

## A density-dependent model of *Cirsium vulgare* population dynamics using field-estimated parameter values

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**Abstract.** Two versions of a stage-structured model of *Cirsium vulgare* population dynamics were developed. Both incorporated density dependence at one stage in the life cycle of the plant. In version 1 density dependence was assumed to operate during germination whilst in version 2 it was included at the seedling stage. Density-dependent parameter values for the model were estimated from annual census data in a factorial grazing experiment. Version 1 of the model produced significant estimates of density dependence under field conditions. The estimated values, when included in a simulation of the dynamics, produced two-point limit cycles under conditions of hard grazing. The limit cycles were most pronounced at the early rosette stage. Comparison of the effects of density dependence at the two different stages in the life cycle revealed a strong difference in predicted dynamics. This emphasizes the importance of determining where density dependence operates under field conditions and the potential problems of arbitrarily assigning it to particular life-history stages. Version 1 of the model produced a good prediction of observed mean plant density across the different grazing treatments ( $r^2=0.81$ ,  $P<0.001$ ).

**Key words:** Population dynamics – Stage-structured model – Density dependence – Field parameter estimates – *Cirsium vulgare*

There have been numerous models of local plant population dynamics incorporating density-independent fecundity and survival values. These models have been developed using difference equations and/or matrix techniques with stage, size or age-structure (Caswell 1989; Silvertown et al. 1993; Watkinson 1987). Such models allow determination of the finite rate of population increase ( $\lambda$ ) either by simulation or by evaluation of the dominant eigenvalue of the transition matrix.

Whilst these density-independent models have been useful in identifying potential rates of population increase at low density, it is clear that for many applications it is important to incorporate density dependence (Watkinson 1987). There is now little doubt that density dependence operates in most plant and animal populations, and that failure to detect it is largely due to the inadequacies of data sets or techniques (Hassell et al. 1989; Holyoak and Lawton 1992; Turchin 1990; Woivod and Hanski 1992). Density dependence has been routinely applied in first order difference equation models but less frequently within stage-structured models (de Kroon et al. 1987; Klinkhamer and de Jong 1989).

For most populations the problem is therefore not one of the existence of density dependence but of its mode of action and strength under different field conditions. Methods of determining the presence of density dependence using regression techniques allow estimates to be made of the value of the density-dependent parameter(s) (Turchin 1990; Turchin and Taylor 1992). These parameter values can then be incorporated into population dynamics models. The primary aim of this study is to determine the values of the parameters of density dependence from annual census data of the spear thistle, *Cirsium vulgare*, and include those values in a stage-structured model. Two versions of the model are developed; one in which density dependence is assumed to operate during germination and one in which it operates on seedling survival. The first version can be linked with an earlier safe-site model for *Cirsium vulgare* (Silvertown and Smith 1989). In this study appropriate regression methods are developed to distinguish between the two versions of the model. The density-dependent function used in the present study is a negative exponential which simplifies the model and allows the effects of incorporating density dependence at the two different life-history stages to be easily compared.

A major limitation of population models is that they are usually developed from data sets in unmanipulated field conditions. An advantage of the present data set is

that it is drawn from a factorial field experiment in which the effect of sheep grazing treatments can be included via effects on the model parameters. Here we examine the relationship between sheep grazing at different times of year and the population dynamics of *Cirsium vulgare* as predicted by the two versions of the density-dependent model. Some of the data used in the present study have already been used to describe the density-independent dynamics of *Cirsium vulgare* under different grazing treatments (Bullock et al. 1994a). The experimental design allows us to make predictions of the fate of *Cirsium vulgare* populations under a variety of different management conditions, which in turn reflect a range of semi-natural habitats.

## Methods

### Field experiment

The sheep grazing experiment was set up at Little Wittenham Nature Reserve in Oxfordshire, England (US 5681 9247) in 1986 (Trewick 1990). The grassland is species-poor and is dominated by *Lolium perenne* and *Agrostis stolonifera* (Bullock et al. 1994b). The experiment is fully factorial (2 summer grazing levels  $\times$  2 winter grazing levels  $\times$  2 spring grazing levels) with two randomized blocks (Table 1). Each treatment replicate is applied to a 50  $\times$  50 m paddock. Winter grazing runs from 1 November to 21 March, spring grazing from 21 March to 21 May and summer grazing from 21 May to 1 November. In winter and spring seasons grazing levels are either ungrazed or grazed by two Suffolk  $\times$  Mule ewes per paddock. In summer two grazing levels are applied by adjusting the stocking rate to produce either a 3 cm or 9 cm sward height (measured weekly).

