ECOGRAPHY 25: 233–243, 2002

Population dynamics in *Oxalis acetosella*: the significance of sexual reproduction in a clonal, cleistogamous forest herb

Henrik Berg

Berg, H. 2002. Population dynamics in *Oxalis acetosella*: the significance of sexual reproduction in a clonal, cleistogamous forest herb. – Ecography 25: 233–243.

I studied demography in three populations of the clonal, cleistogamous herb *Oxalis acetosella* during three growing seasons, to assess the impact of seedling recruitment relative to ramet recruitment on its population dynamics. I followed each plant in permanent plots, and stage-classified it according to origin (sexually or vegetatively derived) and reproductive status. I calculated between-year transition probabilities, and sexual and vegetative fecundities, and used them in projection matrix analyses to simulate the development of populations and obtain the elasticity of each life-history event.

In general, non-flowering adults was the most numerous stage class and flowering new ramets the rarest, whereas the proportions of the other stage classes varied among populations and years. The negative correlation between plant density and survival was not very strong, and mortality seemed to be largely density-independent. Simulated population growth rates (λ) indicated that one of the populations is declining and the other two are growing, although slowly. The highest elasticities were usually those of stasis in adult plants, whereas elasticities of other matrix entries were low and highly variable. λ was positively correlated with the elasticities of seedling production and survival but negatively correlated with the elasticity of adult survival, indicating that seedling recruitment is more favourable for population growth than is adult stasis. There were no correlations between λ on the one hand and the elasticities of ramet production and survival on the other.

The results suggest that recruitment from seedlings is important for the growth and long-term maintenance of *O. acetosella* populations, as a complement to the rather low vegetative propagation. In this context cleistogamy is an adaptive strategy, maximizing total seed output.

H. Berg (bergh@mailer.uni-marburg.de), Dept of Plant Ecology, Evolutionary Biology Centre, Uppsala Univ., Villavägen 14, SE-752 36 Uppsala, Sweden (present address: Dept of Biology, Plant Ecology, Univ. of Marburg, Karl-von-Frisch-Str. 1, D-35043 Marburg, Germany).

Generally, it is assumed that populations of clonal plants are maintained and expanded mainly through vegetative propagation, while recruitment from seeds is of less importance. Allocation to seed production is low, and seedlings will to a large extent be outcompeted by established plants. Seeds should be important mainly for colonizing new sites, e.g. disturbed patches (Tamm 1972, Harper 1977, Barkham 1980, Eriksson 1997, Verburg et al. 2000, and references therein). According to theory, this should be the case especially in woodland species with below-ground clonal growth, "guerilla" growth habit (i.e. extensive vegetative spread), and long-distance seed dispersal (Eriksson 1989).

A plant displaying some of these features is *Oxalis acetosella* L. (Oxalidaceae), which is a long-lived herb with quite extensive rhizomatous growth. It is mostly found in the understorey of more or less undisturbed forest sites, where it can attain very high densities (Packham 1978, Shorina 1985, Grime et al. 1988, Chernenkova and Shorina 1990). However, seed dispersal is exclusively explosive, implying that most propagules are distributed within the population (Packham 1978,

Accepted 26 September 2001

ISSN 0906-7590

Chernenkova and Shorina 1990, Berg 2000). Another way of escaping density-dependent mortality, apart from dispersal in space, is dispersal in time, i.e. the formation of a bank of dormant seeds waiting for conditions appropriate for germination (Harper 1977, Eriksson 1989). In *O. acetosella*, however, seed banks seem to be of little importance, and seedlings are often observed in abundance in natural populations (Bråkenhielm 1977, Packham 1978, Grime et al. 1988, Chernenkova and Shorina 1990).

Oxalis acetosella is cleistogamous, i.e. capable of reproduction by means of both chasmogamous (open, potentially cross-pollinated) and cleistogamous (closed, obligately self-pollinated) flowers ("true" cleistogamy; Lord 1981). Both flower types may occur in a single plant. Despite several studies focusing on the various evolutionary implications of this system (e.g. Darwin 1877, Schemske 1978, Waller 1979, Schoen and Lloyd 1984), few have tried to shed light on the role of cleistogamy in the dynamics of plant populations. The mere fact that *O. acetosella* displays this dimorphic reproductive strategy, together with the lack of mechanisms for long-distance dispersal and dormancy in seeds as well as the frequent occurrence of seedlings, indicates that seed production is of some importance also in established populations. In addition, low root competition (Bråkenhielm 1977) and high shade-tolerance suggest that mortality in this species is largely density-independent, and thus population growth may be influenced by the recruitment of new seedlings.

In earlier studies, data have been gathered on CH (chasmogamous) and CL (cleistogamous) reproductive output and offspring fitness in *O. acetosella* (Redbo-Torstensson and Berg 1995, Berg and Redbo-Torstensson 1998, 2000). The purpose of the present study was to relate information from these studies to demographic data, in order to estimate the significance of the dimorphic reproductive system for the production of seedlings and the relative importance of seedling and ramet (vegetative) recruitment for the growth and maintenance of *O. acetosella* populations. To this end, I collected demographic data in three natural populations of *O. acetosella* during three growing seasons, 1995–1997, and used them in projection matrix analyses of population growth.

Throughout this paper, I will refer to sexual reproduction as just "reproduction", since by definition vegetative propagation cannot be considered as reproduction. Nomenclature follows Karlsson (1998).

Material and methods

The study species

Oxalis acetosella is a low-growing, perennial herb with a slender, branching rhizome rooting adventitiously. The rhizome creeps through the uppermost soil layers or under the litter, and can form clonal patches of up to 0.5 m in diameter. It bears swollen scale leaves acting as storage organs. The green leaves grow in rosettes at the end of the rhizome, or alone along the rhizome. *Oxalis acetosella* is winter-green and capable of growth and seed-set under low light, although growth rate is slow. It is sensitive to drought and strong sunlight and mostly found in shady woodland, where it often dominates the herb layer. Its distribution is through most of Europe and north and central Asia, and in Sweden it is a common understorey plant of moist–mesic coniferous and deciduous forest in the major part of the country (Packham 1978, Grime et al. 1988, Chernenkova and Shorina 1990, Odell and Drakenberg 1991).

CH flowers appear in spring and are pollinated by insects of various taxa (Redbo-Torstensson and Berg 1995). The completely closed and self-pollinated CL flowers are produced mainly in summer and early autumn (Berg and Redbo-Torstensson 1998). For closer descriptions of both flower types, see e.g. Darwin (1877) and Packham (1978). The average *O. acetosella* plant produces more CL flowers than CH flowers, but in both phases there is large temporal and spatial variation in fruit-set (Redbo-Torstensson and Berg 1995, Berg and Redbo-Torstensson 1998).

