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Population dynamics and the effect of disturbance in the monocarpic herb *Carlina vulgaris* (Asteraceae)

Per Löfgren, Ove Eriksson & Kari Lehtilä

Löfgren, P., Eriksson, O. & Lehtilä, K., Department of Botany, Stockholm University, SE-106 91 Stockholm, Sweden

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The population dynamics of short-lived monocarpic perennials are often considered to be influenced by disturbance, providing areas of bare soil. We studied demography of the monocarpic herb *Carlina vulgaris* (Asteraceae), with special emphasis on the effect of disturbance. We used deterministic and stochastic transition matrix models based on the data from eight local populations to analyse the population dynamics. In addition, a field experiment was carried out to determine how disturbance and seed availability affect recruitment. Recruitment of *C. vulgaris* was limited by a combination of seed and microsite availability. Only populations subjected to high disturbance have a positive growth rate. Moderately sized populations are likely to be persistent when the disturbance intensity is high.

Key words: biennials, *Carlina vulgaris*, disturbance, population dynamics, population matrix models, PVA, recruitment

INTRODUCTION

For many short-lived monocarpic perennials, often called as “biennials”, disturbance of the environment is often important for population dynamics, providing areas of bare soil (van der Meijden *et al*. 1992) or lower turf height (Lennartsson 1997). Absence of disturbance in late successional stages is fatal for these plants and most of their habitats are therefore only temporarily suitable. Thus, biennials are often considered to be characteristic of early successional habitats in which they remain for only a single or a few generations (e.g., de Jong & Klinkhamer 1988). As a consequence, their persistence in a regional scale depends on the continuous creation of new sites that are suitable for population development. Populations of biennials may persist for a long period in habitats such as grasslands where there is a high degree of small-scale disturbance by grazing or trampling. Biennials show a wide range of population dynamics. Van der Meijden *et al*. (1992) hypothesized the existence of three main types of biennials (transient, fugitive and persistent) arranged on a scale from short-lived to long-lived populations. Transient and fugitive biennials develop typical metapopulations while persistent species show more of the characteristics of remnant population dynamics (Eriksson 1996). Some have a strict two-year life-span while most species delay flowering from one to several years (van der Meijden *et al*. 1992, Klinkhamer *et al*. 1996). Delayed germination or delay of flowering may permit a monocarpic organism to bridge over years with failing reproduction.

We studied demographic aspects of the short-lived perennial plant species *Carlina vulgaris* (Asteraceae), with special emphasis on the influence of disturbance on recruitment and population dynamics. The distribution of *C. vulgaris* is related to soil moisture conditions for seed germination (Klinkhamer *et al*. 1996). Moreover, the development of local populations of *C. vulgaris* varies greatly among habitats. Populations situated in sand dune habitats show fluctuating patterns whereas populations found in grasslands, which are more homogeneous habitats with fairly constant management regimes, have a more stable population dynamics (van der Meijden *et al*. 1992). Deterministic changes in demographic parameters caused by disturbance, in combination with environmental stochasticity, provide one way to study population dynamics in both time and space (Schemske *et al*. 1994). Such studies are also relevant to conservation biology. We used this approach in an experimental investigation of how disturbance and seed availability affect recruitment under field conditions.

The following questions were addressed: (1) How variable are natural populations of *Carlina vulgaris* with respect to size, age distribution, population growth rate (λ) and elasticities? (2) Is recruitment limited by seed availability and/or disturbance? (3) How are population growth and population survival influenced by population size and degree of disturbance?

METHODS

Natural history *Carlina vulgaris*

Carlina vulgaris is a short-lived monocarpic species inhabiting sand dunes and dry grasslands. The flowering of the plant is determined by the size and not by the age of the individual. Flowering can occur during the first year under favourable conditions, but more commonly the plants will flower in their second year or later (Klinkhamer *et al*. 1991).

In Sweden, flowering starts in late July and lasts until September. Every individual plant carries one to several flower heads. Morphologically the propagules are achenes, but we use the term seed for convenience. Most of the seeds are retained in the flower heads until the heads open on sunny days in autumn or winter. There is little information available about dispersal of the seeds, but the average dispersal distance is most likely very short (a few meters). Seeds germinate in the spring. Studies showed that *Carlina vulgaris* is not very likely to build up large below-ground seed banks because *C. vulgaris* was not found in the seed bank of the study area (Eriksson & Eriksson 1997).