### Life-history of *Cirsium vulgare*

From 1987 to 1992 the abundance and size-distribution of *C. vulgare* rosettes in each paddock were monitored in the second week of April. Survival of various life-history stages and fecundity was also determined in each paddock. Details of these measurements and the plant's life-history are given in Bullock et al. (1994a), a summary of which is provided below and in Fig. 1.

*C. vulgare* is a monocarpic perennial with size-dependent survival and flowering rates. Seedling emergence occurred in early spring (January-April) and was gap-dependent. Three rosette size-classes were recognised: small rosettes (< 10 cm diameter) which die or become medium (10–20 cm) or large rosettes (> 20 cm) by the next year. Medium rosettes were over 1 year old at the census point and died, stayed as medium rosettes or became large rosettes by the next year. Neither small nor medium rosettes flowered in the same year. Large rosettes could flower monocarpically in the same year

Table 1. Design of the grazing experiment

Summer 3 cm	Summer 9 cm		
	Treatment	Winter	Spring
A	–	–	–
B	–	+	+
C	+	–	–
D	+	+	+

A minus sign indicates no grazing during the relevant period. All paddocks were grazed in summer to either 3 cm or 9 cm in height

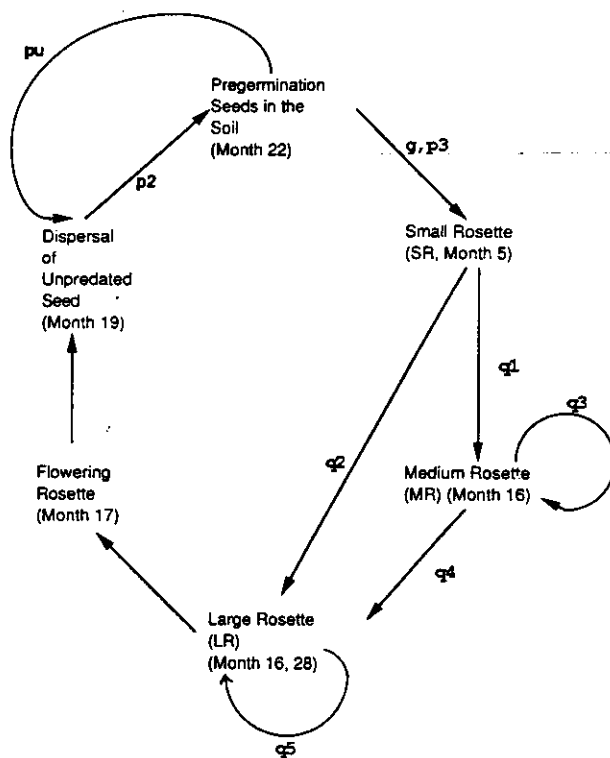


Fig. 1. The life-cycle of *Cirsium vulgare*.  $p_2$ ,  $p_0$  and  $p_3$  refer to the probability of survival of seed before the germination period, seed after the germination period and seedlings to small rosettes respectively;  $g$  indicates the fraction of seeds germinating and  $q_1 - q_5$  refer to the transition probabilities between stages

or die without flowering or remain as large rosettes into the next year. No rosettes regressed to smaller size-classes.

In addition to a size threshold for flowering the proportion of rosettes flowering and the number of flowerheads per plant increased with rosette diameter above the threshold. Seeds were eaten by the larva of the tortricid moth *Eucosma cana* and the percentage of seedheads attacked increased with flowering plant size. Post-dispersal survival of seeds in the soil up to germination and year-to-year survival in the seedbank were measured.

### Model construction

Two versions of a stage-structured model were used, varying in the life-history stage at which density-dependence was incorporated (and therefore varying in the assumed underlying mechanism). The model symbols are summarized in Appendix 1 and related to the life-cycle in Fig. 1.

The model can be divided into two components:

**Seed production, germination and seedling survival.** Immediately after seed-set the number of new viable seeds in year  $t$  ( $N_t$ ) was given by the number of large rosettes in that year ( $L_t$ ), the fraction flowering ( $f$ ) and the average viable seed production of those plants ( $s$ ):

$$N_t = f s L_t \quad (1)$$

The viable new seed was assumed to enter a seed bank with surviving ungerminated seed ( $U$ ) from the previous year. No distinction was made in the model between old seed which had survived for 1 year or more and new seed. The seed in the bank had three fates over the next year – either to germinate or to stay in the seed bank or to die. Any ungerminated seed which remained in the seed bank

was assumed to have a certain probability of survival through the year ( $p_1$ ):

$$U_{t+1} = (1 - \theta_t) p_1 (N_t + U_t) \quad (2)$$

The probability of survival,  $p_1$ , was composed of seed survival prior to germination ( $p_2$ ) and seed survival following the germination period ( $p_3$ ). It was assumed that all the seed in the bank was near the surface so that gaps in the vegetation were experienced in a similar way by new and old seed.