The fruit of both flower types is a capsule usually containing no more than 10 seeds. The seed is explosively dispersed and can be thrown up to a few metres from the mother plant (Packham 1978, Chernenkova and Shorina 1990, Berg 2000). Most seeds germinate in spring in the year after dispersal, but a short-lived seed bank can be formed (Bråkenhielm 1977, Grime et al. 1988, Chernenkova and Shorina 1990). Germination percentage is low in the field, and seedling mortality can be high (Berg and Redbo-Torstensson 2000).

The study sites

Three *O. acetosella* populations in the vicinity of Uppsala, central Sweden, were chosen for the study. The three sites represent different habitats, and all of them were undisturbed during the study period and had a continuous, densely patched cover of the study species. Population 1 (P1) is situated 2 km south of Uppsala (59°49′60″N, 17°41′20″E), in a relatively open and dry forest dominated by deciduous trees, e.g. *Betula pendula* and *Quercus robur*. Dominant field layer species are *Anemone hepatica*, *A. nemorosa*, *O. acetosella*, *Hieracium* sect. *Hieracium* spp., and *Poa nemoralis*. Population 2 (P2) is located ca 300 m east of P1 (59°49′60″N, 17°41′23″E; the two populations are clearly separated). It is in a middle-aged, closed pine plantation with shady and mesic conditions. The tree layer is dominated by *Pinus sylvestris*, the field layer by *Dryopteris filix-mas*, *A. nemorosa*, *O. acetosella*, and *H.* sect. *Hieracium* spp.

Population 3 (P3) is situated 10 km north-east of Uppsala (59°54′30″N, 17°45′00″E), in a shady, moist spruce forest dominated by *Picea abies* but also containing e.g. *Pinus sylvestris* and *Populus tremula*. Dominant field layer species are *A. nemorosa*, *O. acetosella*, *Vaccinium myrtillus*, and *Deschampsia flexuosa*. This site has a slightly shorter growing season than the two others (see also Berg and Redbo-Torstensson 1998).

Basic demography

I established 10 permanent plots in each of the three populations. I marked each plot with two plastic tubes, driven into the ground, onto which a quadratic metal frame with a 2.5 × 2.5 cm mesh grid could be attached. The grid formed a 10 × 10 coordinate system; the observation area in each plot was thus 25 × 25 cm.

In early May 1995, at the start of the growing season, I registered every *O. acetosella* plant in all 30 plots, and tagged it with a piece of plastic straw slipped over a petiole (or, for leafless plants, over the above-ground part of the rhizome). I counted the leaves as a measure of size/resource status, since flower production has been found to be positively related to leaf number (Berg and Redbo-Torstensson 1998). I then visited the plots two to four times per month during the growing season, until mid-October. I also registered and tagged all seedlings (seed-derived plants in their first year above ground; with cotyledons) and new ramets (presumably vegetatively derived plants in their first year above ground) appearing during the season. I counted the leaves in new ramets but not in seedlings, since almost all seedlings had only one leaf or just cotyledons. I also noted the reproductive status of each plant – CH-, CL-, or non-flowering – to obtain the probabilities of reproduction. The coordinate system and the tagging made it possible to follow each plant for several years. When a tagged plant could not be recovered, or had been lacking green parts for more than two months, I registered it as "dead"; thus, survival probabilities were obtained. I repeated this in 1996 and 1997, from early May to mid-October. Each year, I summed the total plant number per plot to calculate population density, in order to relate this variable to e.g. reproduction and survivorship.

Matrix models

Stage classification

After data collection, I classified the plants for simulations of population growth with projection matrix models (Caswell 1989). Initially, my intention was to classify the plants according to origin (sexually or vegetatively derived), age, and size (leaf number), but soon I found that there was no real age or size limit for reproduction. Only seedlings lacked the ability to produce flowers during the study period; in the other groups even very small plants were able to reproduce. Therefore, I divided the plants into five stage classes, based on origin and reproductive status: 1) seedlings; 2) non-flowering new ramets; 3) flowering new ramets; 4) non-flowering adult plants; and 5) flowering adult plants. I considered this classification appropriate since the aim of the study was to compare the importance of reproduction and vegetative propagation.

Transition probabilities and fecundities

I considered seedlings and ramets adult when they had survived their first winter above ground. Thus, for each plant there were only three possible transitions between years: death, or survival to the non-flowering or to the flowering adult stage. The transition from seedling to flowering adult was rare, but nevertheless possible (see Table 1).

I calculated sexual fecundity values for each plot by dividing the number of seedlings in each year by the number of flowering plants in the preceding year ("anonymous reproduction"; Caswell 1989). I assigned equal sexual fecundities to flowering new ramets and adults, since I could not tell from which stage class a seedling had been derived. This assignment was probably correct, since I had found in an earlier study on *O. acetosella* that new ramets and adults do not differ in mean number of mature fruits (Berg unpubl.).

I similarly obtained vegetative fecundities for each plot from the numbers of non-flowering and flowering new ramets in each year divided by the number of potentially ramet-producing plants in the preceding year (all plants in the plot except seedlings). I assigned equal vegetative fecundities to non-flowering and flowering new ramets and adults, according to results from a study on vegetative propagation in *O. acetosella* (Berg unpubl.).

Simulations

I carried out matrix simulations using Excel software Karismat (Lehtilä pers. comm.) and a MATLAB model (Horvitz et al. pers. comm.). I analysed each population with a deterministic model for each transition interval (1995–1996 and 1996–1997), yielding the asymptotic population growth rate (λ), the stable stage distribution, the reproductive value of each stage class, and the elasticities of all matrix entries (transition probabilities and fecundities). The stable stage distribution gives the proportion of individuals in each stage class as the population reaches the asymptotic growth rate. The reproductive value is a measure of the potential value of an individual of a certain class for the current or future production of new individuals; a new population will grow faster the higher the reproductive value is of the class to which its founder individuals belong. The elasticity gives the relative change in λ resulting from a small change in a matrix entry, and is thus a measure of the proportional contribution to the population's fitness of that life-history event (Silvertown et al. 1993, Horvitz and Schemske 1995). For detailed information on matrix models, see Caswell (1989).