Field study

The study was performed in semi-natural pastures with long continuity of grazing, located about 60 km SSW of Stockholm, in south-east Sweden. Populations were found in two separate areas (Långmaren, 58°50´N, 17°24´E, and Nyckelby, 58°50´N, 17°23´E), situated about one kilometer apart.

The study consisted of two parts; a recruitment experiment and a population study based on demographic data in unmanipulated field populations. In the recruitment experiment, sixteen plots were laid out in the beginning of May 1997 at one of the sites. Each plot contained four subplots (30 × 30 cm) that were treated in the following ways: (1) disturbance and seed addition (100 seeds) of *Carlina vulgaris*, (2) disturbance and no seed addition, (3) no disturbance, and seed addition (100 seeds) of *C. vulgaris* and (4) no disturbance and no seed addition. In the disturbed areas all above-ground vegetation was removed. Eight of the plots were situated within established *C. vulgaris* populations while the other eight plots were placed in similar habitats where *C. vulgaris* did not occur. The number of seedlings was recorded in June and the survival in the end of August.

In the demographic study, eight populations of different size were chosen in June 1997, numbered as 1–6 for the Långmaren populations and 7–8 for the Nyckelby populations. The distance between the neighbour populations ranged from 50 to a few hundred metres in each area. Seven to ten sample plots (1 m^2) were laid out randomly in all the populations. Rosettes and seedlings were individually tagged with small numbered flags and their size was measured. Rosette diameter times leaf number was used as an index of the size of the rosettes. In the middle of August, all tagged individuals in the plots were again measured and the rosettes which had started flowering were noted. The total number of individuals in different life-history stages (*see* below) was counted in the sampled plots.

Formulation of transition matrix models

Since this study was carried through only one season, we made three basic assumptions in order to carry out a demographic analysis. First, we assume that the rosette size in June gives a reasonable estimate of the rosette size at the end of the previous growing season. The second assumption is that the number of dead rosettes with remnants of flowers gives a good representation of the number of flowering rosettes the previous year. Dead rosettes of *Carlina vulgaris* are very persistent (O. Eriksson & P. Löfgren, personal observation). Third, winter mortality of rosettes is assumed to be of little importance. The rosettes of *C. vulgaris* have been found to have high survival probability (Klinkhamer *et al.* 1996) and high overwintering survival (Kemppainen 1990).

The demographic data were analysed by transition matrices (Caswell 1989). These analyses yield the stable stage distribution, the population growth rate (λ) and sensitivities (s_{ij}). Sensitivity measures how much λ is influenced by a change in a matrix element a_{ij} and it can be defined as the partial derivate of λ with respect to the element a_{ij} of the projection matrix (McDonald & Caswell 1993):

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \tag{1}$$

However, since proportional values are a more useful measure than absolute values when comparing populations, elasticies were used instead of sensivities. Elasticity is defined as the proportional change in λ resulting from a proportional change in a_{ij} (de Kroon *et al.* 1986):

$$e_{ij} = \frac{a_{ij} s_{ij}}{\lambda} \tag{2}$$

All *Carlina vulgaris* individuals were classified into three life stages: (1) small vegetative rosettes (size index 45 or less), (2) large vegetative rosette (size index 46 or more), and (3) flowering plants. The size below which individuals did not appear to flower was chosen as a limit between class 1 and 2 (cf. Ehrlén 1995). Seedling fate was followed by labelling seedlings in the early summer and following their fate throughout the season. Seedlings were included in small vegetative rosettes, as they grew to that size already in the early summer. On the other hand, seedlings never flowered or reached the size of large rosettes in our populations.

Transition probabilities between the stages (Fig. 1) for one time interval were calculated from the field data for each of the eight populations. The fecundities (F_1-values) were calculated by dividing the number of naturally occuring seedlings in the early summer × summer survival by the number of flowering plants the previous season. F_2-values (transition from flowering plants directly to large rosettes) are not shown in tables and figures, since they were always zero. The flowering plants were thus at least three years old.