The fraction of seed germinating in year  $t$  ( $g_t$ ) was mainly determined by the proportion of bare ground which was known to be dependent on grazing (Silvertown and Smith 1989; Bullock et al. 1994a). In version 1 of the model it was assumed that  $g$  was also a function of the number of all *C. vulgare* rosettes; thus a density-dependent mechanism was assumed, operating with intensity  $a$ , in which rosettes were envisaged to exponentially reduce the fraction of ground available for germination, and therefore the fraction of seeds able to germinate, from a maximum of  $m$ :

$$g_t = m \exp[-a(S_t + M_t + L_t)] \quad (3)$$

For simplicity, rosettes of all size-classes were assumed to reduce  $m$  equally (Eq. 3). The number of small rosettes ( $S$ ) following seed-set depended on the probability of seed surviving prior to germination ( $p_2$ ), the fraction of seed germinating ( $g$ ) and the probability of seedling survival from germination to small rosettes ( $P_3$ ):

$$S_{t+1} = g_t p_2 p_3 (N_t + U_t) \quad (4)$$

In version 2 of the model,  $g$  was assumed to be equal to  $m$  and density-dependent mortality was assumed to occur amongst seedlings. Therefore  $p_3$  was now reduced from a maximum value,  $p_{\max}$ , by the number of germinated seed:

$$p_3 = p_{\max} \exp[-\alpha m (N_t + U_t)] \quad (5)$$

Note that  $p_3 = p_{\max}$  in version 1 of the model.

**Survival of rosettes.** Medium rosettes in year  $t+1$  ( $M_{t+1}$ ) were derived from medium rosettes in year  $t$ , with a transition probability of  $q_3$ , and from small rosettes in year  $t$ , with a transition probability of  $q_1$ :

$$M_{t+1} = (q_1 S_t) + (q_3 M_t) \quad (6)$$

Large rosettes in year  $t+1$  were derived from small, medium and nonflowering large rosettes in year  $t$  with transition probabilities of  $q_2$ ,  $q_4$  and  $q_5$  respectively:

$$L_{t+1} = (q_2 S_t) + (q_4 M_t) + (q_5 L_t) \quad (7)$$

### Detection of density dependence

Linear regression methods were employed for detecting and determining the values of the density-dependent parameters. These were modifications of the standard Ricker equation regression [ $\ln(N_{t+1}/N_t)$  against  $N_t$ ] in which the degree of density dependence was given by the gradient of the regression (Turchin 1990). For version 1 of the model, estimation of  $a$  (Eq. 3) required a regression of  $\ln(S_{t+1}/L_t)$  against all rosettes ( $R_t$ , Appendix 2), whilst for version 2 the intensity of density dependence,  $\alpha$  (Eq. 5), was estimated from the slope of the regression of  $\ln(S_{t+1}/L_t)$  against  $L_t$ . (Although it should be noted for version 2 that the slope of the regression is equal to  $\alpha m f s$  - see Appendix 2).

## Results

### Detection of density dependence and estimation of parameter values

Estimates of the parameter values for both versions of the model are given in Appendix 3 based on field data

**Table 2.** Values of  $\lambda$  across the eight treatments (A-H see Table 1) in two blocks, based on simulation over 50 generations with no density dependence ( $a=0$ )

	Treatment							
	A	B	C	D	E	F	G	H
Block 1	0.601	0.917	1.587	2.606	0	0.610	1.449	2.432
Block 2	1.340	1.476	1.245	2.475	0.769	0.959	1.517	2.358

**Table 3.** Magnitude of slope of regression of  $\ln(S_{t+1}/L_t)$  against  $R_t$  ( $a$ , version 1) and  $\ln(S_{t+1}/L_t)$  against  $L_t$  ( $\alpha m f s$ , version 2) for all treatments except E

#### Model version 1

Treatment	$a$	$r^2$	$P$ (6 df)
A	0.0742	0.09	NS
B	0.0075	0.25	NS
C	0.0277	0.52	<0.05
D	0.0097	0.39	<0.1
F	0.0156	0.21	NS
G	0.0346	0.58	<0.05
H	0.0187	0.34	NS (0.13)

#### Model version 2

Treatment	$\alpha m f s$	$r^2$	$P$
A	0.1667	0.15	NS
B	0.0073	0.18	NS
C	0.0169	0.18	NS
D	0.0038	0.03	NS
F	0.1667	0.15	NS
G	0.0258	0.21	NS
H	0.0068	0.03	NS

Treatment replicates were combined to give a sample size of 8 (the number of large rosettes was not recorded in the first year). All slopes were negative except for version 2, treatment G NS,  $P > 0.1$

The data are shown in Fig. 2 for version 1 treatments C, D, G and H

reported in Bullock et al. (1994a). These values were initially used in a density-independent simulation ( $a=0$ ) of the model to generate values for the finite rate of increase ( $\lambda$ , Table 2).