In addition, I performed stochastic simulations where both matrices were assigned equal probability of sampling. In this model, I set the initial stage distribution to the values of 1995 (see Fig. 1a) and calculated the average population growth rate (ln λ), the stationary stage distribution, and the extinction probability from 100 simulations of 100 yr (Caswell 1989; cf. also Ehrlén 1995). The average growth rate and the stationary stage distribution are the equivalents of the asymptotic growth rate and the stable stage distribution, respectively.

For each interval, I also performed a deterministic simulation for each plot. I did this to be able to analyse the spatial and temporal variation in population growth rates, and the relationships between elasticities and growth rates. In addition, I divided the elasticity matrix of each interval-plot into five sections, representing the main population processes: 1) seedling production (row 1 in the matrix; Table 2); 2) ramet production (rows 2 and 3); 3) seedling survival to the adult stage (rows 4 and 5, column 1); 4) survival of new ramets to the adult stage (rows 4 and 5, columns 2 and 3); and 5) adult survival (rows 4 and 5, columns 4 and 5). Within each section, I summed the elasticities to be able to analyse the relationships of these processes to each other and to population growth rate (cf. Silvertown et al. 1993, Oostermeijer et al. 1996). In this paper, I report elasticities but not sensitivities, since the former make it easier to compare the impact of different life-history events on population growth (Eriksson 1988, Caswell 1989, Horvitz and Schemske 1995).

Statistical analysis

All analyses were performed using SYSTAT 7.0 (Wilkinson 1997). I log-transformed the response variable plant density (plants m^{-2}) and subjected it to ANOVA (GLM) with each plot as an observation, and population, plot nested within population, year, and the interaction between population and year as explanatory variables. I assumed population a fixed factor, and plot and year random factors. I analysed the variation among populations and years in the distribution of plants among stage classes with χ^2-tests.

I arcsine-transformed the response variables CH and CL flower production and survival (probabilities), and tested them with the same type of ANOVA as for plant density. I also analysed the relationships of these variables to density with Pearson correlation. For survival, I only analysed the data from 1995 and 1996, since

Table 1. Projection matrices for three natural populations of *Oxalis acetosella* near Uppsala, central Sweden, and for two transition intervals. Entries are the probabilities of a plant in stage class j in year t (horizontal) to contribute to stage class i in year t+1 (vertical). 1: seedlings; 2: non-flowering new ramets; 3: flowering new ramets; 4: non-flowering adult plants; 5: flowering adult plants. 1st row: sexual fecundities; 2nd and 3rd row: vegetative fecundities; 4th and 5th row: transition probabilities. P1: deciduous forest; P2: pine forest; P3: spruce forest.

	1995–1996					1996–1997				
Stage	1	2	3	4	5	1	2	3	4	5
P1										
1	0.000	0.000	0.408	0.000	0.408	0.000	0.000	0.292	0.000	0.292
2	0.000	0.196	0.196	0.196	0.196	0.000	0.126	0.126	0.126	0.126
3	0.000	0.038	0.038	0.038	0.038	0.000	0.036	0.036	0.036	0.036
4	0.288	0.449	0.000	0.461	0.149	0.212	0.576	0.474	0.660	0.310
5	0.000	0.232	0.867	0.166	0.603	0.000	0.162	0.474	0.136	0.540
P2										
1	0.000	0.000	0.621	0.000	0.621	0.000	0.000	0.681	0.000	0.681
2	0.000	0.150	0.150	0.150	0.150	0.000	0.073	0.073	0.073	0.073
3	0.000	0.037	0.037	0.037	0.037	0.000	0.027	0.027	0.027	0.027
4	0.260	0.605	0.000	0.367	0.100	0.435	0.632	0.421	0.487	0.288
5	0.008	0.211	0.900	0.312	0.796	0.000	0.092	0.421	0.244	0.692
P3										
1	0.000	0.000	0.940	0.000	0.940	0.000	0.000	0.091	0.000	0.091
2	0.000	0.259	0.259	0.259	0.259	0.000	0.156	0.156	0.156	0.156
3	0.000	0.022	0.022	0.022	0.022	0.000	0.000	0.000	0.000	0.000
4	0.346	0.704	0.000	0.580	0.250	0.588	0.634	0.125	0.704	0.362
5	0.000	0.099	0.000	0.164	0.607	0.000	0.065	0.500	0.093	0.580

Fig. 1. Distribution of plants among stage classes in three natural populations of *Oxalis acetosella* near Uppsala, central Sweden, 1995–1997. Stage classes: 1: seedlings; 2: non-flowering new ramets; 3: flowering new ramets; 4: non-flowering adult plants; 5: flowering adult plants. Populations: 1: deciduous forest; 2: pine forest; 3: spruce forest. a) Observed distribution (numbers) in each year. b) The stable stage distribution (proportions) obtained from deterministic matrix simulations for each transition interval. c) The stationary stage distribution (proportions) obtained from stochastic matrix simulations for the whole period.