Simulation of temporal variation

The demographic data were analysed both by projections of each transition matrix (to examine the spatial variation in λ) and by stochastic simulations (to examine the temporal development of the populations). In the stochastic simulations, the spatial variation between the populations was assumed to represent variation between years. Since the locations of the populations had different moisture conditions, the spatial variation could be assumed to represent the variation of weather conditions and grazing intensity between years. The eight matrices were assigned equal probabilities of sampling in the simulation process. For

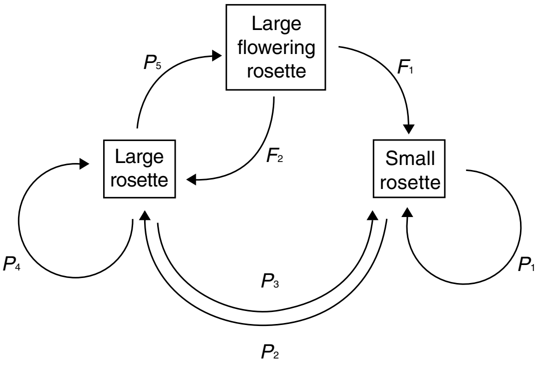

Fig. 1. Life-cycle graph of *Carlina vulgaris* with transition probabilities (P_i) and fecundities (F_i) between life-stages.

each time step, one of the eight matrices was randomly selected (since they are given equal probabilities), giving a temporal variation in population growth. The simulations yield stationary distributions of population structures to which all populations converge (Caswell 1989). The estimated eight local population sizes, and the proportion of stages within these, were used as initial values in the simulations, resulting in eight different simulations. All simulations were repeated 50 times for periods of either 10 or 50 years (in the same way as described below in "Effects of disturbance").

Effects of disturbance

We used vegetation height as an indicator of disturbance, since cattle grazing and trampling are the most important disturbing factors in the study area and both have a strong impact on height of the vegetation. All the sampled plots in the eight populations were assigned to a disturbance category based on the vegetation: (1) Closed: the vegetation is higher than the rosettes of *Carlina vulgaris*; (2) Medium: the vegetation is of approximately the same height as the rosettes of *C. vulgaris*; and (3) Open: the vegetation is lower than the rosettes of *C. vulgaris*.

The model populations in the simulation of disturbance effect were created in the following way. From each of the eight populations, only one plot from every disturbance category was selected, if they were present. This was done in order to avoid pseudoreplication. All the plots from the same category were then pooled together. As in the other simulations, the data were analysed both by deterministic matrix models and by stochastic models.

The simulations were performed with different initial population sizes, one for each of the natural population sizes and with five different degrees of disturbance. In these disturbance regimes the three categories closed/medium/open vegetation were given different probabilities to appear in the simulations (Table 1).

Caswell (1989) presents a method to determine the effect of a certain variable on the population growth rate λ. The effect of disturbance can, thereby, be separated into contributions of different elements of the matrix. The change in each element due to disturbance, $\delta a_{ij(\mathrm{d})}$, is the product of the difference in transition probabilities between disturbed and undisturbed categories, $a_{ij(\mathrm{d})} - a_{ij(\mathrm{ud})}$, and the proportion of individuals in this class that are exposed to disturbance, δd_j.

$$\delta a_{ij(d)} = \delta d_j \left(a_{ij(\mathrm{d})} - a_{ij(\mathrm{ud})} \right) \qquad (3)$$

The contribution from each matrix column is the sum of changes in each matrix element due to disturbance, weighted by the sensitivity of λ to that element. By inserting Eq. 3 into Eq. 1 and rearranging the terms we derive the contribution of disturbance acting on each class to λ.

$$\frac{\delta h}{\delta d_j} = \sum_{i=0}^{k} s_{ij} \left(a_{ij(\mathrm{d})} - a_{ij(\mathrm{ud})} \right) \qquad (4)$$

The effect of disturbance on λ, from a certain class, is thus the sum of contributions due to change in each matrix element of this column. In this analysis the category with vegetation of medium height was chosen as "undisturbed" (because there were very small differences between the closed and medium categories). The category with open vegetation was chosen as "disturbed".

The simulations were evaluated with respect to three different response variables: (i) population growth rate and (ii) probability of survival to 50 years. To obtain (i) the disturbance, regimes were simulated 50 times for a period of ten years while the probabilities of survival (ii) were obtained by repeating the simulation 100 times for 50 years. The population growth rate was approximated by average maximum likelihood estimator of population growth rate (Caswell 1989). The maximum likelihood estimator $\overline{\ln \lambda}$ of $\ln \lambda$ is given by:

$$\overline{\ln \lambda} = \frac{\ln N(T) - \ln N(1)}{T - 1}. \qquad (5)$$

We analyzed the effect of population size and different disturbance regimes on (i) population growth rate and (ii) probability of survival to 50 years.

