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Population dynamics of *Agrimonia eupatoria* and *Geum rivale*, two perennial grassland species

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Abstract

The population dynamics of two polycarpic perennials, *Agrimonia eupatoria and Geum rivale*, characteristic of semi-natural grasslands in Scandinavia, were examined in south-eastern Sweden. The perennial forbs were studied for several years in two populations each, located in habitats characteristic for the species in the study area. Demographic transition probabilities varied significantly between populations and among years for the species. Transition matrix modelling yielded λ-values (population growth rates) that ranged from 0.89 to 1.14 for *A. eupatoria* and from 0.94 to 1.04 for *G. rivale*. The elasticity analysis showed that stasis in the adult stage classes contributed most to λ. The life-table response experiment analysis produced similar results as the elasticity analysis, where stasis together with progression in the adult stage classes made a large contribution to the observed spatial variation in λ. Simulations of expected time to extinction were in the order of centuries for the study populations. Seedling recruitment was enhanced by seed addition and small scale disturbance in populations. For the intermediately abundant and more patchily distributed *A. eupatoria*, a regional survey of local populations was conducted in the study area which revealed that most populations were relatively small (< 100 individuals) and restricted to grassland fragments in road verges. Furthermore, an attempt was made to estimate fruit dispersal from local populations.

Introduction

An important issue for both long term predictions about population fates and insights about the evolution of life histories is understanding how structured populations respond to spatial and temporal variation (Horwitz and Schemske 1995; Oostermeijer et al. 1996; Menges and Dolan 1998; Ehrlén 1999). The population dynamics of long-lived plants are difficult to study within the temporal and spatial scales usually considered in demographic investigations (Inghe and Tamm 1985; Crawley 1990; Eriksson 1994; Valverde and Silvertown 1997a). Many perennials are characterised by the long periods that ramets spend in a vegetative stage and the often infrequent recruitment from seedlings (Harper 1977; Cook 1985; Eriksson 1989, 1994; Meyer and Schmid 1999a, 1999b). The survival (stasis and retrogression) and growth (progression) of established plants are often more important to population growth than fecundity (Silvertown et al. 1993, 1996; Alvarez-Buylla et al. 1996).

Patterns of population development can be simulated by transition matrix models incorporating demographic data from real populations (Caswell 1989). These models are useful for analysing the status of species, e.g. the probability of local population extinction, and hence of interest in conservation biology (Nunney and Campbell 1993; Schemske et al. 1994; Menges 1998). Simulations of extinction risks, based on demographic data, have been done for a few species (Menges 1990; Eriksson 1994; Nantel et al. 1996; Menges 2000), confirming that extinction risks are related to life-cycle structure and population size (Caswell 1989). Besides data on spatiotemporal variation in demography, the identification of factors that determine recruitment rates are of interest, e.g. to gather data on the importance of seed input for the dynamics and survival of local populations (Eriksson and Ehrlén 1992). Factors influencing the number of populations may be as important as within-population dynamics in determining whether a species persists or becomes extinct (Schemske et al. 1994). The metapopulation concept, a system of local populations interconnected by dispersal, has usually been applied in studies of species living in a fragmented habitat. The dynamics of metapopulations are closely linked with the processes of population turn-over, i.e. colonisation and extinction of local populations (Husband and Barrett 1996; Hanski and Gilpin 1997).

In Sweden (as in most of Europe), semi-natural grasslands are presently declining (Eriksson et al. 1995; Ihse 1995). The destruction and fragmentation of semi-natural grasslands results in fewer and smaller habitat patches with fewer and smaller populations. These nutrient-poor grassland habitats are of interest due to their species-richness (Eriksson and Eriksson 1997). It has been suggested that "linear elements" of the landscape, e.g. road verges, ditches and hedges, may function as marginal habitats for grassland plants and aid in the dispersal between their "real" habitats (Verkaar 1990; van Dorp 1996; Kiviniemi and Eriksson 1999). Linear elements are also subject to a general decline (Ihse 1995). The perennial species in focus of this study, *Agrimonia eupatoria* L. and *Geum rivale* L, are common in these fragmented habitats in south-eastern Sweden. In the study area (the Ludgo Parish), the populations of *A. eupatoria* have become highly fragmented with the majority of the populations located in marginal grassland fragments. Based on estimations of the extinction threshold (i.e. the minimum amount of habitat needed for a species to maintain a persistent metapopulation), *A. eupatoria* may at present be declining in the study area (Eriksson and Kiviniemi 1999).

The main objective of this study was to examine population dynamics for two relatively long-lived species (one clonal), occurring in defined small populations, in order to contribute to generalisations regarding the dynamics and extinction risks of perennial plant populations. Both species possess adhesive fruits that can be dispersed externally in animal fur (Kiviniemi 1996). *Agrimonia eupatoria* was studied during six years in two road verge populations, hence this study provide data of population dynamics in linear elements (dispersal corridors). *Geum rivale* was studied in four years in two populations, one population located in a semi-natural grassland and another in a deciduous forest. The observed variation in demographic parameters was incorporated into matrix models in order to project population growth and dynamics of the species. A regional survey of the local populations was conducted for *A. eupatoria*, which in contrast to *G. rivale*, has a patchy distribution in the study area. The number and size of populations were censused over three years. Seed dispersal is of interest for the persistence of a metapopulation, therefore an attempt was made to estimate the "natural" dispersal of *A. eupatoria* fruits from local populations (which was conducted in the two study populations).

Specifically, the aims were (1) to examine the spatiotemporal variation in demographic transition probabilities, population structure and population growth rate (λ); (2) to examine the sensitivity of population growth rate to changes in specific transitions in the life-cycle; (3) to estimate extinction risks for the study populations and how such risks were related to initial population size and (4) to examine effects of seed addition within local populations. The implications of the results for the survival of the perennial plant species in fragmented landscapes are discussed.

Methods

Species

Agrimonia eupatoria L. and *Geum rivale* L. are polycarpic hemicryptophytic perennials belonging to the family Rosaceae, subfamily Rosoideae. Besides open grassland, both species also occur in wood edges and road verges. *Geum rivale* also grows in semi-open deciduous forests. *Agrimonia eupatoria* develops rather coarse stems (usually single stems) from a subterranean rhizome, up to one metre in height, with a basal rosette of leaves and with racemose inflorescences, i.e. single flowers arranged spirally around the stem with the lowermost flowers opening first. The species begins to flower at mid-summer (July) and the flowering period is long. The fruiting unit of *A. eupatoria* is a receptacle with hooked bristlets on the edge usually enclosing one seed (hereafter termed fruit). Mean fruit weight is 18.0 mg (S.D. = ± 6.21, n = 50).