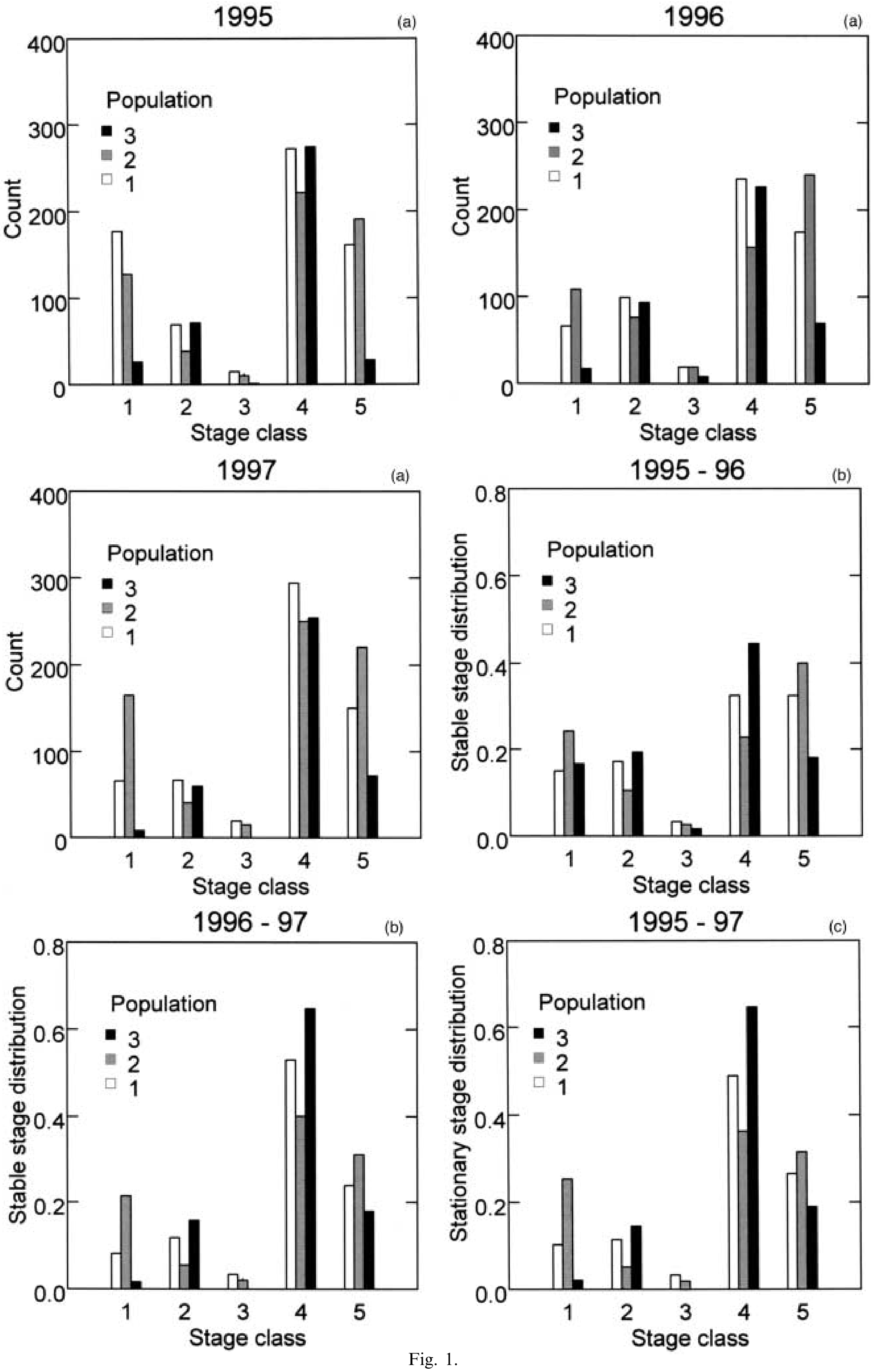
1995 (a)
1996 (a)
1997 (a)
1995 - 96 (b)
1996 - 97 (b)
1995 - 97 (c)
Population
■ 3
▨ 2
□ 1
Count
Stable stage distribution
Stationary stage distribution
Stage class
0
100
200
300
400
0.0
0.2
0.4
0.6
0.8
1
2
3
4
5

Fig. 1.

Table 2. Elasticities of the matrix entries of Table 1. 1: seedlings; 2: non-flowering new ramets; 3: flowering new ramets; 4: non-flowering adult plants; 5: flowering adult plants. 1st row: sexual fecundities; 2nd and 3rd row: vegetative fecundities; 4th and 5th row: transition probabilities. P1: deciduous forest; P2: pine forest; P3: spruce forest. The two highest elasticities of each interval-population are in bold text.

	1995–1996					1996–1997				
Stage	1	2	3	4	5	1	2	3	4	5
P1										
1	0.000	0.000	0.004	0.000	0.037	0.000	0.000	0.002	0.000	0.015
2	0.000	0.035	0.007	0.065	0.065	0.000	0.014	0.004	0.065	0.029
3	0.000	0.010	0.002	0.020	0.020	0.000	0.006	0.002	0.025	0.011
4	0.041	0.073	0.000	**0.142**	0.046	0.018	0.069	0.016	**0.358**	0.076
5	0.000	0.054	0.039	0.074	**0.268**	0.000	0.023	0.020	0.089	**0.159**
P2										
1	0.000	0.000	0.003	0.000	0.052	0.000	0.000	0.005	0.000	0.072
2	0.000	0.014	0.004	0.031	0.054	0.000	0.003	0.001	0.021	0.016
3	0.000	0.006	0.001	0.012	0.021	0.000	0.002	0.001	0.014	0.011
4	0.053	0.053	0.000	0.071	0.034	0.077	0.028	0.007	**0.161**	0.074
5	0.003	0.030	0.032	**0.097**	**0.432**	0.000	0.008	0.013	0.152	**0.334**
P3										
1	0.000	0.000	0.004	0.000	0.048	0.000	0.000	0.000	0.000	0.010
2	0.000	0.046	0.004	0.106	0.043	0.000	0.021	0.000	0.088	0.024
3	0.000	0.002	0.000	0.005	0.002	0.000	0.000	0.000	0.000	0.000
4	0.052	0.121	0.000	**0.233**	0.041	0.010	0.098	0.000	**0.446**	0.063
5	0.000	0.028	0.000	0.106	**0.159**	0.000	0.014	0.000	0.083	**0.143**

winter mortality between 1997 and 1998 could not be determined. I used logistic regression, with individual plants as data points, to analyse the effects of stage class and leaf number, considered independent of population and year, on the probabilities of CH and CL flowering and survival. I set the response variables to 0 (non-flowering and death, respectively) or 1 (flowering and survival, respectively). For the analysis of flower production, the stage classes were only seedlings, new ramets, and adults, without a distinction between non-flowering and flowering plants.

I used the λs obtained from the matrix simulations for each interval-plot in an ANOVA analysing the variation in population growth rate on different scales. In this analysis, the explanatory variables were population, plot nested within population, transition interval, and the population × interval interaction. I analysed the relationship between λ and plant density with Pearson correlation. I also tested the correlation between λ and the elasticity of each entry, using the values from the simulations for each interval-plot, and I did the same using the summed elasticities of the five matrix sections. Such correlation analyses may reveal relationships of life-history events to population growth and to each other, e.g. costs and trade-offs (Silvertown et al. 1993, Horvitz and Schemske 1995, Oostermeijer et al. 1996).

Results

Basic demography

Plant density and stage distribution

The mean plant density ($\pm$ SD) of *O. acetosella* in the 30 plots from 1995 to 1997 was 883.6 ± 341.8 plants m^{-2} (range: 240–1840; $n = 90$). P3 had a lower density (646.9 ± 210.1 plants m^{-2}) than P1 and P2 (1003 ± 280.5 and 1001 ± 385.7 plants m^{-2}, respectively; $F_{2,27} = 5.06$, $p < 0.01$). Plant density also varied among plots nested within populations ($F_{27,54} = 18.89$, $p < 0.001$). There was no variation among years, but an interaction of population × year was detected ($F_{4,54} = 5.59$, $p = 0.001$).