RESULTS

Seedling establishment

There were no differences in seedling establishment between occupied and unoccupied areas (Wilcoxon Matched Pair Test, $p > 0.05$); and they were, therefore, pooled in the following analysis. In the control plots where no seeds had been sown, only one established seedling was recorded. Disturbance enhanced seedling establishment (Fig. 2). In the undisturbed treatment there were three plots in which no seeds germinated, all found in unoccupied areas. The seedlings had a very high survival during their first season (> 95%). This resulted in very similar values in number of plants counted (of those which were sown in the spring) in June and August.

Transition probabilities

A total of 260 individuals, ranging from 18 to 45 per population, were tagged in the demographic study. In all the populations, the probability of

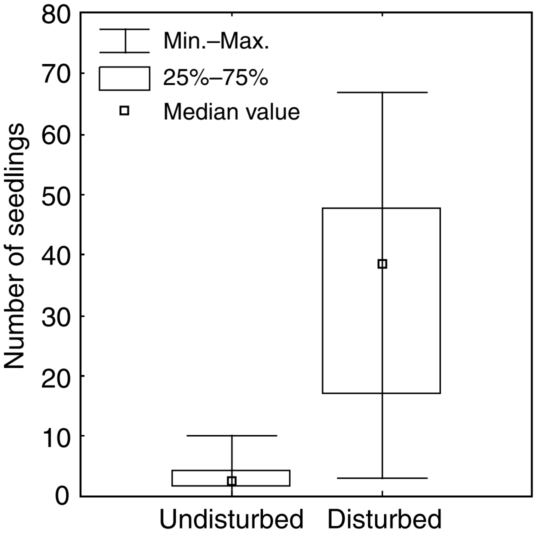

Fig. 2. Number of established seedlings in the recruitment experiment, in disturbed and undisturbed plots where seeds had been added. One hundred seeds of *Carlina vulgaris* were added in both treatments. Wilcoxon Matched Pair Test: $p < 0.05$, $n = 16$.

Table 1. The probabilities of different disturbance categories in a simulation study of disturbance effects on the dynamics of *Carlina vulgaris*.

Disturbance regime	Closed	Medium	Open
1	0.60	0.30	0.10
2	0.40	0.35	0.25
3	0.33	0.33	0.33
4	0.25	0.35	0.40
5	0.10	0.30	0.60

Table 2. Transition probabilities between life-stages in *Carlina vulgaris* in eight natural populations.

Population	Transition					
	F_1	P_1	P_2	P_3	P_4	P_5
1	0.167	0.593	0.407	0	0.444	0.556
2	2.800	0.500	0.250	0	0.222	0.667
3	0.177	0.630	0.370	0	0.182	0.818
4	0	0.500	0.500	0.063	0.438	0.500
5	2.600	0.467	0.467	0	0.273	0.727
6	0.333	0.250	0.750	0	0.429	0.571
7	0.222	0.800	0.067	0.077	0.333	0.539
8	1.000	0.688	0.188	0	0.429	0.571

rosettes to survive through the summer was high (0.75–1.0), whereas in five of the eight populations recruitment F_1 (from flowering individuals to small rosettes) was low (0–0.33) (Table 2). In the other three populations F_1 was 1 or higher. The transition probabilities for small rosettes to remain in the same stage (P_1) and large rosettes to start flowering (P_5) were very high throughout the population data. Retrogression from large to small rosettes (P_3) was only present in two populations, and it occurred to a very limited extent.

Population growth

The analysis of deterministic matrices showed λ-values for the populations ranging from 0.65 to 1.22 (mean = 0.85, SD = 0.19), and the values were above 1 only in two populations (Table 3). There was no significant correlation between the λ-values and the size of the populations (Spearman rank correlation test, $p > 0.05$). The stochastic simulations gave population mean λ-values from 0.877 to 0.887 (mean = 0.882, SD = 0.004). The risk of extinction in 50 years decreased with increasing size of the population (Fig. 3).

Stable stage distributions and elasticities

The stage distribution generated from the simple projection matrices differed strongly from those observed, except in two cases (population 3 and 6; Fig. 4). In three of the populations (number 1, 3 and 8) the small rosettes dominated, followed by the large vegetative rosettes. In population 2 and 7 the situation was the opposite. The last three populations (4, 5 and 6) show some kind of intermediate stage distribution.

Table 3. Population size, population growth rate and the elasticities of P_1 (persistence of small rosettes) of the eight natural populations of *Carlina vulgaris*.