Geum rivale is a clonal herb that has a well-developed branched rhizome, which is actually an organ intermediate between a rhizome and an overground steam (caudex) (Taylor 1997). The growing parts of the rhizome produce above-ground shoots, leaf rosettes. The rosettes are initially interconnected, but as the older parts of the rhizome decay, they may become separate parts (ramets). The species begins to flower in May, erect stems (one to several) up to a half metre in height, are developed from the rosettes with usually two to five pendent flowers. The fruits are achenes with a hairy hooked style and have an average weight of 1.2 mg (S.D. = ± 0.25, n = 50). The nomenclature used is according to Lid and Lid (1994).

Field studies

The field work was performed during 1993–1998 in the surroundings of Tovetorp Zoological Research Station situated in the Ludgo Parish in the eastern part of Södermanland County in southern Sweden, about 100 km SSW of Stockholm (17 °8′E, 58 °56′N). The study area includes arable land and pastures as well as deciduous and coniferous forests.

Demography

Demographic studies of *A. eupatoria* were conducted in two populations (five kilometres apart). The populations were monitored during 1993–1998 and both populations occurred at road verges along gravelled roads adjacent to arable fields. The study populations differed in size, the smaller population (A) consisted of c. 150 individuals (vegetative or reproductive), whereas the larger population (B) consisted of about 1000 individuals. In population A, *A. eupatoria* grew only on one side of the road along a distance of less than 10 meters and quite isolated from other *A. eupatoria* populations (two kilometres to the nearest population). In population B, *A. eupatoria* occurred on both sides along a distance of c. 100 meters and not so far from other populations (c. 400 meters). Common species in the road verge populations were *Achillea millefolium, Agrostis capillaris, Anthriscus sylvestris, Artemisia vulgaris, Festuca ovina, Galium verum, Pimpinella saxifraga, Poa pratense, Potentilla reptans* and various *Trifolium* species (Kiviniemi and Eriksson 1999). In 1993 permanent plots (0.25 m^2) were established in the two populations, three in population A and five in population B. Mapping was conducted during (1) flowering and (2) fruit maturation. The number of leaves, flowers and fruits of the individuals were recorded. The size of the plants was measured as height of stem. The plants were identified by their position (grid position) and followed individually throughout the study. During the study, the size (height) of the vegetative plants of *A. eupatoria* ranged between 3 and 54 cm (overall median size = 18, n = 206). The size distribution of the reproductive plants was normally distributed with an overall mean size of 57 cm (S.D. = ± 19, n = 442).

The demographic studies of *G. rivale* were conducted during 1993–1996 in two populations (five kilometres apart). One population (C) was studied in a deciduous forest (a few hundred plants) adjacent to a gravelled road, and the other population (D) was studied in a semi-natural grassland (> 1000 plants). Common species in the deciduous forest population were *Anemone nemorosa, Betula pubescens, Corylus avellana, Fragaria vesca, Geranium sylvaticum, Quercus robur* and various *Ranunculus* species. In the semi-natural grassland population commonly occurring species were *Achillea millifolium, Agrostis capillaris, Anthoxanthum odoratum, Fragaria vesca, Galium verum, Luzula campestris, Potentilla erecta and Rumex acetosa* (Eriksson and Eriksson 1997). In 1993 permanent plots (0.25 m^2) were established in the two populations, three in population C and three in population D (one more plot was established in population D in 1994). The mapping of the plants was done as for *A. eupatoria* (described above). The size of the plants was measured as the rosette diameter. The size distribution of the rosettes in the deciduous forest population C was normally distributed, which was not the case for semi-natural grassland population D. During the study, the individual rosettes in population C ranged between 21 and 63 cm (overall $\bar{x}$ = 39 cm, S. D. = ± 8, n = 244). In population D, the overall median size of the rosettes was 9 cm (range = 3–23, n = 648).

Seed addition experiment

In this study, seed addition was only conducted for *G. rivale*. Seedling recruitment was examined in both populations. In 1993, seeds (achenes) were sown in disturbed and undisturbed plots (0.04 m^2). In disturbed plots the vegetation was removed by hand and the ground was laid bare. Four replicate plots were used per treatment (i.e. disturbed and undisturbed plots) and the number of seeds sown was 100 (4 replicates × 2 treatments × 2 populations × 100 seeds = 1600 seeds totally). Two control plots per treatment were used in both populations (with no addition of seed). Seedling recruitment was monitored for two years (1994–1995). For *A. eupatoria*, thorough studies of seedling recruitment (with the same methodology as for *G. rivale*) has been carried out along road verges in the study area (Kiviniemi and Eriksson (1999), K. Kiviniemi in prep.).

Regional survey of Agrimonia eupatoria *populations*

In the Ludgo Parish (about 103 km^2), *Agrimonia eupatoria* occurs in 28 of 103 km^2 squares whereas *G. rivale* occurs in 101 of 103 km^2 squares. A total of 57 populations (based on a survey by H. Berglund, unpubl.) in the Ludgo Parish have been revisited during 1994 to 1998. The populations were visited once a year during August–September. In 1994, the populations were visited and the occurrence of the species was recorded. Since 1995 the number of vegetative and reproductive individuals have been recorded in the populations. Apparent extinctions were thus based on repeated counts of the number of vegetative and flowering stems. New foundings of populations were observed during the study (new colonisations were not actively looked for in this study). The minimum distance between two populations was c. 150 meters, but usually it was several hundred meters to kilometres.

Enclosure experiment of Agrimonia eupatoria *populations*

An attempt was made to estimate the relative proportion of fruit dispersal from individual plants in the two study populations by use of net enclosures. *Agrimonia eupatoria* possess adhesive fruits that can be dispersed in fur by various mammals (e.g. small rodents, hares, roe deers, fallow deers). The objective of the experiment was to examine the natural tendency of fruits to merely come loose and fall down without any interference of dispersal agents. The experiment was based on the assumption that dispersal would be reduced by the use of enclosures. A total of 71 inflorescences (71 individuals) were enclosed with a net, 21 in the smaller population (A) and 50 in the larger population (B). The mesh size of the net was 1 mm. The experiment was started in the end of July and was conducted to the end of September in 1995. For the enclosed inflorescences, the number of fruits attached to the inflorescence and the number of fruits that had fallen off the inflorescence were counted. Individual plants located in the permanent plots in population A and B, functioned as controls in the experiment.