In order to examine the effects of grazing treatment on the regression-estimated values of  $a$ , the two treatment blocks were combined (Table 3) giving eight comparisons of  $\ln(S_{t+1}/L_t)$  against  $R_t$  (four from each treatment replicate; the proportion of large rosettes was not recorded in the first year). Treatment E was omitted from the analysis because in 6 of the 12 censuses there were no plants present.

For version 1 treatments C and G provided the best evidence for density-dependence (both values of  $a$  significantly greater than 0,  $P < 0.05$ , Table 3, Fig. 2) with treatment D marginally non-significant ( $P < 0.1$ ). In contrast, none of the  $\ln(S_{t+1}/L_t)$  against  $L_t$  regressions (version 2 of the model) were significant.

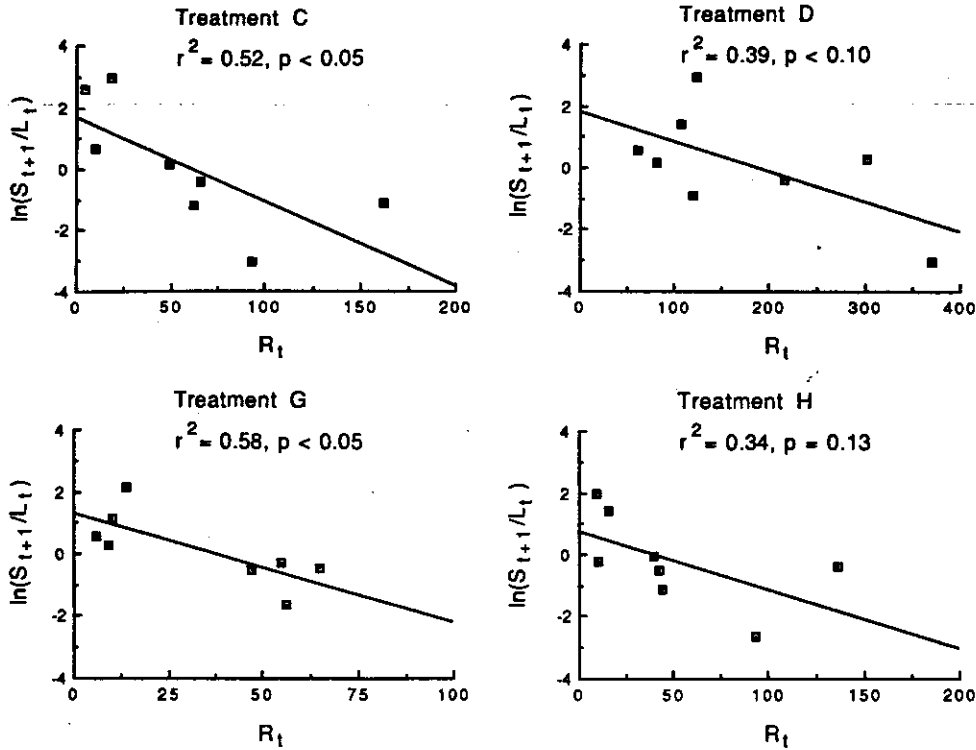


Fig. 2. Linear regressions of  $\ln(S_{t+1}/L_t)$  against  $R_t$  for treatments C, D, G and H in block 1 and 2 of the experiment (Table 1). The  $r^2$  values and significance level (6 *df*) are given for each regression. The full set of relevant regression data is given in Table 3

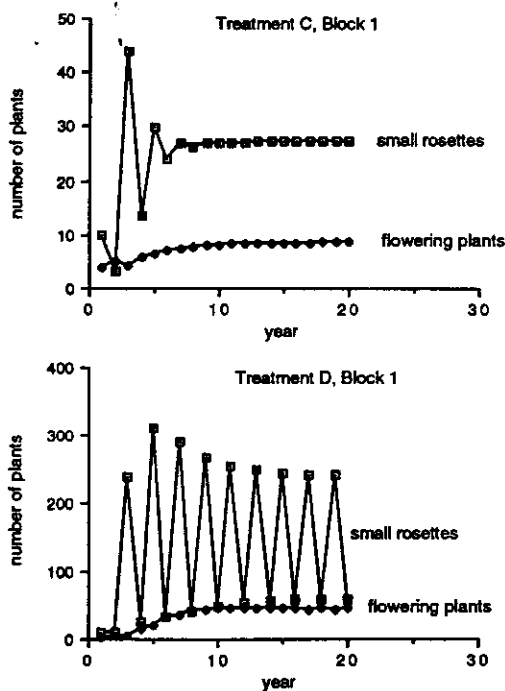


Fig. 3. The population dynamics of *Cirsium vulgare* under different grazing conditions. The dynamics of small rosettes (< 10 cm) and flowering plants are depicted for treatments C and D in Block 1. The simulations began with 10 rosettes in each of the three size-classes. The values at equilibrium are given in Table 4

