some seeds. This gives a survival rate of viable seeds of 24% which was unaffected by the grazing treatments (Table 3).

Because transition 9 includes germination some of the 200 seeds put out in each paddock for the assessment of survival were lost through germination (mean = 14.4). As expected from previous results more seeds germinated in the winter grazed paddocks ( $F_{1,7} = 10.8, P < 0.05$ ). However there was no winter grazing effect on the number of whole seeds retrieved ( $F_{1,7} = 0.19, \text{NS}$ ) which was low (mean = 23.6), or on their percentage viability (mean = 46.5%,  $F_{1,7} = 0.04, \text{NS}$ ). The percentage viability of these seeds was again lower than that of the original set of seeds due to the same factors that acted upon the transition 8 seeds but also to the 9% loss of viable seeds through germination. Allowing for this loss of viable seeds through germination the loss of viable seeds through other causes during transition 9 was unaffected by the grazing treatments (Table 3).

#### MATRIX MODELS

Harder grazing in any season raised the finite rate of population increase ( $\lambda$ ) (Table 3). This result was similar to the grazing effects on thistle numbers (Table 2) and regression analysis showed that  $\lambda$  and thistle numbers (meaned over the six years) were correlated (Fig. 6). Small rosette survival, medium rosette survival and large rosette survival were all increased by winter grazing (Table 3). The last transition was affected because winter grazing decreased the flowering rate of large rosettes (Table 3). The seed to seed, seed to small rosette and large rosette to seed transitions were unaffected by the treatments (Table 6). Winter and spring grazing and harder summer grazing all significantly increased the large rosette to small rosette transition. There were significant interactions of spring  $\times$  winter ( $F_{1,7} = 8.96$ ,



**Fig. 4** The effect of rosette diameter in June 1992 on the number of flowerheads produced by those rosettes that flowered that year. The relationship is described by a linear regression.

**Table 6** The results of ANOVA on the main effects of the grazing treatments on the four matrix transitions formed by combining several transitions (see Methods). Interaction effects are not shown and the numbers show the mean value over the eight paddocks of that main treatment. The F-values of the ANOVAs are shown

Characteristic	Winter grazing			Spring grazing			Summer grazing		
	+	–	F	+	–	F	3 cm	9 cm	F
Seed to Seed	0.012	0.014	0.23	0.015	0.010	0.90	0.010	0.015	0.74
Seed to Small rosette	0.004	0.001	5.26	0.004	0.001	3.13	0.002	0.002	0.05
Large rosette to Seed	80.2	193.2	2.17	187.3	86.1	1.79	169.6	103.8	0.73
Large rosette to Small rosette	28.4	8.0	20.80**	27.7	8.7	18.01**	28.6	7.9	21.48**

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Degrees of freedom are all 1,7.

$P < 0.05$ ) and summer  $\times$  winter ( $F_{1,7} = 5.87$ ,  $P < 0.05$ ) both due to positive synergistic effects of grazing in more than one season (means not shown).  
The triangular ordination of  $e_F$ ,  $e_L$  and  $e_G$  is shown in Fig. 7. All comparisons between grazing treatments (e.g. D vs. H, which differed only in summer grazing intensity; see Table 1), except those involving treatment E, indicate that heavier grazing in a particular season increased  $e_F$ , decreased  $e_L$  and had a comparatively small effect on  $e_G$ .