Population	Size (No. ind.)	λ	elasticity (P_1)
1	104	0.754	0.453
2	36	1.044	0.219
3	86	0.754	0.605
4	140	0.651	0.450
5	399	1.224	0.158
6	120	0.777	0.100
7	227	0.830	0.890
8	64	0.792	0.638

In population 2, 5 and 6, most of the elements had similar elasticity values (~ 0.20; data not shown) while in the rest of the populations, the small rosettes staying in the same stage had the highest elasticity values (0.450–0.890; Table 3), compared to the other transition elasticities (< 0.15; data not shown).

Disturbance

The matrices that were constructed from the three categorized classes of disturbance were analysed with respect to λ and elasticities. The transition probabilities in the matrices differed mostly in the elements F_1 and P_2 (Table 4). The probability of remaining as a small rosette (P_1) increased with openness. The production of establishing offspring through seeds (F_1) was high in open habitats but low in areas with vegetation of closed and medium height. Only the open habitat had a population growth rate which was higher than 1 (Table 5). The categories showed the same pattern of elasticities as the eight populations, in that changes in the transition of remaining as a small rosette (P_1) had the largest effect on λ in all categories.

The stochastic simulations showed a distinct effect of disturbance on the population dynamics. The average λ increased from 0.769 to 1.011 with increasing the degree of disturbance (Fig. 5). The survival probability in 50 years could be shown to depend both on degree of disturbance (Fig. 6) and on the size of the population (Fig. 7).

The influence of disturbance was separated into contributions from different elements of the matrices (medium and open categories) and examined for effects on the population growth rate (Table 6). The most important element was the negative effect of vegetation of medium height on seed production and seedling establishment (F_1). The open category did not have any values which distinctly differed from the rest in the matrix. Most of the values in the open category were positive. This means that disturbance has a positive effect on most contributions to population growth rate. In the category with vegetation of medium height most of the values were negative,

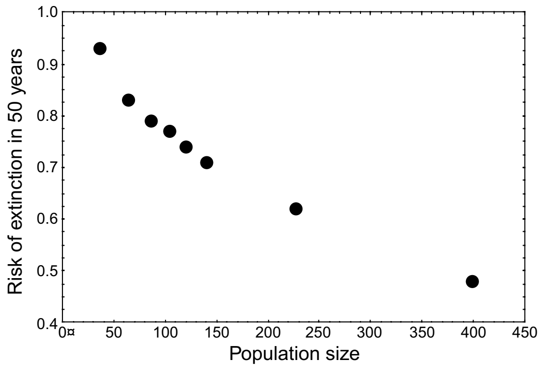

Fig. 3. The risk of extinction in 50 years in relation to the initial size of the populations in *Carlina vulgaris*. The stochastic simulations were repeated 100 times and spanned over a time-interval of 50 years. Spearman rank correlation test: $p < 0.05$, $n = 8$.

i.e. lack of disturbance affects the contribution to growth rate negatively. The F_1-value was almost ten times larger than any other value (negative) in the matrix and was of greatest importance to the population growth rate.

DISCUSSION

The results show that disturbances and vegetation height have a major effect on recruitment, population growth rate and population persistence in the biennial *Carlina vulgaris*. In the model simulations only populations subjected to the highest degree of disturbance had a positive population growth rate. Thus, disturbance is necessary to obtain a positive population growth.

Table 4. Transition probabilities between the life-stages of *Carlina vulgaris* in three model populations categorized after the type of vegetation, related to the disturbance regime.

	Disturbance Category		
Transition	Closed	Medium	Open
F_1	0.136	0.133	2.100
P_1	0.471	0.667	0.792
P_2	0.529	0.333	0.125
P_3	0	0	0
P_4	0.417	0.333	0.389
P_5	0.583	0.667	0.611

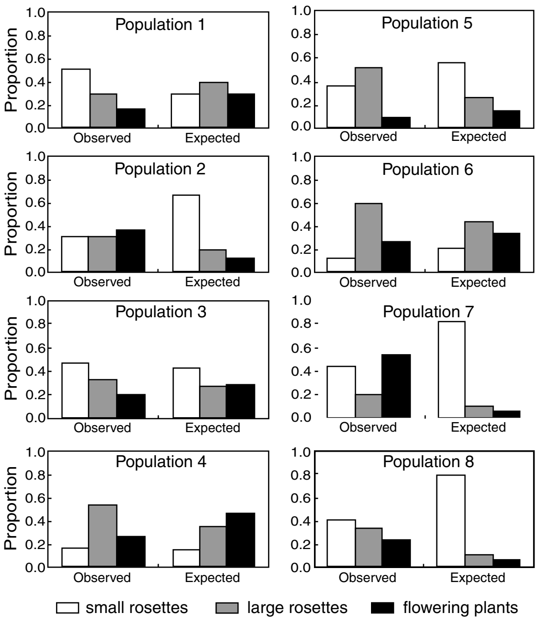

Fig. 4. The observed stage distributions and the expected stable stage distribution in eight populations of *Carlina vulgaris*.