#### Range of possible dynamics with field-estimated density dependence

The exploration of biologically possible dynamics focused on treatments C, D, G and H as these were shown

Table 4. The predicted number of new seed ( $N$ ), ungerminated seed ( $U$ ), small and medium rosettes ( $S$ ,  $M$ ) and flowering plants ( $F$ ) at equilibrium under density-dependent conditions (version 1 of model, density-dependent parameter values given in Table 3)

	Treatment					
	C	D <sub>1</sub>	D <sub>2</sub>	G	H <sub>1</sub>	H <sub>2</sub>
Block 1						
N	3477	53714	55945	5539	21452	20569
U	60.2	1044	1062	101.8	397	401
S	27.2	60.9	239.6	17.84	37.2	110.1
M	8.73	66.1	30.5	5.73	30.9	16.4
F	8.52	46.4	44.5	5.34	23.4	22.5
Block 2						
N	1749	50868	52346	1885	15867	15847
U	30.1	982	990	33.6	303	303
S	13.4	80.6	197	19.9	65.1	67.6
M	4.30	56.1	33.0	6.37	21.6	21.1
F	3.04	42.5	41.3	6.18	20.0	20.0

$D_1$ ,  $D_2$  and  $H_1$ ,  $H_2$  refer to the two points in the limit cycle in these treatments

Examples of the dynamics are given in Fig. 3

to have values of  $a$  significantly different from 0 (or close to significance – the regression for treatment H gave  $P=0.13$  but was included for comparison). Results of simulations with version 1 of the model under density-dependent conditions, employing the parameter values in Appendix 3 (and therefore the  $\alpha$  values in Table 2), are given in Table 4 and Fig. 3.

For version 1, treatments D and H produced two-point limit cycles for each replicate (Table 4, Fig. 3), which were most pronounced at the small and medium

rosette stages. For example, the small rosettes fluctuated almost four-fold in numbers in treatment D, block 1, compared with virtually no change amongst the large rosettes (Fig. 3). The other two treatment conditions (C and G) resulted in a stable equilibrium in both blocks.

Exploration of the parameter space of  $a$  and  $\lambda$  for version 1 revealed that only  $\lambda$  had an effect on the dynamics. Two-point limit cycles occurred above a value of approximately  $\lambda = 2.05$  up to the observed maximum of  $\lambda = 2.6$  (in fact, two-point cycles still occurred at  $\lambda = 3.0$ ) over the whole range of estimated  $a$  values (0.007–0.035, Table 3). Although none of the regressions were significant for version 2, a similar exploration of the parameter space was undertaken. This again revealed a strong dependence on  $\lambda$  and, in contrast to version 1 of the model, a much larger stable equilibrium region, which went well beyond the maximum observed value of  $\lambda = 2.6$  (it was still stable at  $\lambda = 3.0$ ).

#### Comparison of model stage-class distribution and equilibrium with observed field values

It was only possible to make a comparison using version 1 of the model as none of the density-dependent parameter estimates were significant for version 2. There was a significant positive relationship ( $r^2 = 0.81$ ,  $P < 0.001$ ) between the observed mean rosette numbers (per treatment

replicate) and the predicted equilibrium values from version 1 of the model (Table 5). In all cases the model predicted a higher proportion of large ( $\geq 10$  cm) than small rosettes (Table 6). Although only two out of eight field observations supported this trend, five of the eight comparisons between predicted and observed were not significantly different from each other. Treatments 1D, 2C and 2D all showed significant differences ( $G = 22.4$ , 4.86 and 23.5 respectively, 1 *df*).