Demographic analyses

The demographic data were analysed by matrix modelling, a method treated in detail by Caswell (1989). The individuals of *A. eupatoria* were divided into four stage classes: seedlings, juveniles (stem height < 10 cm), vegetative and reproductive (see life-cycle graph, Figure 1). The rosettes of *G. rivale* were divided into five stages: seedlings, juveniles, small vegetative, large vegetative and reproductive (Figure 2). The vegetative plants were divided at the middle of the size distribution, in population C at 39 cm and in population D at 8 cm (i.e. small vegetative plants were < 39 cm in population C and < 8 cm in population D). Juveniles (< 25 cm in population C and < 3 cm in population D) had a more slender growth form compared to "new" leaf rosettes produced by vegetative growth. *Geum rivale* was surpressed by grazing in the semi-natural grassland (Taylor 1997), therefore were the vegetative plants divided differently (regarding size) in the two populations. The seeds of *A. eupatoria* seem not to be capable of being dormant and viable in soil (i.e. dispersal in time) whereas the seeds of *G. rivale* seem to have a short-term persistence in soil (K. Kiviniemi in prep.). Most seeds of *G. rivale* persist only until start of next growing season (Grime et al. 1988). In the matrix analysis, it was assumed that seedling numbers in one year resulted from the previous year's reproduction. Thus, seeds produced in year *t* were assumed to develop into seedlings in the year *t*+1.

The transition matrix model used was $\boldsymbol{n}_t+1 = \boldsymbol{A}\times\boldsymbol{n}_t$ where $\mathbf{n}_t$ is the column vector describing the stage structure of the population at time t, and **A** is the matrix including the transition probabilities from one stage class to another and the reproductive contribution of each stage class. Transition probabilities were calculated as the proportion of the individuals in each stage class at time t, which, at time t+1, had changed to the other classes, or remained in the same stage class. For *A. eupatoria*, ten transition matrices were made, i.e. five one year intervals × two populations (Appendix 1). For *G. rivale* six transition matrices were made, i.e. three one year intervals × two populations (Appendix 2). For both species, log-linear models were used in order to analyse effects of population (site) and year on demographic fate, i.e. the variability of demographic transition probabilities (Table 1). The fate of the stage classes was analysed as: mortality vs. changing stage class for seedlings; changing stage class vs. not changing stage class/mor-

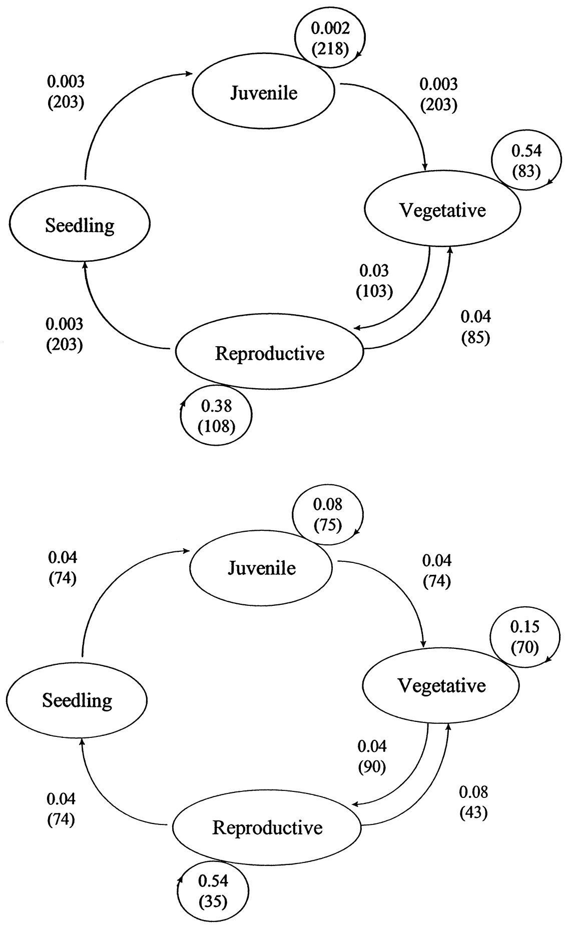

Figure 1. Life-cycle graph for *Agrimonia eupatoria* including four life cycle stages, seedlings, juveniles, vegetative and reproductive individuals. (a) The small population A. (b) The large population B. The figures on the arrows are elasticity values (average from five matrices). The coefficients of variation (temporal variation) for the elasticities are shown within brackets.

tality, or not changing stage class vs. changing stage class/mortality for vegetative and reproductive individuals. For both species, in a few instances, adult plants shrunk in size during certain years. For *A. eupatoria*, totally six individuals shrunk (< 10 cm in height), and for *G. rivale*, four plants in population C shrunk (< 25 cm in rosette diameter). These plants were all categorised as adults during shrinkage.

Projections of each individual transition matrix (deterministic or stable simulation) were conducted in order to obtain the stable stage distribution, the growth rate of the population (λ), and the sensitivity (s_{ij}) of λ to changes in matrix elements (a_{ij}) ($s_{ij} = \delta\lambda/\delta a_{ij}$) (Caswell 1989). Sensitivity predicts the impact of hypothetical alterations in a_{ij} on population growth rate. In order to compensate for differences in absolute values of a_{ij}, elasticity, defined as the proportional change in λ resulting from a proportional change in a_{ij}, was used as a sensitivity measure (de Kroon et al. 1986). Elasticities are additive, summing to one for a single matrix, and hence comparable among stages. Life-table response experiment analyses (LTRE's) (Caswell 1989; Horwitz et al. 1997; Ehrlén 1999) were also conducted in order to examine between-site variation in population growth rate within each year (i.e. several matrices are incorporated in the analyses). This analysis examine which matrix elements contributed most to the observed difference in λ between sites, i.e. populations. The difference in λ is decomposed into contributions from

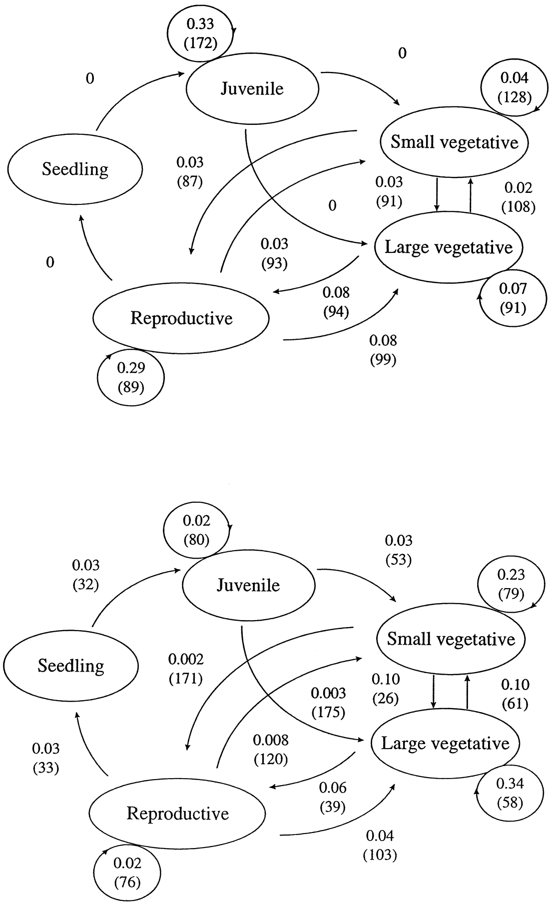

Figure 2. Life-cycle graph for *Geum rivale* including five life cycle stages, seedlings, juveniles, small vegetative, large vegetative and reproductive plants. (a) The deciduous forest population C. (b) The semi-natural population D. The figures on the arrows are elasticity values (average from three matrices). The coefficients of variation (temporal variation) for the elasticities are shown within brackets.