The distribution of plants among stage classes differed among populations ($\chi^2 = 525.9$) and among years ($\chi^2 = 111.7$; DF = 8, $n = 4961$, $p < 0.001$; Fig. 1a). In P1 and P3, non-flowering adults was by far the most numerous stage class, whereas P2 had a relatively high proportion of flowering adults. In P2, seedlings was always the third largest stage class, while in P1 the third place shifted between seedlings and non-flowering new ramets. In P3, seedlings and flowering plants were relatively rare.

Reproduction

Adult plants had a higher probability (0.16; $n = 3486$) of producing CH flowers than seedlings (0.00; $n = 759$) and new ramets (0.03; $n = 718$). There was also a positive relationship between leaf number and flowering probability (Table 3). CH production differed between populations, with the highest flowering probability in P2 and the lowest in P3, but there was also variation among plots within populations. It also varied among years, with the highest probability in 1996 and the lowest in 1997, but there was a population × year interaction (Table 4).

Adults had a higher probability (0.33) of producing CL flowers than seedlings (0.00) and new ramets (0.14).

Table 3. The effects of stage class and leaf number on the probabilities of production of chasmogamous (CH) and cleistogamous (CL) flowers (1995–1997), and of plant survival (1995 and 1996), in three natural populations of *Oxalis acetosella* near Uppsala, central Sweden. The data were analysed with logistic regression, with individual plants as data points ($n(1995-1997) = 4963$, $n(1995+1996) = 3285$). Odds ratios are given with confidence intervals within parentheses.

		CH flower prod.		CL flower prod.		Survival	
	DF	Odds ratio	p	Odds ratio	p	Odds ratio	p
Stage class	1	8.96 (5.88–13.66)	<0.001	4.82 (4.01–5.80)	<0.001	1.70 (1.61–1.80)	<0.001
Leaf number	1	1.94 (1.77–2.13)	<0.001	2.36 (2.18–2.56)	<0.001	1.36 (1.23–1.52)	<0.001

Table 4. The effects of population, plot nested within population, year, and the interaction between population and year on the probabilities of production of chasmogamous (CH) and cleistogamous (CL) flowers (1995–1997), and of plant survival (1995 and 1996), in three natural populations of *Oxalis acetosella* near Uppsala, central Sweden. The data were analysed with factorial ANOVA, with each plot as an observation ($n(1995-1997) = 90$, $n(1995+1996) = 60$).

	CH flower prod.				CL flower prod.			Survival			
	DF	MS	F	p	MS	F	p	DF	MS	F	p
Population	2	0.38	11.42	<0.001	0.84	14.05	<0.001	2	0.06	2.37	ns
Plot (population)	27	0.03	3.74	<0.001	0.06	6.48	<0.001	27	0.03	3.59	0.001
Year	2	0.14	16.55	<0.001	0.06	6.08	<0.005	1	0.18	24.14	<0.001
Population × year	4	0.06	6.65	<0.001	0.01	1.19	ns	2	0.01	1.08	ns
Error	54	0.01			0.01			27	0.01		

Like in the CH phase, there was a positive relationship between leaf number and CL production (Table 3). The probability of producing CL flowers was highest in P2 and lowest in P3, but there was variation among plots within populations. Flowering probability was highest in 1996 and lowest in 1995, and there was no population × year interaction (Table 4).

Since both CH and CL production were related to leaf number, production in the two phases were highly correlated (odds ratio (CI) = 10.46 (8.58–12.74), DF = 1, n = 4963, $p < 0.001$); plants producing CH flowers had a higher probability of producing CL flowers in the same year than plants not producing CH flowers. Plant density did not affect the probability of producing CH or CL flowers ($r = 0.149$ and 0.157, respectively; DF = 1, n = 90, $p > 0.05$).

Plant survival

The main causes of death seemed to be drought and frost, since nearly all mortality occurred during dry periods in summer and during winter. Survival was negatively correlated with plant density ($r = -0.347$, DF = 1, n = 60, $p < 0.01$), although there was no effect of density on mean leaf number (linear regression: $r^2 = 0.002$, DF = 1, n = 90, $p > 0.05$). When I analysed each stage class separately with Pearson correlation, plant density had no effect on survival in any of the stage classes (DF = 1, n = 29–60, $p > 0.05$). Signs of predation were very scarce.

The stage classes differed in survival, which was highest in flowering new ramets (85.9%; n = 71) and flowering adults (88.5%; n = 863), and lowest in seedlings (31.7%; n = 521). In non-flowering new ramets and adults, survival was 73.5% (n = 446) and 72.7% (n = 1384), respectively. Leaf number influenced survival, which was lower in plants with one leaf than in plants with more leaves (Table 3). The observation that flowering plants had higher survival than non-flowering plants may be attributed to the higher mean leaf number of the former group (2.4 vs 1.7; $t = 24.92$, DF = 4175, $p < 0.001$).

There was no difference in overall survival among populations, but a difference was detected among plots within populations. Survival was higher in 1996 than in 1995, and there was no population × year interaction (Table 4). When analysing each stage class separately, I found no among-population or between-year variation in survival for seedlings and new ramets; the variation could be attributed to the adult plants. Non-flowering adults had higher survival in 1996 than in 1995 ($F_{1,27} = 7.98$, $p < 0.01$), and so had flowering adults ($F_{1,26} = 7.27$, $p < 0.025$). In flowering adults, survival was slightly lower in P1 than in the other populations ($F_{2,26} = 3.79$, $p < 0.05$).

Matrix models

Population growth rates

Table 1 shows the transition probabilities and fecundities for each population in each interval, that were used in matrix simulations of population growth. The deterministic and the stochastic models gave basically the same predictions regarding growth rates and extinction probabilities (Table 5). P1 had a λ below 1 in both intervals and a negative ln λ for the whole period, which means that the population is declining and will go extinct if conditions stay the same. P2 had a $\lambda > 1$ in both intervals and a positive ln λ, implying that the population is increasing under prevailing conditions. P3 is also growing according to the ln λ, although its λ was above 1 in the first interval and below 1 in the second. All λ values are close to unity, which means that changes are fairly slow.

The ANOVA analysing the variation in λ on different scales showed that it did not differ among populations ($F_{2,27} = 1.67$, $p > 0.05$), nor among plots within populations ($F_{27,27} = 1.49$, $p > 0.05$). There was also no difference in λ between intervals ($F_{1,27} = 3.18$, $p > 0.05$), and no population × interval interaction ($F_{2,27} = 0.91$, $p > 0.05$). I found no correlation between λ and plant density ($r = -0.099$, DF = 1, n = 60, $p > 0.05$).