#### Discussion

The use of stage-structure in population models, combined with density dependence, leads to important results concerning the stability of the field populations whose dynamics we attempt to understand (Guckenheimer et al. 1976; de Kroon et al. 1987). To illustrate the effect of population structure consider the simple Ricker model of  $N_{t+1} = \lambda N_t \exp(-aN_t)$  in which it can be shown that two-point limit cycles begin at  $\ln(\lambda) = 2.0$  or  $\lambda = 7.39$ . If such a model were to be used for the *Cirsium vulgare* populations (e.g. with  $N$  giving the number of all rosettes), the predicted dynamics, given the field estimated values of  $\lambda$  (Table 2), would all be well within the stable equilibrium region. In contrast, version 1 of the present model, with its inherent time-lags, reduced the critical value of  $\lambda$  at which two-point cycles began to about 2.05, resulting in populations in two of the grazing treatments (D and H) falling within the two-point limit cycle parameter space. This result is important in the context of previous debate concerning the likelihood of plant populations showing limit cycles or chaotic dynamics (Watkinson 1980; Pacala 1986; Symonides et al. 1986; Silvertown 1991; Rees and Crawley 1991). Unlike the present study, these authors focused on annual plants for which the Ricker model would be appropriate. In this debate the role of self-thinning and seed dormancy has been considered, revealing that both can reduce the likelihood of limit cycles and chaos (Watkinson 1980; Pacala 1986; Thrall et al. 1989). In the present model there was no explicit description of self-thinning and seed dormancy was included in a very simplified form (Eq. 2). The model output suggests that seed dormancy is relatively unimportant in *Cirsium vulgare* dynamics (Table 4) and an elasticity analysis by Bullock et al. (1994a) showed that seed dormancy had little effect on  $\lambda$  in these popula-

**Table 5.** Comparison of the observed mean number of all rosettes (per treatment replicate) with the equilibrium number from version 1 of the model

Treatment	Block 1		Block 2	
	Observed	Model	Observed	Model
A	8.5	0	—	—
B	7.0	0	167	156
C	99.2	57.2	70.7	48.1
D	240	345	259	318
E	—	—	—	—
F	33.7	0	27.7	0
G	26.5	42.0	42.8	42.6
H	38.0	157	62.5	155

For treatments D and H the model value was the mean of the two-point limit cycle equilibria  
3 of the 16 comparisons were ignored (the two E values as before and A, Block 2, because it had two 0 values)

**Table 6.** Comparison of observed (obs) and predicted (pred) numbers of different sized rosettes in treatments C, D, G and H in experimental blocks 1 and 2

	C pred	C obs	D pred	D obs	G pred	G obs	H pred	H obs
Block 1								
< 10 cm	27.2	64.4	150	163	17.8	16.4	73.7	113
$\geq 10$ cm	30.0	51.4	195	96.4	24.2	14.0	84.1	92
Block 2								
< 10 cm	13.4	34.2	139	179	19.9	22.2	66.4	139
$\geq 10$ cm	34.7	37.4	180	104	22.6	21.0	88.1	152

Two size-classes were compared (< 10 cm, S and  $\geq 10$  cm, M and L)

tions. However, a definitive statement on the role of dormancy can only be given when a more realistic algorithm for ungerminated seed has been developed.

The treatments which resulted in a prediction of unstable dynamics (D and H) were those which were grazed in both spring and winter (Table 1) and in which the sward was expected to be most open. Under these treatment conditions  $\lambda$  was at its highest, primarily due to the increased probability of seedling survival ( $p_3$ ). In fact,  $p_3$  served as a good predictor of  $\lambda$  ( $\lambda = 0.431 + 3.301p_3$ ,  $r^2 = 0.783$ ). For two-point cycles the greatest likelihood of detection came not from large rosettes but from the small and medium rosettes (Table 4, Fig. 3). This showed that it is important to examine all stages of the life-history of the plant to maximize the chance of discovering unstable dynamics.

De Kroon et al. (1987) undertook similar analyses for model populations of *Hypochaeris radicata*. In their study, mowing was the management regime and density dependence was incorporated at both germination and seedling establishment, which were in turn functions of gaps in the vegetation. The density dependence in the present study has only been incorporated at one point in the life-cycle at a time (unlike de Kroon et al. 1987 and Law's model in Watkinson 1987) in order to compare the effects on population behaviour.

An alternative method of incorporating density dependence during germination would have been to use a safe-site model (e.g. Klinkhamer and de Jong 1989; Silvertown and Smith 1989). Such models assume a particular distribution of seed amongst a certain number of safe sites in which germination is guaranteed for a small number of the seeds in a safe site. Version 1 of the present model was clearly similar to a safe-site model and might be mechanistically described in such terms. A quantitative comparison with the earlier *Cirsium vulgare* model of Silvertown and Smith (1989) is impeded by the difficulty of determining the density and size of safe sites (gaps for germination) in the field. Therefore one either makes assumptions about the minimum size of gaps for germination, the density of those gaps and the distribution of seed, or they are experimentally determined in the field. This then allows a conversion from minimum gap size and gap density to fraction of space available for germination and fraction of seeds germinating, i.e. parameters  $m$  and  $g$  in the present model.

The fact that only version 1 of the model produced significant estimates of density dependence might lead one to believe that version 1 encapsulates a more appropriate model of density dependence compared to version 2. However, it is possible that the particular regression used for version 1 could also be appropriate to an entirely different density-dependent mechanism and one should be cautious about the link between the significance of the regression and the assumed mechanism in the field.