Both in the natural and in the model populations, small rosettes staying in the same stage had very high elasticites, which imply a great importance for population growth and development. However, recruitment (F_1) was the critical element in the projection matrix, which exhibited large negative effects on population growth rate in the model population in vegetation of medium height with low disturbance.

The degree of disturbance had a greater effect than the initial population size on population persistence. This suggests that even small populations, from a demographic point of view, can be long-lived if they are exposed to a high degree of disturbance. When comparing the extinction risks

Table 5. Population growth rate and elasticities of P_1 (persistence of small rosettes) of three model populations.

	Disturbance Category		
	Closed	Medium	Open
λ	0.692	0.759	1.030
Elasticity (P_1)	0.320	0.657	0.477

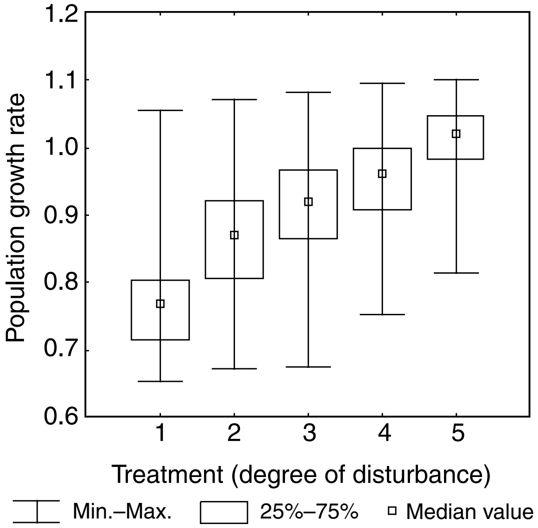

Fig. 5. The population growth rate of *Carlina vulgaris* in relation to degree of disturbance in model populations based on field data. Three matrices of different level of disturbance (combined to give five disturbance regimes; Table 1) were analysed in 50 simulations over a time-interval of 10 years. Spearman rank correlation test: $p < 0.05$, $n = 1992$).

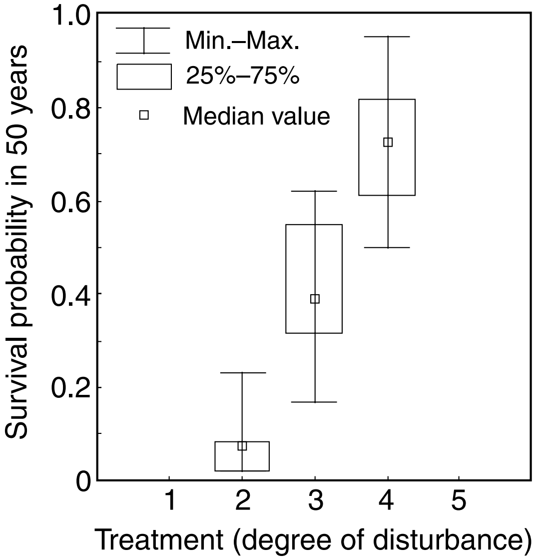

Fig. 6. Survival probability of *Carlina vulgaris* populations in relation to disturbance. The stochastic simulation were repeated 50 times and spanned over a time-interval of 50 years. Disturbance regimes 1 (no one survived) and 5 (all survived) are not shown in the graph. Spearman rank correlation test: $p < 0.05$, $r = 0.908$.