Simulated stage distributions and reproductive values

Figure 1b shows the stable stage distributions obtained from the deterministic simulations, and Fig. 1c, the stationary stage distributions resulting from the stochastic simulations. On the whole, they show the same pattern as the observed distributions (Fig. 1a), with high proportions of non-flowering adults in P1 and P3, relatively high proportions of seedlings and flowering adults in P2, and low proportions of seedlings and flowering plants in P3. This means that the population structures will not change much if current conditions prevail.

The reproductive values are shown in Fig. 2. Flowering plants had the highest values in most interval-populations; the low value of flowering new ramets in P3 is due to the rarity of this stage class in that population (Table 1, Fig. 1). The values of seedlings were equally low in all interval-populations, because of their high mortality and low probability of transition to the flowering adult stage (Table 1).

Elasticities

Table 2 shows the elasticity matrix obtained from the deterministic simulations. In most interval-populations, stasis in adult plants had by far the highest elasticities. The elasticities of the other entries varied substantially among interval-populations.

When testing the correlations between λ and the elasticity of each entry, I found that the elasticities of flowering adults producing seedlings and seedlings becoming non-flowering adults were positively correlated with λ ($r = 0.316$ and 0.315, respectively; DF = 1, n = 60, $p < 0.025$). The elasticity of stasis in non-flowering adults was negatively correlated with λ ($r = -0.417$, DF = 1, n = 60, $p = 0.001$). None of the other elasticity entries was correlated with λ (DF = 1, n = 60, $p > 0.05$).

I also tested the three elasticities correlated with λ for variation on different scales, with the same type of ANOVA as for λ (see above). The elasticities of flowering adults producing seedlings and seedlings becoming non-flowering adults were higher in P2 than in the other populations ($F_{2,27} = 10.00$, $p < 0.001$ for both elasticities; Table 2). These elasticities did not vary significantly among plots within populations or between intervals, and there were no population × interval interactions. The elasticity of stasis in non-flowering adults was lower in P2 than in the other populations ($F_{2,27} = 4.98$, $p < 0.05$), but showed variation also among plots within populations ($F_{27,27} = 2.15$, $p < 0.05$). This elasticity was higher in 1996–1997 than in 1995–1996 ($F_{1,27} = 18.57$, $p < 0.001$), and there was no population × interval interaction. I also analysed the relationships between these three elasticities and plant density with Pearson correlation, and found no correlation (DF = 1, n = 60, $p > 0.05$).

The test of correlations of the summed elasticities of each of the five matrix sections with each other and with λ gave much the same picture (Table 6); λ was positively correlated with the elasticities of seedling production and seedling survival, and negatively correlated with the elasticity of adult survival. The elasticities of seedling production and survival were negatively correlated with the elasticities of ramet production and survival, and so was the elasticity of adult survival. The elasticities of seedling production and survival were highly correlated, as were the elasticities of ramet production and survival.

Table 5. Results from matrix simulations of growth of three natural populations of *Oxalis acetosella* near Uppsala, central Sweden, for two transition intervals. P1: deciduous forest; P2: pine forest; P3: spruce forest. For each matrix both a deterministic simulation, yielding the asymptotic population growth rate (λ) for each transition interval, and a stochastic simulation, yielding the average population growth rate (ln λ) for the whole period, were performed. The ultimate extinction probability is 1 for interval-populations with a negative average growth rate. For calculation of 95% confidence interval (CI) for ln λ, see Caswell (1989).

Population	λ 1995–1996	 1996–1997	ln λ with CI 1995–1997	Extinction probability
P1	0.979	0.989	-0.023 ± 0.000	1
P2	1.092	1.050	0.069 ± 0.000	0
P3	1.117	0.973	0.052 ± 0.001	0

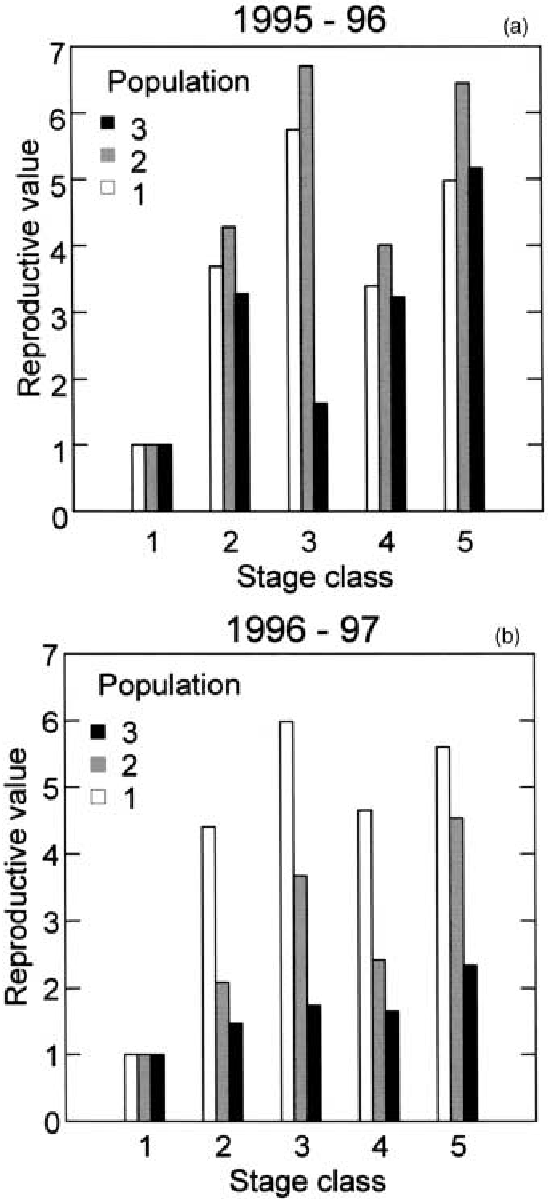

Fig. 2. Reproductive values of each stage class in three natural populations of *Oxalis acetosella* near Uppsala, central Sweden, obtained from deterministic matrix simulations for the transition intervals a) 1995–1996 and b) 1996–1997. Stage classes: 1: seedlings; 2: non-flowering new ramets; 3: flowering new ramets; 4: non-flowering adult plants; 5: flowering adult plants. Populations: 1: deciduous forest; 2: pine forest; 3: spruce forest.