Table 1. Results from log-linear analyses of effects of population and year on demographic fate of *Agrimonia eupatoria* and *Geum rivale*. Demographic fate was dying, not changing stage class or changing stage class (see Methods). Significant effects on transitions probabilities are given as * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$.

Stage	Population	Year
Agrimonia eupatoria		
Seedling	**	***
Juvenile	**	*
Vegetative	*	***
Reproductive	**	***
Geum rivale		
Seedling	***	N.S.
Juvenile	N.S.	N.S.
Small vegetative	***	**
Large vegetative	***	N.S.
Reproductive	***	N.S.

each matrix element. The equation used was:

$$\mathrm{LTRE}_{ij} = (a_{ij}^{A} - a_{ij}^{(A+B)/2}) \times (\delta\lambda/\delta a_{ij})\big|_{(A+(A+B)/2)/2} \qquad (1)$$

where **A** and **B** are different matrices (populations). The equation describe the LTRE-effect from actual differences in a matrix element weighted by the sensitivity of λ to that element. The sensitivity is evaluated at a mean matrix, "midway" between the two matrices being compared (Caswell 1989). For the two species, for each of the transition years one mean matrix was produced from the two populations (sites) and the deviation from this was calculated. Thus, elasticity and LTRE analyses both depend on the matrix transition elements (vital rates). LTRE analysis express variation in λ as a function of observed variation in the vital rates, whereas elasticities project how much λ would change in response to hypothetical changes in vital rates independent of any actual past variation in those rates (Caswell 2000).

The demographic data for the two species were analysed by stochastic models where matrices were assigned equal probability of sampling (Caswell 1989). Stochastic population simulations do not yield a stable stage distribution, but instead they generate a distribution of population structure distributions. Average population growth rate and stage distribution were calculated from 3000 simulations of 50 years each. For *A. eupatoria*, the initial population size was 100 individuals for population A and 1000 individuals for population B. For *G. rivale*, the initial size was 400 individuals for population C and 1000 for population D. The stage structures obtained by deterministic and stochastic analysis were compared to those observed in the field (χ^2-test on mean values). The stage structures were based on the total number of individuals observed in the permanent plots in the populations during the study.

Stochastic simulations were also performed in order to simulate the expected time to extinction in relation to initial population size (N_0) (Caswell 1989). The range of N_0 examined was 10–5000. The range of N_0 examined differed between the simulation series due to differences in population size between the study populations, and for *A. eupatoria* also with respect to the observed population sizes in the Ludgo Parish. For the simulation series, the expected time to extinction was calculated from 100 simulations with 1000 years each. In the stochastic simulations the initial population sizes were distributed among stage classes in proportions equal to those observed in field (averages from five matrices and three matrices, respectively). Thus, calculations were influenced by the initial size distribution, e.g. stochastic λ, in order to simulate the future development of the study populations. The simulations were made with the software PopMat (K. Lehtilä, unpubl.).

Results

Demographic variation

The demographic study of *A. eupatoria* was based on mappings of a total 240 individuals encountered in the study plots during six years and a total of 397 plants of *G. rivale* during four years. Plant densities (based on observations in permanent plots) ranged between 50–122 plants per m^2 for *A. eupatoria* and between 89–244 plants per m^2 for *G. rivale*. The overall median number of fruits produced per reproducing individual (not normally distributed) of *A. eupatoria* in population A and B was 31 (range = 0–197), n = 183) and 46 (range = 0–423, n = 230), respectively. Large individuals (> 40 cm in height) were able to reproduce during successive years. The overall median number of fruits produced per flower in the two *G. rivale* populations C and D was 60 (range = 25–118, n = 46) and 42 (range = 30–60, n = 18). For *A. eupatoria*, the demographic transition probabilities of the stage classes varied among years and between populations (Table 1). For *G. rivale* the transition probabilities differed significantly more often between populations (Table 1). The mortality of most stage classes was indifferent to year and population (Log-linear model: mortality vs. changing/not changing stage class). However, the juvenile mortality of *A. eupatoria* varied significantly among populations and the mortality of small vegetative rosettes of *G. rivale* varied significantly among years (Log-linear model: $P < 0.01$). Annual mortality of seedlings and juveniles varied between 0 – 89% for *A. eupatoria* and between 0–100% for *G. rivale*. Average annual mortality did not exceed 8% for adults, and 2% for reproductive ones.

Matrix analyses

Stage distribution

Adult plant stages accounted for c. 80% of the observed individuals in three of the four study populations (69% in population B) (Figures 3a and 3b). The simulated stage structures (i.e. the stable stage structure generated by deterministic analysis and the distribution of stage structures generated by stochastic models) and the observed stage structure of the road verge populations of *A. eupatoria* had an overall similar pattern for the larger population (B) (Figure 3a). The observed stage structure of the smaller population (A) deviated significantly from the stable stage structure (χ^2-tests on mean values, $\chi^2 = 24.1$, df = 3, $P < 0.001$), e.g. vegetative plants were under-represented in the observed stage structure. The observed stage structures of the *G. rivale* populations (Figure 3b) deviated significantly from the stable stage structures (Population C: $\chi^2 = 72.1$, df = 4, $P < 0.001$; D: $\chi^2 = 20.1$, df = 4, $P < 0.001$) and the distribution of stochastic stage structures (C: $\chi^2 = 22.5$, df = 4, $P < 0.01$; D: $\chi^2 = 25.0$ df = 4, $P < 0.001$). For example, in both populations small vegetative rosettes were over-represented. Thus, the observed stage structures of three of the study populations deviated from the simulated ones, which implies that the stage structure of the populations will change if the conditions during the study prevail.

Population growth

Simple projection matrices generated population growth values (λ) that ranged from 0.89–1.14 for *A. eupatoria* ($\bar{x} = 1.00$, S.D. = ± 0.08, n = 10) (Table 2). The smaller population (A) was projected to be declining whereas the larger population (B) was projected to be growing. For *G. rivale*, the stable simulation generated λ-values that ranged from 0.94–1.04 ($\bar{x} = 1.00$, S.D. = ± 0.03, n = 6) (Table 3). The λ-values from the stochastic simulations were similar to those projected with the deterministic models (Tables 2 and 3).