Although none of the density-dependent regressions were significant for version 2, exploration of the parameter space of  $\lambda$  and  $\alpha$  was justified in that  $\lambda$  was the determinant of the switch from a stable equilibrium to other types of dynamics ( $a$  or  $\alpha$  contributes to the equilib-

rium value). Thus, in order to compare versions 1 and 2 of the model, one only has to assume existence of density-dependence in version 2 (however small the values of  $a$  or  $\alpha$ ). This comparison revealed the relative stability of version 2 of the model. This is perhaps surprising when one considers the similarity of the two versions. Manipulation of the equations (ignoring the relatively small component of  $U_t$  compared with  $N_t$ , Table 4) reveals the primary difference in the two versions:

$$\begin{aligned} S_{t+1}/F_t &= y \exp(-a R_t) \text{ version 1} \\ S_{t+1}/F_t &= y \exp(-b N_t) \text{ version 2} \end{aligned}$$

where  $y = m p_2 p_{\max} s$  and  $b = \alpha m$

In version 1 the number of small rosettes in year  $t+1$  produced per flowering plant in year  $t$  was reduced by all rosettes in year  $t$ ; whilst in version 2 the equivalent per capita production of small rosettes in year  $t+1$  was reduced by the number of new seeds in year  $t$ . Thus, only the large rosettes in year  $t$  contributed to the density dependence (by a certain fraction flowering and producing seed) in version 2, whereas all rosette stages contributed to the density dependence in version 1. So, for these two model versions, density-dependence effects from the larger number of stages was more destabilizing. From these results it is clear that a thorough study of the way in which stage structuring can interact with assumed types of density dependence is required, and, linked to that, an assessment undertaken in the field of the existence and intensity of these assumed density-dependent responses.

There are two related applications of the models presented in this paper. First, they can be used to predict the relative levels of *C. vulgare* infestation in fields under different grazing management treatments. Second, they can be used to predict population dynamics in any one field, given a certain management regime. It is difficult (and probably not sensible) to test the efficacy of the latter in the present case because of the short time-series. However, it has been possible to consider the relationship between observed mean population size (per treatment) and predicted equilibrium population size. In making this comparison it should be noted that all the early stage parameter values used to quantify the model (Appendix 3, Table 2) were based on data independent of the observed rosette numbers. The population equilibria in version 1 of the model explained over 80% of the between-treatment variation in mean observed numbers of *C. vulgare*. The ratios of small to large rosettes predicted by the model were less satisfactory than the predictions of total rosette density. In three out of eight cases the predicted ratio of small:large rosettes was significantly different from that observed in the field. The greatest departure from prediction came in the hardest grazed plots (1D and 2D, Table 6), where the model predicted a higher proportion of large rosettes whilst the observed pattern was one of a higher proportion of small rosettes. These were also the only two cases where the observed ratio of small:large rosettes was significantly different from 1:1. In other words, the values of large rosette survival were too high. The most obvious explanation of this are direct effects of grazing which were not incor-

porated into the treatment parameter values. Thus this apparent failing of the model can be turned into a virtue by identifying an area of model parameterization where more fieldwork may be required.

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**Appendix 1.** Summary of the symbols and abbreviations used in the two versions of the model

#### Stage variables

<i>N</i>	new viable seed
<i>U</i>	ungerminated seed
<i>S</i>	small rosettes
<i>M</i>	medium rosettes
<i>L</i>	large rosettes
<i>F</i>	flowering plants
<i>R</i>	all rosettes

#### Fecundity and mortality parameters

<i>s</i>	average viable seed production per plant
<i>p</i> <sub>1</sub>	probability of survival of ungerminated seed throughout year ( <i>p</i> <sub>u</sub> , <i>p</i> <sub>2</sub> )
<i>p</i> <sub>2</sub>	probability of seed surviving before germination
<i>p</i> <sub>u</sub>	probability of seed survival after germination period
<i>p</i> <sub>3</sub>	probability of seedling survival from germination to small rosettes ( <i>p</i> <sub>max</sub> - maximum value of <i>p</i> <sub>3</sub> )

#### Transition probabilities

<i>q</i> <sub>1</sub>	small to medium rosettes
<i>q</i> <sub>2</sub>	small to large rosettes
<i>q</i> <sub>3</sub>	medium to medium rosettes
<i>q</i> <sub>4</sub>	medium to large rosettes
<i>q</i> <sub>5</sub>	large to large rosettes

#### Other parameters

<i>a</i> , <i>a</i>	intensity of density-dependence (versions 1 & 2)
<i>λ</i>	finite rate of population increase
<i>f</i>	fraction of large rosettes flowering
<i>m</i>	maximum fraction of seeds able to germinate
<i>g</i>	actual fraction of seeds germinating