Discussion

These results enable me to make suggestions regarding the impact of the different life-history events on population growth and maintenance in *O. acetosella*, in particular the relative significance of seedling and ramet recruitment. However, it is important to note that they are the results of a study for only three years, and should thus be interpreted with some caution. This goes especially for the simulated population growth rates and extinction probabilities.

Looking first at basic demography, the stage structure varied substantially among populations and years (cf. Shorina 1985). Adults generally dominated, but there was variation in the relationship between seedling and new ramet numbers; in P2, seedling production was higher than ramet production in all three years, while in P3 it was always lower, and in P1 this relationship varied. This agrees with the probabilities of reproduction in the different populations (see also Berg and Redbo-Torstensson 1998).

When examining elasticities, I found that stasis in adult plants clearly had the highest values, though varying among populations. This is to be expected in a species with a dominance of adults and high life-expectancy (Damman and Cain 1998, de Kroon et al. 2000). The entries related to production and survival of seedlings and new ramets had in general low and highly variable elasticities, which is also not surprising (Damman and Cain 1998). However, as de Kroon et al. (2000) point out, the life-history events that have the highest elasticities are not always the most important for population growth. The elasticities of adults producing seedlings and seedlings surviving to non-flowering adults were positively correlated with λ, which means that the populations/plots having the highest seedling recruitment also had the highest growth rates (cf. Silvertown et al. 1993, Horvitz and Schemske 1995, Oostermeijer et al. 1996, Valverde and Silvertown 1998). This is obvious for P2, which had relatively high proportions of flowering plants and seedlings, and a high ln λ. The elasticity of stasis in non-flowering adults was, on the contrary, negatively correlated with λ, because this stage class has a relatively low reproductive value (Fig. 2).

The summed elasticities of seedling production and survival were also positively correlated with λ, while the summed elasticity of adult survival was negatively correlated with λ. A negative relationship between stasis and population growth has been found also in other perennial species (Silvertown et al. 1993, Oostermeijer et al. 1996, Valverde and Silvertown 1998), and in this case it must be explained by a high proportion of non-flowering plants among the adults. In contrast, a successful reproductive pathway (e.g. high seedling production, good recruitment from seedlings to the adult stage) will favour population growth (de Kroon et al. 1987, 2000). The same does not seem to be true for vegetative propagation; there was no correlation between λ and the elasticities of production or survival of new ramets. A lack of correlation between clonal growth and population growth rate was found also by Silvertown et al. (1993) for several species.

The negative correlation between the elasticities of seedling and ramet production could suggest a trade-off

Table 6. Matrix of Pearson correlation coefficients among λ and the elasticities (e) of the five main population processes, pooled for deterministic matrix simulations of growth of three natural populations (10 plots each) of *Oxalis acetosella* near Uppsala, central Sweden, and for two transition intervals (1995–1996 and 1996–1997). 1: seedling production; 2: ramet production; 3: seedling survival; 4: survival of new ramets; 5: adult survival. DF = 15, n = 60. Asterisks denote the statistical significance of each correlation coefficient: *: $p < 0.025$; **: $p < 0.01$; ***: $p < 0.001$.

	λ	e1	e2	e3	e4
e1	0.318 *				
e2	0.142	−0.417 **			
e3	0.318 *	1.000 ***	−0.417 **		
e4	0.083	−0.463 ***	0.980 ***	−0.463 ***	
e5	−0.296 *	−0.031	−0.892 ***	−0.031	−0.863 ***

between reproduction and vegetative propagation (Silvertown et al. 1993; cf. also Eriksson 1997). Correspondingly, the negative correlations between the elasticities of production and survival of new ramets on the one hand, and the elasticity of adult survival on the other, may indicate a high cost of vegetative propagation. Such a cost was found by Eriksson (1988) in *Argentina anserina*, with no equivalent cost of reproduction. However, de Kroon et al. (2000) have advised caution in explaining negative elasticity correlations with trade-offs between life-history traits.

As for the predicted development of the populations, they seem to go in different directions according to the simulated growth rates, although in the ANOVA λ did not differ significantly among populations (cf. Ehrlén 1995). P1 is slowly decreasing, possibly due to relatively high mortality of flowering adults which is not compensated for by seedling or ramet recruitment. This may be due to the drier and more exposed conditions in this population. P2 obviously has good conditions for reproduction, and is slowly increasing due to fairly efficient seedling recruitment. This population is probably younger than the others since it grows in a tree plantation, which may in part explain the relatively high seedling production (cf. de Kroon et al. 1987, Eriksson 1997). P3, which is in a dark and cool, more stable habitat, has comparatively low reproduction and relies more on ramet recruitment, in line with theory and previous findings on clonal herbs (Tamm 1972, Barkham 1980, Eriksson 1989, Silvertown et al. 1993, Damman and Cain 1998).

However, judging from the elasticity analyses, all three populations are apparently to some extent dependent on seedlings for their expansion. This can be explained from life-history characteristics of *O. acetosella*. Adult survival in the present study was lower and more variable than expected for a perennial forest plant, ranging from 67 to 88% depending on population and year (cf. Tamm 1972, Harper 1977, Damman and Cain 1998). Furthermore, the relationship between plant density and mortality was not very strong, and density did not affect leaf number or flowering probability. This is likely due to the sensitivity of this species to density-independent factors such as drought and frost (shallow, thin root system), and to its high tolerance to shade and root competition (Bråkenhielm 1977, Grime et al. 1988). Thus, since long-term survival of established plants is unsecure, and limited by factors other than light and space, recruitment of seedlings into populations is probably necessary as a complement to the rather low ramet production (see also Shorina 1985, Chernenkova and Shorina 1990). Another indication of this is the observation that ramets may reproduce already in their first year above ground. Moreover, even seedlings of *O. acetosella* can produce CL seeds (Bråkenhielm 1977, Chernenkova and Shorina 1990, Berg unpubl.), although this was not observed in the present study. In other clonal species, seedling recruitment has also been found to be important for population maintenance, apart from its obvious effects on genetic diversity (de Kroon et al. 1987, Kéry et al. 2000, Verburg et al. 2000).