Elasticity

In both populations of *A. eupatoria*, λ was projected to be most sensitive to matrix elements representing the likelihood of adults remaining in the same class (Figure 1). Reproductive individuals remaining reproductive contributed 54% to λ in the larger population (B). In the smaller population (A), vegetative plants remaining vegetative contributed most to λ (54%), and together with stasis in reproductive plants, these two transitions contributed 92% to λ. Fecundity and recruitment through seedlings affected λ little in both populations (Figure 1). The coefficients of variation (CV) among years for the elasticities ranged from 35% to 218% in the two populations (with greater CVs in population A).

The adult stage classes also contributed much to λ in the *G. rivale* populations (Figure 2). In the deciduous forest population (C), reproductive plants remaining reproductive contributed 29% to λ whereas vegetative plants remaining vegetative contributed 57% in the semi-natural grassland population (D). Transitions between these stage classes were also of importance for the *G. rivale* populations. For example, transitions between small and large vegetative plants contributed 20% to λ in the semi-natural grassland population (D) (Figure 2b). The mean elasticity for juveniles was 33% (CV = 172%) in the deciduous population (C) (Figure 2a). There were a few juveniles that remained in the juvenile stage till the end of the study (Appendix 2). Fecundity and recruitment through seedlings affected λ little in both populations. The coefficients of variation (CVs) for the elasticities ranged from 87% to 172% in population C and 26% to 175% in population D.

Life-table response experiment analyses

Matrix entries that have been most influential in determining the spatial variation in λ within years (Tables 4 and 5) were besides stasis in the adult stage classes (e.g. *A. eupatoria*: a_{44}; *G. rivale*: a_{55}), also progression in the adult stage classes (*A. eupatoria*: a_{43}; *G. rivale*: a_{54}). For *G. rivale* (Table 5), also the matrix transition from seedlings to juveniles (a_{21})

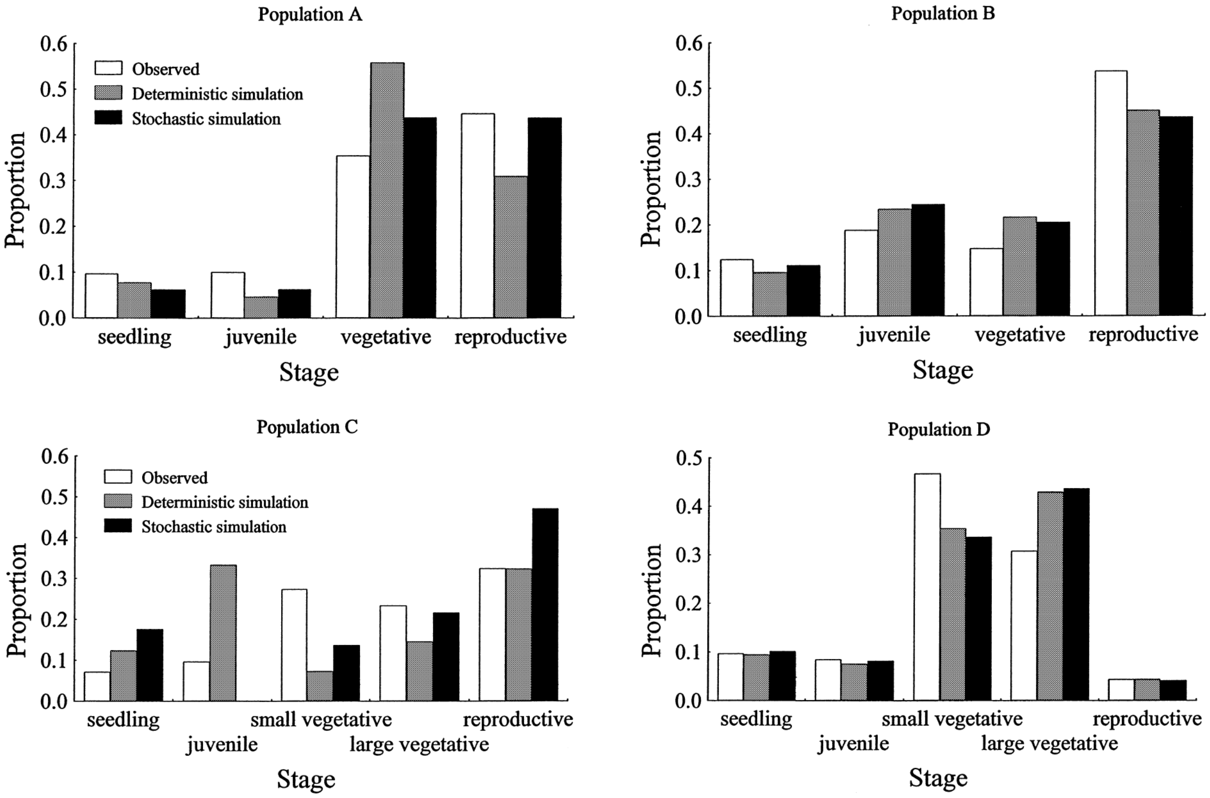

Figure 3. Observed and simulated population structure in two populations of (a) *Agrimonia eupatoria* (population A and population B) and (b) *Geum rivale* (population C and population D). Observed population structures and stable stage structures are mean values from five and three transition matrices respectively. The distributions of stage structure yielded by stochastic simulation are mean values based on 3000 simulations of 50 years each.

Table 2. Population growth rates, λ, of *Agrimonia eupatoria* for two populations during six years. λ-values were obtained by projection matrices and by stochastic models including five matrices with equal probability of sampling.

Year Deterministic simulation	Population A	Population B
93–94	1.02	1.14
94–95	0.95	1.07
95–96	0.89	0.99
96–97	0.98	1.08
97–98	0.93	0.96
Stochastic simulation	0.96	1.04

contributed to the difference in λ between populations.

Expected time to extinction

There was an exponential relationship between the initial population size and expected time to extinction. For the smaller *A. eupatoria* population (A), mean

Table 3. Population growth rates, λ, of *Geum rivale* for two populations during four years. λ-values were obtained by projection matrices and by stochastic models including three matrices with equal probability of sampling.