**Appendix 2** i. Derivation of regression of  $\ln(S_{t+1}/L_t)$  against all rosettes (*R*<sub>*t*</sub>) for estimation of intensity of density dependence in version 1 of model

$$g_t = m \exp(-aR_t) \quad (3)$$

Substitute for *g*<sub>*t*</sub> in Eq. 4:

$$S_{t+1} = m \exp(-aR_t) p_2 p_3 (N_t + U_t) \quad (4a)$$

Given *U*<sub>*t*</sub> is very low compared with *N*<sub>*t*</sub> (Table 4) *U*<sub>*t*</sub> is ignored and *m*, *p*<sub>2</sub> and *p*<sub>3</sub> combined as *p*<sub>4</sub>:

$$S_{t+1} = p_4 \exp(-aR_t) N_t \quad (5a)$$

Substitute for *N*<sub>*t*</sub> in 5a from Eq. 1:

$$S_{t+1} = p_4 \exp(-aR_t) f s L_t \quad (6a)$$

Combine *p*<sub>4</sub>, *f* and *s* as *p*<sub>5</sub>, divide by *L*<sub>*t*</sub> and take logarithms:

$$\ln(S_{t+1}/L_t) = \ln(p_5) - aR_t \quad (7a)$$

ii. Derivation of regression of  $\ln(S_{t+1}/L_t)$  against *L*<sub>*t*</sub> for version 2  
From Eqs. 3 and 5

$$g_t = m \text{ and } p_3 = p_{\max} \exp[-am(N_t + U_t)]$$

Ignoring *U*<sub>*t*</sub> and substituting Eq. 5 into 4:

$$S_{t+1} = m p_2 p_{\max} \exp(-amN_t) N_t \quad (8a)$$

Substitute RHS of Eq. 1 for *N*<sub>*t*</sub>:

$$S_{t+1} = m p_2 p_{\max} \exp(-amf s L_t) f s L_t \quad (9a)$$

Combine *m*, *p*<sub>2</sub>, *p*<sub>max</sub>, *f* and *s* (*p*<sub>6</sub>), divide by *L*<sub>*t*</sub> and take logarithms:

$$\ln(S_{t+1}/L_t) = \ln(p_6) - amf s L_t \quad (10a)$$

**Appendix 3.** Field parameter estimates from different grazing treatments (A–H, listed in Table 1), following Bullock et al. (1993a). Explanation of the parameter abbreviations (*s*, *m*, *p*<sub>3</sub>, *q*<sub>1</sub>–*q*<sub>5</sub> and *f*) are given in Appendix 1. Blocks 1 and 2 refer to the two blocks in the grazing experiment. *p*<sub>2</sub> and *p*<sub>u</sub> were found to be unaffected by the treatments and taken as constants (*p*<sub>1</sub> = *p*<sub>2</sub> × *p*<sub>u</sub> = 0.24 × 0.08)

#### Block 1

	1A	1B	1C	1D	1E	1F	1G	1H
<i>s</i>	274	2888	408	1207	1193	727	1038	916
<i>m</i>	0.113	0.131	0.556	0.431	0.063	0.069	0.256	0.488
<i>p</i> <sub>3</sub>	0.167	0.095	0.281	0.594	0.0 <sup>1</sup>	0.182	0.220	0.487
<i>q</i> <sub>1</sub>	0.084	0.084	0.246	0.246	0.084	0.084	0.246	0.246
<i>q</i> <sub>2</sub>	0.056	0.056	0.164	0.164	0.056	0.056	0.164	0.164
<i>q</i> <sub>3</sub>	0.15	0.15	0.234	0.234	0.15	0.15	0.234	0.234
<i>q</i> <sub>4</sub>	0.35	0.35	0.546	0.546	0.35	0.35	0.546	0.546
<i>q</i> <sub>5</sub>	0.473	0.312	0.567	0.652	0.576	0.312	0.671	0.586
<i>f</i>	0.5	0.67	0.40	0.31	0.39	0.67	0.29	0.38

<sup>1</sup> None of the seedlings survived to form small rosettes

#### Block 2 (values of *q*<sub>1</sub>–*q*<sub>4</sub> as for Block 1)

	2A	2B	2C	2D	2E	2F	2G	2H
<i>s</i>	1672	985	576	1231	1190	1360	305	794
<i>m</i>	0.375	0.456	0.456	0.469	0.113	0.163	0.381	0.438
<i>p</i> <sub>3</sub>	0.217	0.343	0.260	0.467	0.111	0.192	0.492	0.700
<i>q</i> <sub>5</sub>	0.586	0.473	0.851	0.652	0.577	0.709	0.586	0.662
<i>f</i>	0.38	0.50	0.10	0.31	0.39	0.25	0.38	0.30

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