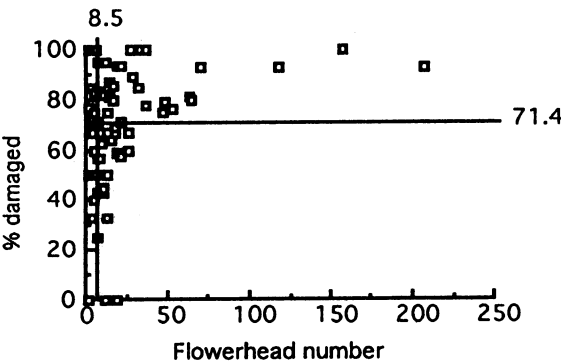
### Discussion

All grazing treatments significantly affected  $\lambda$ , which increased with harder grazing. We found that  $\lambda$ , calculated from experimental observations, correlated with the mean size of the population present in each paddock (Fig. 6). The experimental design has allowed us to uncover some of the mechanisms behind this correlation. Because grazing treatments were seasonal, different treatments affected different parts of the life cycle. Seedling emergence and survival of seedlings and rosettes (Table 3) were increased under increased grazing in particular seasons. These effects probably arose through a relaxation of interspecific competition as the dominant grasses were grazed and the thistles were not. This is suggested by the effects of winter and summer grazing on the proportion of sowing points with a canopy (Table 4) and the correlation of the lack of a canopy with seedling

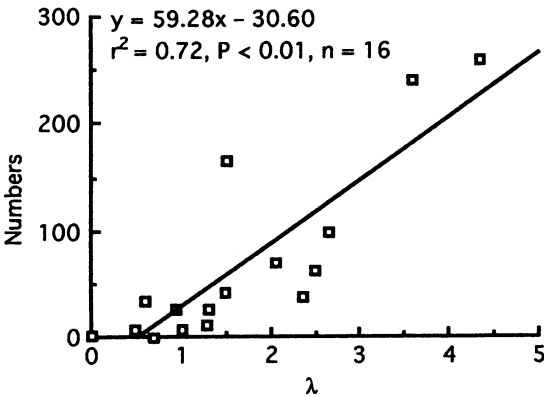
emergence. Silvertown & Smith (1989) found that emergence in *C. vulgare* was increased in artificial gaps. The effect of litter in decreasing emergence and grazing in decreasing litter (Table 4) as well as the canopy effect suggests that the mechanism of the response of seeds and seedlings to gap conditions may be complex and that gaps may need to be defined by a number of factors.

Grazing effects on seedling and adult plant survival can be positive (Bakker, Dekker & de Vries 1980; Forcella & Wood 1986; Louda, Potvin & Collinge 1990) or negative (Silander 1983) depending on whether plants or their competitors suffer more from grazing. The exact effect can depend on the intensity of grazing (Silvertown *et al.* 1992) and, as in this study, on the size or age class of the plants; with a loss in sensitivity to grazing with increased size (Silander 1983). Seedling survival in this study was increased by winter and spring grazing, those treatments that would have decreased grass cover during the period of seedling growth. It is less clear why only winter grazing increased the survival of small and medium rosettes but this grazing treatment was the most effective in decreasing the densities of the two dominant grass species *Lolium perenne* and *Agrostis stolonifera* (J. M. Bullock *et al.*, unpublished data) and thus may have been the most effective in reducing competition from the grasses.

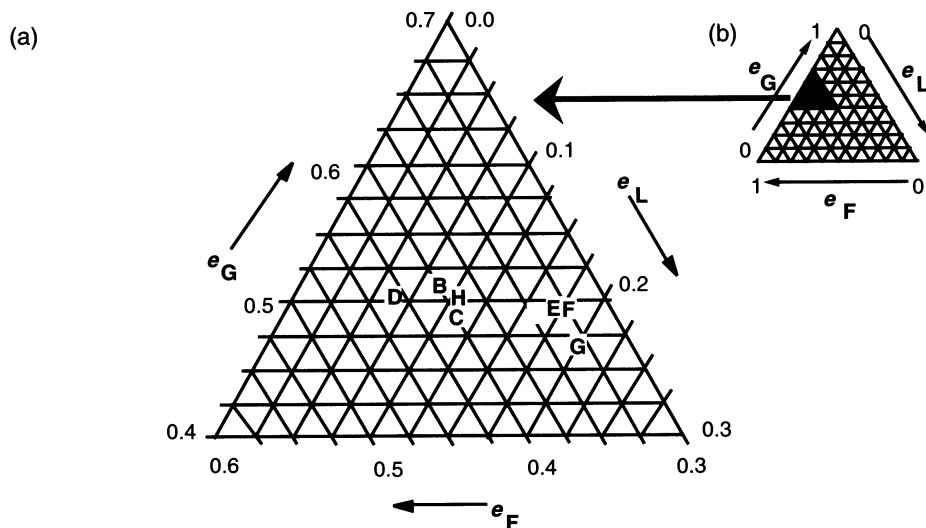
The effects of winter grazing on some transitions affecting seed production were complex, but all were