Year Deterministic simulation	Population C	Population D
93–94	1.00	1.02
94–95	0.99	1.04
95–96	1.00	0.94
Stochastic simulation	0.97	1.00

expected time to extinction was 124 years for a population size of 100 individuals (Figure 4). The expected time to extinction levelled out around 200 years for populations of more than 1000 individuals. For an initial population size of ten individuals in the larger population (B), the risk of extinction in 1000 years was zero. For the deciduous forest population (C) of *G. rivale*, the expected time to extinction levelled out around 240 years for populations of more

Table 4. Life-table-response experiment analysis of *Agrimonia eupatoria*. The LTRE-effect from differences in a matrix element a_{ij} to the differences in λ between the populations, population B - population A. The values are the observed differences in λ between the populations distributed among the matrix elements. Stage classes: 1 = seedlings, 2 = juveniles, 3 = vegetative and 4 = reproductive.

Matrix elements (a_{ij})	1993–94 (0.12)	1994–95 (0.12)	1995–96 (0.10)	1996–97 (0.10)	1997–98 (0.03)
a_{14}	0.048	0.012	0	0.004	0.011
a_{21}	0.060	−0.001	0	0.025	0.010
a_{22}	0.036	0.009	0	0.018	0.018
a_{32}	−0.022	0.024	0	0.030	−0.024
a_{33}	0.005	−0.093	−0.052	−0.014	−0.126
a_{43}	−0.001	0.151	0.092	0.023	0.141
a_{34}	0.032	−0.061	−0.071	−0.057	−0.026
a_{44}	−0.037	0.076	0.126	0.072	0.026
Σa_{ij}	0.12	0.12	0.10	0.10	0.03

Table 5. Life-table-response experiment analysis of *Geum rivale*. The LTRE-effect from differences in a matrix element a_{ij} to the differences in λ between the populations, population D - population C. The values are the observed differences in λ between the populations distributed among the matrix elements. Stage classes: 1 = seedling, 2 = juveniles, 3 = small vegetative, 4 = large vegetative and 5 = reproductive.

Matrix elements (a_{ij})	1993–94 (0.02)	1994–95 (0.05)	1995–96 (-0.06)
a_{15}	0.080	0.092	0.022
a_{21}	0.129	0.119	0.041
a_{22}	0.018	−0.033	−0.063
a_{32}	−0.006	0.060	0.022
a_{42}	0	0.043	0.019
a_{33}	0.178	0.008	0.010
a_{43}	−0.113	0.052	0.065
a_{53}	−0.130	−0.089	−0.057
a_{34}	0.033	0.061	−0.050
a_{44}	0.085	0.056	0.176
a_{54}	−0.157	−0.179	−0.136
a_{35}	0.029	0.013	−0.030
a_{45}	0.030	0.071	0.152
a_{55}	−0.128	−0.116	−0.152
Σa_{ij}	0.05	0.07	0.02

than 1000 plants (c. 200 years for a population of 400 plants) (Figure 5a). For population D, located in a semi-natural grassland, the expected time to extinction levelled out around 1300 years for population sizes of more than 500 plants (Figure 5b).

Seed addition experiment

In the seed-sowing experiment with *G. rivale* (Table 6), the number of seedlings recruited was significantly affected by site (population) and disturbance. There was a significant interaction between site and disturbance, i.e. disturbance had a positive effect for seedling recruitment in the semi-natural grassland population (D), but not for the deciduous forest population (C). Four seedlings emerged in the control plots (two seedlings in each population), none of the seedlings recruited.

Regional survey of Agrimonia eupatoria populations

Agrimonia eupatoria has a patchy distribution in the Ludgo Parish. A total of 66 occurrences of *A. eupatoria* populations have been observed in the study area, out of which 57 occurrences were reported before this study (–1992) (H. Berglund unpubl.) and nine “colonisations” have occurred during this study (1994–98). 22 populations have gone extinct in the

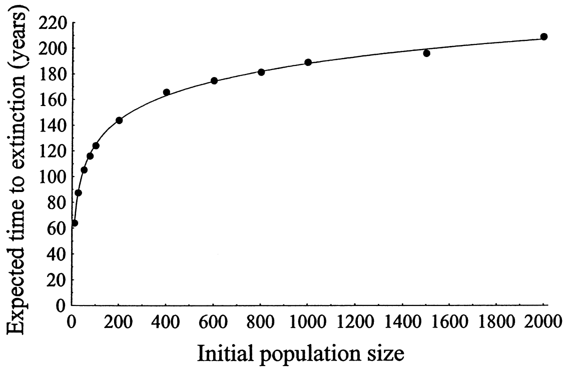

Figure 4. Expected time to extinction for *Agrimonia eupatoria* in relation to initial population size (N_0) for the small road verge population A. The expected time to extinction was obtained from stochastic modelling of five transition matrices with equal probability of sampling.

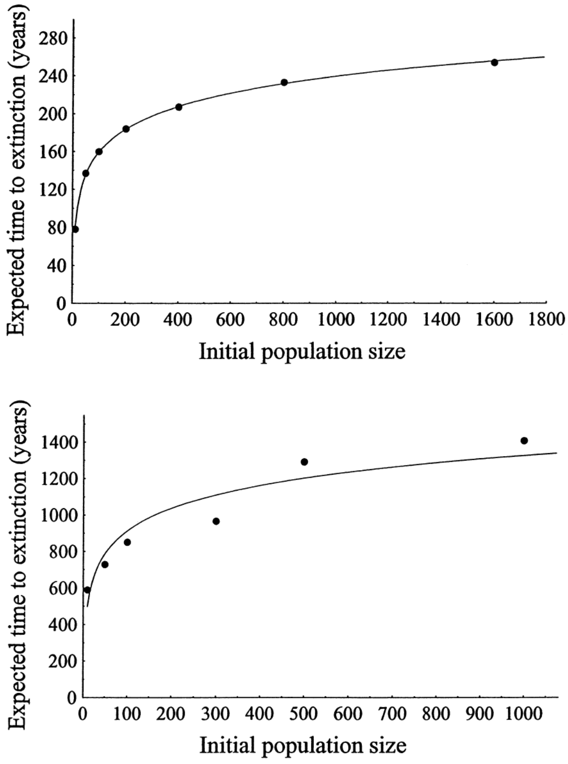

Figure 5. Expected time to extinction for *Geum rivale* in relation to initial population size (N_0) for (a) the deciduous forest population C and (b) the semi-natural grassland population D. The expected time to extinction was obtained from stochastic modelling of three transition matrices with equal probability of sampling.

Ludgo Parish (six populations during this study), i.e. 44 populations were left in 1998. The majority of the populations in the study area were quite small (Figure 6). In 1998, 63% of the populations had less than 100 individuals. The overall mean size of the populations with less than 50 individuals was 23 individuals (S.D. = ± 13.5, n = 79). The smallest population observed during 1994–98 had only two individuals which grew in a abandoned pasture. Three populations were quite large with more than 1000 individuals. These large populations were located in road verges that were regularly mown. In 1998, 88% (n = 44) of the populations were road verge populations.