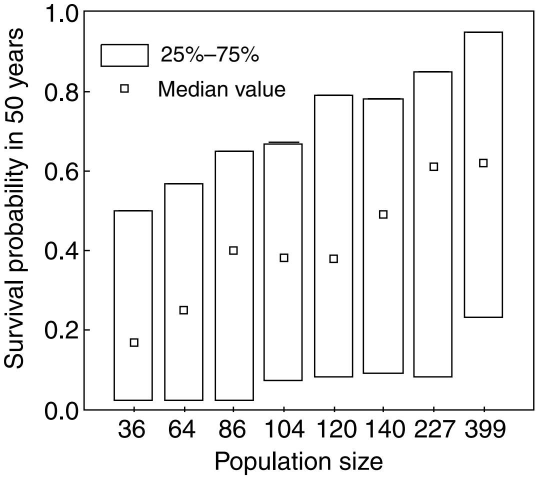

Fig. 7. The survival probability for of model populations of *Carlina vulgaris* in relation to the initial size of the natural populations. The stochastic simulations were repeated 50 times and spanned over a time-interval of 50 years. Spearman rank correlation test: $p < 0.05$, $r = 0.391$.

between the natural and the model populations, the simulations with the highest degree of disturbance have an approximately equal survival probability as in a large population (about 400 individuals). In the other end of the scale, the model population exposed to the lowest degree of disturbance did not survive for many years or did not persist at all, while the second lowest degree (with a little more disturbance) had similar values as the smallest natural population (36 individuals). Both population size and disturbance in the form of grazing and trampling in grassland areas creates long-lived populations of *Carlina vulgaris*. Accordingly, in these habitats *C. vulgaris* can be characterised as a persistent type of biennial plant as proposed by van der Meijden *et al*. (1992).

In accordance with Klinkhamer *et al*. (1996), the results show that there is a very low number of establishing seedlings produced per flowering plant. They suggested three possible reasons for this: few seeds survive until the time of germination; a high fraction of the seeds remain dormant; there is a high early seedling mortality. The authors ruled out the second alternative based on the finding that the germination of *Carlina* seeds are relatively insensitive to light quality (van Tooren & Pons 1988). Light response of seeds is not always related to dormancy, but contribution of seed bank to dynamics of extant populations in our study area is probably small because *C. vulgaris* has not been found in the seed bank (Eriksson & Eriksson 1997, O. Eriksson unpubl.). The results of the present study suggest that seedling mortality also is of little importance in explaining the small numbers of seedlings. The first alternative, that a few seeds survive until the time of germination, is probably of greatest importance. Almost 40% of the seeds germinated in disturbed areas in the experiment, so, provided that disturbance is frequent, it seems that seed production is the crucial factor limiting seedling number.

The results suggest that recruitment is limited either by the number of seeds (disturbance of vegetation alone had little or no effect on the number of seedlings establishing naturally) or the occurrence of safe sites (more of the added seeds germinated in the disturbed plots), or both. To get a more accurate understanding of the individual importance of the two factors, an experiment is needed that incorporates a range of seed and safe site densities in various spatial and temporal scales (Eriksson & Ehrlén 1992). However, it is likely that *Carlina vulgaris* suffers from dispersal limitation both at a local and at a regional scale, as have been found for other species inhabiting dry semi-natural grasslands in the study area (Eriksson 1997, 1998).

Schemske *et al.* (1994) suggested that there are three fundamental issues to take into consideration when deciding an appropriate course of action for recovery of endanged plant species and when evaluating recovery plans. The first issue is to understand the biological status of the species, which means to collect demographic information to determine whether the number of individuals and populations of the species are increasing, decreasing or stable. The second subject concerns the life history stages which have the greatest effect on population growth and species persistence. The information concerning the aspects of species biology which constitute the greatest threat to survival is of great importance. The third and last issue deals with the biological causes of variation in those life history stages that have a major demographic impact. It is also of great concern to extend population studies to include a regional ”metapopulation” perspective in biennial plants. Menges (1990, 1992) showed that even though separate populations have a positive population growth rate, the species could not be expected to survive (on a regional basis), when among-patch dispersal does not occur.

This study illustrates that it is possible to get useful information and knowledge also from short-term demographic studies. Even though a longer investigation on the species would be of great interest to evaluate the accuracy of the preditions given by shorter studies, we suggest that it is possible to get information for a rough understanding of population dynamics of annual and short-lived perennials in shorter studies. We substituted spatial for temporal variation. The important assumption that must be considered here is that the environmental variation in populations corresponds with the course of events in simulations.

Table 6. Effect of changes in transitions on population growth rate of *Carlina vulgaris* populations in two disturbance categories.