**Fig. 5** Seed predation. The effect of flowerhead number per plant on the percentage of flowerheads attacked by the seed predator *Eucosma cana*. The scatter of points is divided by the median values of both variables.



**Fig. 6** The correlation between  $\lambda$  and the number of thistles (meaned over the six years) in a paddock. The relationship is described by a linear regression.



**Fig. 7** (a) Ordination of fecundity ( $e_F$ ), stasis ( $e_L$ ) and growth ( $e_G$ ) elasticities for *C. vulgare* populations from the treatments A–H. (b) All the populations fall within the shaded region of this demographic triangle.

caused purely by the grazing effect on the survival of small and medium rosettes. The elucidation of these mechanisms illustrates the importance of using size-structured demographic analysis (e.g. Caswell 1989; Cochran & Ellner 1992). Survival, transition rates to other size classes, flowering probability, flower production and seed predation were all dependent on a measure of plant size; be it rosette diameter or flower number. Size-dependent mortality has often been reported (Werner & Caswell 1977; van der Meijden & van der Waals-Kooi 1979; Gross 1981) and there is a large literature concerning minimum size thresholds for flowering and size-dependent flower production (Samson & Werk 1986; Klinkhamer, Meelis, de Jong & Weiner 1992) including work by van Leeuwen (1983) and Klinkhamer, de Jong & Meelis (1987) who have shown the last two processes occurring in populations of *Cirsium vulgare*.

Size-dependent seed predation is less often studied (but see Crawley 1983, p. 64). This study suggested that a disproportionate number of flowerheads were damaged by *Eucosma cana* on the largest thistles (Fig. 5), although there was no simple linear relationship. Winter grazing increased the survival of small and medium rosettes (Table 3) and thus increased the proportion of small flowering plants and decreased the mean number of flowerheads per plant (Table 3, Fig. 4). Because the proportion of heads attacked was highest on the biggest plants, winter grazing decreased the mean percentage of damaged flowerheads (Table 3). The moth *Depressaria pastinacella*, which feeds on umbels of *Pastinaca sativa*, attacked more flowers on larger plants (Thomson 1978) and increased stem diameter in *Cirsium palustre* increased the probability of attack by the stem-boring moth *Epiblema scutulana* (van Leeuwen 1983). The exact mechanisms causing size-dependent predation vary but in this study the facts that almost all plants were attacked, but size

affected the proportion of flowerheads attacked, indicate that either larger plants attracted disproportionately more moths or individual moths laid fewer eggs on smaller plants.

Triangular ordination of elasticities clearly showed that  $\lambda$  became more sensitive to small changes in fecundity and less sensitive to small changes in stasis (i.e. survival of rosettes from one year to the next in the same size class) as grazing intensity increased. This is consistent with our findings that grazing increased recruitment, either increasing seedling emergence (winter grazing or harder summer grazing) or increasing seedling survival (spring grazing). Silvertown *et al.* (1993) showed that triangular ordination of  $e_F$ ,  $e_L$  and  $e_G$  was a useful way of comparing the demography of different species, which segregated in the triangle according to habitat and life history. All our populations of *Cirsium vulgare* fell within the region of the demographic triangle (Fig. 7b) containing other semelparous herbs (Silvertown *et al.* 1993). This indicates that the transitions due to growth and fecundity were more important to  $\lambda$  than was stasis. The fact that grazing intensity determined the precise position of each *C. vulgare* population within the region occupied by semelparous herbs in general shows that the demographic triangle may be successfully applied in comparisons of populations of a single species as well as in interspecific comparisons.

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