Enclosure experiment of Agrimonia eupatoria populations

There was a significant effect of net enclosures on the number of fruits attached on *A. eupatoria* individuals (Figure 7). In both populations significantly more fruits were still attached on enclosed individuals in the end of September, whereas a large proportion of the fruits were lost ("dispersed") on control individuals (without nets). The percentage of fruits attached on control plants did not differ between the two populations (P = 0.55).

Discussion

It is a well known fact that the dynamics of populations of the same species may vary over time and space which is related to the underlying differences in demographic transition rates (Ehrlén 1999). This study showed that the populations of both these long-lived species exhibited stable dynamics. The stage structures of the populations were dominated by adult plant stages with a high average survival (usually more than 90%). Projected population growth rates (λ-values) varied moderately for both species, even though transition probabilities between stage classes varied significantly between populations and among years. The life-cycle structure of long-lived species can often buffer the effect of environmental variability, which will result in a rather stable dynamics of local populations (Eriksson 1996). If the conditions during the study prevail, adult plant stages will continue to dominate the structure and dynamics of these plant populations.

The population growth rates (λ) of *A. eupatoria* and *G. rivale* are similar to what has been reported in other studies of perennial herbs (Charron and Gagnon 1991; Silvertown et al. 1993; Ehrlén 1995; Eriksson and Eriksson 2000) summarised demographic data for 66 perennial species and concluded that fecundity and

Table 6. Recruitment of *Geum rivale* in the two study populations. The values represent the mean proportion of seeds (n=100 seeds in 4 replicate plots) developing into seedlings (that persisted to the end of the experiment) within disturbed and undisturbed plots. The P-values from log-linear models, regarding the effect of site (population), treatment, and the interaction of site and treatment on seedling recruitment, are presented. Significant effects are given as * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$.

Site (population)	Recruitment in disturbed plots (± S.D.)	Recruitment undisturbed plots (± S.D.)	Site (S)	Analyses Disturbance (D)	S × D
Deciduous forest (C)	0.003 (0.005)	0.005 (0.006)	***	***	*
Semi-natural grassland (D)	0.063 (0.043)	0.005 (0.010)			

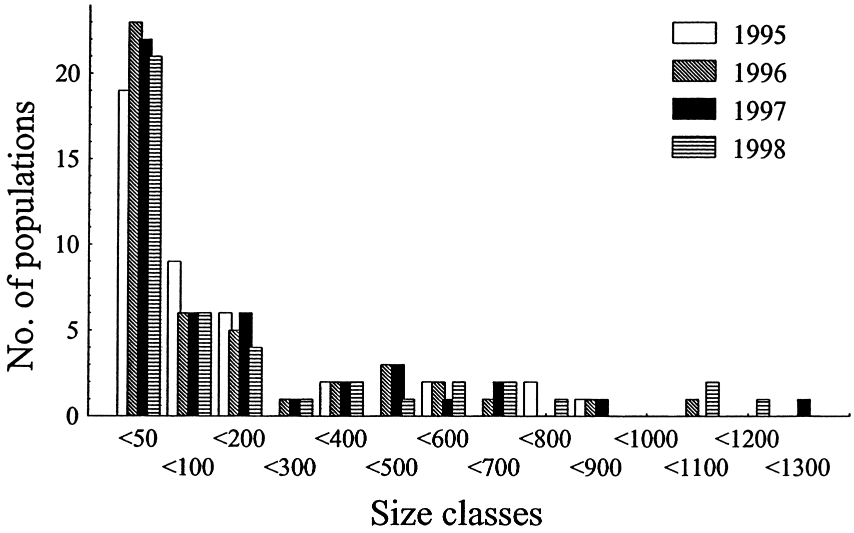

Figure 6. The observed size distribution of *Agrimonia eupatoria* populations during 1995–1998 in the Ludgo Parish (County of Södermanland) in southern Sweden. The size classes refer to the number of adult individuals (vegetative and/or reproductive individuals) counted in the populations during the years.

growth were more important for herbs, i.e. contributed most to λ, whereas survival was more important for woody plants. However, they showed that λ was also more sensitive to survivorship for forest herbs. For both perennial species in this study, λ was projected to be most sensitive to transitions among the most frequent classes in the study populations, which were the adult stage classes. Survival, (stasis and retrogression) had higher elasticity values, ranged between 75–96%, than growth (progression) and fecundity together. Thus, demographically the two study species behave more like woody plants (Silvertown et al. 1993). However, several studies on perennial herbs have reported the same pattern regarding sensitivity of λ to survivorship (Bengtsson 1993; Ehrlén 1995; Horwitz and Schemske 1995; Oostermeijer et al. 1996; Menges and Dolan 1998; Eriksson and Eriksson 2000). In the life-table response experiment analysis, adult stage classes also contributed most to the observed variation in λ within each year. The transitions with the highest contributions to the observed difference in λ between populations were also the ones with the highest elasticity values, i.e. hypothetical future changes in these transitions were projected to affect λ the most. However, the transitions that contribute the most to the difference in λ are not necessarily the ones with the highest elasticity values (Horwitz et al. 1997; Caswell 2000).

In the stochastic simulation the effects of a variable environment was examined by introducing temporal variation by randomly selecting from a set of transition matrices. Expected time to extinction was in the order of centuries for the study populations (Eriksson 1994; Ehrlén 1995). Out of 100 populations not one was projected to become extinct within 100 years. Even though these estimates of expected time to extinction cannot be taken at face value, they indicate that local populations are not subjected to a high

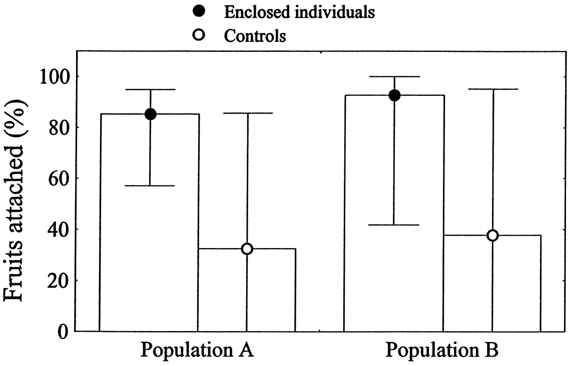

Figure 7. Seed dispersal in two road verge populations of *Agrimonia eupatoria*. Median values and ranges (min - max) of the proportion of attached fruits on enclosed individuals (nets) and controls (without nets) in the two study populations A and B. This was possible to measure for 20 of the enclosed plants in population A, and for 44 plants in population B. Individual plants located in the permanent plots in population A and B, functioned as controls in the experiment, 31 and 38 individuals respectively. Effects of the net treatment (Mann-Whitney U-test): Population A: $P < 0.001$, $n = 51$; Population B: $P < 0.001$, $n = 82$).

extinction risk if the conditions prevailing during the study also prevail in the future. For the small population of *A. eupatoria* (projected to be declining) it would take several decades for a population with an initial size of ten individuals to become extinct. Hence, environmental stochasticity seems not to be a very important feature of the dynamics of the populations. In general, small populations suffer a greater risk of extinction due to stochasticity. Fluctuations in population size may subject small populations to a high extinction risk (Soulé 1987; Nunney and Campbell 1993; Menges 1998, 2000).