	Small rosette	Large rosette	Flowering
Medium category			
Small rosette	–0.0385	0	–0.2126
Large rosette	0.0500	–0.0066	0
Flowering	0	–0.0046	0
Open category			
Small rosette	0.0375	0	0.0976
Large rosette	–0.0938	0.0068	0
Flowering	0	0.0057	0

In our study site, the dry meadow vegetation has been maintained for centuries by continuous disturbance of mowing and grazing. Variation in disturbance regime may well change the environment from closed to open, or vice versa, very fast. The other extreme is the successional development, where the vegetation is sparse around individuals of a young population and gets slowly closed when a population becomes older. To get direct information on the temporal variation, one could estimate the successional development and variation of disturbance regime for the whole community and use the same data for many species.

The weaknesses in this study are the lack of empirical data on temporal variation, and the lack of data for winter mortality and size-class transformations over the winter. Overwintering mortality is probably of little importance in *Carlina vulgaris* (Kemppainen 1990, Klinkhamer *et al.* 1996), and spatial variation of disturbance was used in the simulations instead of temporal variation. It must be noted that the effect of temporal variation in disturbance can be estimated with this method, but a longer study is needed to measure the impact of yearly variation in weather conditions. Despite these caveats, this study has shown the great importance of disturbance for population persistence in *C. vulgaris*.

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REFERENCES

Caswell, H. 1989: *Matrix population models: construction, analysis and interpretation.* — Sinauer, Sunderland, MA, USA. 328 pp.

de Jong, T. J. & Klinkhamer, P. G. L. 1988: Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coast sand-dune area. — *J. Ecol.* 76: 366–382.

de Kroon, H., Plaisier, A., van Groenendael, J. & Caswell, H. 1986: Elasticity: the relative contribution of demographic parameters to population growth rate. — *Ecology* 67: 1427–1431.

Ehrlén, J. 1995: Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. — *J. Ecol.* 83: 297–308.

Eriksson, Å. 1998: Regional distribution of *Thymus serpyllum*: management history and dispersal limitation. — *Ecography* 21: 35–43.

Eriksson, Å. & Eriksson O. 1997: Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. — *Nordic J. Bot.* 17: 469–482.

Eriksson, O. 1996: Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. — *Oikos* 77: 248–258.

Eriksson, O. 1997: Colonization dynamics and relative abundance of three plant species (*Antennaria dioica*, *Hieracium pilosella* and *Hypochoeris maculata*) in dry semi-natural grassland. — *Ecography* 20: 559–568.

Eriksson, O. & Ehrlén, J. 1992: Seed and microsite limitation of recruitment in plant populations. — *Oecologia* 91: 360–364.

Kemppainen, E. 1990: *Idänverijuuren, ketonukin, kurhon ja vanakelton biologiasta Suomessa.* — Ph. Lic. Thesis, Dept. Bot., University of Helsinki.

Klinkhamer, P. G. L., de Jong, T. J. & de Heiden, J. L. H. 1996: An eight year study of population dynamics and life-history variation of the "biennial" *Carlina vulgaris*. — *Oikos* 75: 259–268.

Klinkhamer, P. G. L., de Jong, T. L. & Meelis, E. 1991: The control of flowering in the monocarpic perennial *Carlina vulgaris*. — *Oikos* 61: 88–95.

Lennartsson, T. 1997: *Demography, reproductive biology, and adaptive traits in* Gentianella campestris *and* G. amarella. — Ph.D. Thesis, Agraria 46, Swedish University of Agricultural Sciences, Uppsala, Sweden.

McDonald, D. B. & Caswell, H. 1993: Matrix methods for avian demography. — *Curr. Ornithol.* 10: 139–185.

Menges, E. S. 1990: Population viability analysis for an endangered plant. — *Conserv. Biol.* 4: 52–62.

Menges, E. S. 1992: Stochastic modeling of extinction in in plant populations. — In: Fiedler, P. L. & Jain, S. K. (eds.), *Conservation biology. The theory and practice of nature conservation, preservation and management*: 253–275. Chapman & Hall, New York.

Schemske, D. W., Husband, B. C., Ruckelhaus, M. H., Goodwillie, C., Parker, I. M. & Bishop, J. G. 1994: Evaluating approaches to the conservation of rare and endangered plants. — *Ecology* 75: 584–606.

van der Meijden, E., Klinkhamer, P. G. L., de Jong,T. J. & van Wijk, C. A. M. 1992: Meta-population dynamics of biennial plants: how to exploit temporary habitats. — *Acta Bot. Neerl.* 41: 249–270.

van Tooren, B. F. & Pons T. L. 1988. Effects of temperature and light on the germination of chalk grassland species. — *Funct. Ecol.* 2: 303–310.