Then, what parts do the CH and CL flowering modes play in seedling production? From the present study, I have obtained the percentages of the flowering plants producing CH and CL flowers, respectively, for each population and year. By applying data from earlier studies on CH and CL fruit- and seed-set (Berg and Redbo-Torstensson 1998) and seed germination (Berg and Redbo-Torstensson 2000) in these populations, it can be approximated that ca 15% of the seedlings in P1, ca 30% of the seedlings in P2, and ca 45% of the seedlings in P3 are of CH origin. Since CH and CL seedlings do not differ in survivorship (Berg and Redbo-Torstensson 2000), these would be the contributions of the CH phase to the adult plant populations, though varying greatly among years (Berg and Redbo-Torstensson 1998). These contributions are quite substantial, in contrast to theoretical predictions about cleistogamy (Darwin 1877, Schoen and Lloyd 1984). Both phases show large spatial and temporal variation in reproductive success, but they complement each other by having partly divergent fitness responses to environmental variation, and so optimize total seed-set (Berg and Redbo-Torstensson 1998). Thus, I may conclude that this dimorphic reproductive strategy, maximizing seed output and thus seedling recruitment, has significance for the growth and long-term maintenance of *O. acetosella* populations.

Acknowledgements – I would first like to thank my former supervisor Peter Redbo-Torstensson, who came up with the idea of this study and gave comments on the original manuscript, and Stefan Björklund, technician at the Dept of Plant Ecology, for making the plot frame with grid. Many thanks to Galina Semenova and Galina Pokarzhevskaya for translation of Russian literature, and to Kari Lehtilä, Carol Horvitz, Shripad Tuljapurkar, and John B. Pascarella for permission to use their matrix programs. My gratitude also to Stefan Andersson, T. M. Culley, Bengt Carlsson, Tesfaye Bekele, Brita Svensson, and Diethart Matthies for valuable advice and discussions. The study was economically supported by the Swedish Natural Science Research Council (NFR).

References

Barkham, J. P. 1980. Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*). I. Clonal growth, seed reproduction, mortality and the effects of density. – J. Ecol. 68: 607–633.

Berg, H. 2000. Differential seed dispersal in *Oxalis acetosella*, a cleistogamous perennial herb. – Acta Oecol. 21: 109–118.

Berg, H. and Redbo-Torstensson, P. 1998. Cleistogamy as a bet-hedging strategy in *Oxalis acetosella*, a perennial herb. – J. Ecol. 86: 491–500.

Berg, H. and Redbo-Torstensson, P. 2000. Offspring performance in *Oxalis acetosella*, a cleistogamous perennial herb. – Plant Biol. 2: 638–645.

Bråkenhielm, S. 1977. Vegetation dynamics of afforested farmland in a district of south-eastern Sweden. – Acta Phytogeogr. Suec. 63.

Caswell, H. 1989. Matrix population models. – Sinauer.

Chernenkova, T. V. and Shorina, N. I. 1990. *Oxalis acetosella* L. – In: Pavlov, V. N., Rabotnov, T. A. and Tikhomirov, V. N. (eds), Biological flora of the Moscow region, part 8. Moscow Univ. Press, pp. 154–172, in Russian.

Damman, H. and Cain, M. L. 1998. Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. – J. Ecol. 86: 13–26.

Darwin, C. 1877. The different forms of flowers on plants of the same species. – John Murray.

de Kroon, H., Plaisier, A. and van Groenendael, J. 1987. Density dependent simulation of the population dynamics of a perennial grassland species, *Hypochaeris radicata*. – Oikos 50: 3–12.

de Kroon, H., van Groenendael, J. and Ehrlén, J. 2000. Elasticities: a review of methods and model limitations. – Ecology 81: 607–618.

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

Eriksson, O. 1988. Ramet behaviour and population growth in the clonal herb *Potentilla anserina*. – J. Ecol. 76: 522–536.

Eriksson, O. 1989. Seedling dynamics and life histories in clonal plants. – Oikos 55: 231–238.

Eriksson, O. 1997. Clonal life histories and the evolution of seed recruitment. – In: de Kroon, H. and van Groenendael, J. (eds), The ecology and evolution of clonal plants. Backhuys Publishers, pp. 211–226.

Grime, J. P., Hodgson, J. G. and Hunt, R. 1988. Comparative plant ecology. – Unwin Hyman.

Harper, J. L. 1977. Population biology of plants. – Academic Press.

Horvitz, C. C. and Schemske, D. W. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. – Ecol. Monogr. 65: 155–192.

Karlsson, T. 1998. Förteckning över svenska kärlväxter. – Sv. Bot. Tidskr. 91: 241-560, in Swedish.

Kéry, M., Matthies, D. and Spillmann, H.-H. 2000. Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. – J. Ecol. 88: 17–30.

Lord, E. M. 1981. Cleistogamy: a tool for the study of floral morphogenesis, function and evolution. – Bot. Rev. 47: 421–449.

Odell, G. and Drakenberg, B. 1991. Atlas över skogsmarksväxters förekomst i Sverige. Reports in forest ecology and forest soils 64. – Dept of Forest Soils, Swedish Univ. of Agricult. Sci., in Swedish.

Oostermeijer, J. G. B. et al. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. – J. Ecol. 84: 153–166.

Packham, J. R. 1978. Biological flora of the British Isles: *Oxalis acetosella* L. – J. Ecol 66: 669–693.

Redbo-Torstensson, P. and Berg, H. 1995. Seasonal cleistogamy: a conditional strategy to provide reproductive assurance. – Acta Bot. Neerl. 44: 247–256.

Schemske, D. W. 1978. Evolution of reproductive characteristics in *Impatiens* (Balsaminaceae): the significance of cleistogamy and chasmogamy. – Ecology 59: 596–613.

Schoen, D. J. and Lloyd, D. G. 1984. The selection of cleistogamy and heteromorphic diaspores. – Biol. J. Linn. Soc. 23: 303–322.

Shorina, I. I. 1985. Seasonal dynamics of coenopopulations of *Oxalis acetosella* in relation to its biology. – In: Serebrjakova, I. I. (ed.), Dynamics of plant coenopopulations. Nauka, pp. 36–45, in Russian.

Silvertown, J. et al. 1993. Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. – J. Ecol. 81: 465–476.

Tamm, C. O. 1972. Survival and flowering of perennial herbs III. The behaviour of *Primula veris* on permanent plots. – Oikos 23: 159–166.

Valverde, T. and Silvertown, J. 1998. Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. – J. Ecol. 86: 545–562.

Verburg, R., Maas, J. and During, H. J. 2000. Clonal diversity in differently-aged populations of the pseudo-annual clonal plant *Circaea lutetiana* L. – Plant Biol. 2: 646–652.

Waller, D. M. 1979. The relative costs of self- and cross-fertilized seeds in *Impatiens capensis* (Balsaminaceae). – Am. J. Bot. 66: 313–320.

Wilkinson, L. 1997. SYSTAT 7.0 for Windows. – SPSS.