In the matrix models, fecundity and recruitment through seedlings did not have any profound significance for the population growth rate in the study populations. However, for the long-term maintenance of plant populations opportunities for successful recruitment is needed. Neither of the study species possess a permanent seed bank that could buffer against negative impact of environmental variability (Venable and Brown 1993). Results from seed-sowing indicated that seedling recruitment in *G. rivale* was enhanced by "immigration" of seed in both study populations and by small scale disturbances in the seminatural grassland. *Geum rivale* is able to compete in grassland and other open habitats where it can develop dense populations largely as a result of vegetative growth (Taylor 1997). The results are congruent to what has been found for *A. eupatoria* in grassland fragments in road verges, and with previous studies for several grassland species within the study area (Eriksson and Eriksson 1997; Kiviniemi and Eriksson 1999), Kiviniemi in prep.).

The regional survey revealed that the majority of the populations of *A. eupatoria* were relatively small (contained less than 100 individuals). *Agrimonia eupatoria*, associated with the former hay meadows (Ekstam et al. 1988) is now almost entirely restricted to grassland fragments in road verges. The mowing management of the road verges in the study area is surely of importance for the long-term persistence of *A. eupatoria* and other grassland species in these habitats (Milberg and Persson 1994). Mowing machinery may also be an important vector of dispersal along road verges. In road verge grassland in the Netherlands, mowing had a positive effect on the population growth rate of *Hypochoeris radicata*, a rosette-forming perennial, by stimulating fecundity and recruitment and thus population size (de Kroon et al. 1987). New colonisations of *A. eupatoria* populations have been observed during the survey (even though they were not actively looked for), and several populations have also gone extinct in the study area. Loss of grassland fragments in road verges constitute a deterministic change in the local environment of *A. eupatoria*. Populations face a risk of extinction due to road graders (scrapers) that destroy these marginal sites and plant populations within them, irrespective of population size.

Evidence for dispersal limitation has been found for many plants inhabiting fragmented habitats (Primack and Miao 1992; Quinn et al. 1994; Kiviniemi and Eriksson 1999; Ehrlén and Eriksson 2000; Eriksson and Eriksson 2000). The enclosure experiment of *A. eupatoria* in the two study populations indicated that many fruits may be dispersed away from populations, which could decrease the average fitness of the populations (Valverde and Silvertown 1997a). However, if the local populations of *A. eupatoria* function as a metapopulation, seed dispersal would aid in the regional persistence of the species. There is still not so much evidence for metapopulation structure in plants (van der Meijden et al. 1992; Ouborg 1993; Overton 1994; Eriksson 1996; Husband and Barrett 1996; Valverde and Silvertown 1997b; Husband and Barrett 1998).

In this study, the overall stable dynamics and the low projected extinction risks of the investigated study populations imply their ability to persist in a variable environment, as long as their local environment does not change drastically (e.g. catastrophes caused by road graders in road verge habitats). Stasis and growth in the adult stage classes, which were the most frequent stage-classes, contributed most to population growth, and are therefore life-cycle stages that are of importance for the maintenance of the populations. Experimental seed addition within populations indicated that recruitment was both seed and microsite limited (Eriksson and Ehrlén 1992; van der Meijden et al. 1992). Earlier studies have revealed that both species have a good dispersal potential (in space) (Kiviniemi 1996; Kiviniemi and Telenius 1998; Kiviniemi and Eriksson 1999), which is of importance in a fragmented habitat (Tilman et al. 1994) Traits that influence the colonisation capacity of patches (e.g. dispersal characteristics and seed production) and the survival within patches (longevity) are important for the regional dynamics of species (Ehrlén and Van Groenendael 1998). The availability of suitable habitat patches is also crucial for the long-term persistence of species. Thus, the abundance of a species reflects both changes in the size and the number of populations. In order to understand these patterns, more information on both the dynamics of local populations and metapopulations are needed.

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Appendix 1

Transition probability matrices for the two populations of *Agrimonia eupatoria*.

Table tablea. Population A

Stage at time *t*+1	Stage at time *t*			
	Seedling	Juvenile	Vegetative	Reproductive
1993–1994	n = 13	n = 14	n = 28	n = 37
Seedling	0	0	0	0.189
Juvenile	0.154	0.357	0	0
Vegetative	0	0.429	0.5	0
Reproductive	0	0	0.464	1.0
1994–1995	n = 7	n = 7	n = 20	n = 50
Seedling	0	0	0	0.08
Juvenile	1.0	0.143	0	0
Vegetative	0	0.0	0.95	0.32
Reproductive	0	0	0	0.68
1995–1996	n = 4	n = 8	n = 35	n = 34
Seedling	0	0	0	0.265
Juvenile	0.75	0.625	0	0
Vegetative	0	0	0.857	0.206
Reproductive	0	0	0.029	0.735
1996–1997	n = 9	n = 8	n = 37	n = 26
Seedling	0	0	0	0.269
Juvenile	0.111	0.5	0	0
Vegetative	0	0	0.568	0.115
Reproductive	0	0	0.324	0.885
1997–1998	n = 7	n = 5	n = 24	n = 35
Seedling	0	0	0	0.057
Juvenile	0.286	0.2	0	0
Vegetative	0	0.4	0.875	0.371
Reproductive	0	0	0.042	0.629

Table tableb. Population B

Stage at time *t*+1	Stage at time *t*			
	Seedling	Juvenile	Vegetative	Reproductive
1993–1994	n = 5	n = 7	n = 11	n = 39
Seedling	0	0	0	0.538
Juvenile	0.6	0.714	0	0
Vegetative	0	0.286	0.545	0.051
Reproductive	0	0	0.454	0.949
1994–1995	n = 21	n = 8	n = 10	n = 42
Seedling	0	0	0	0.214
Juvenile	0.952	0.5	0	0
Vegetative	0	0.375	0.8	0.095
Reproductive	0	0	0.2	0.905
1995–1996	n = 9	n = 24	n = 15	n = 41
Seedling	0	0	0	0.049
Juvenile	0.556	0.625	0	0
Vegetative	0	0	0.733	0.049
Reproductive	0	0	0.2	0.951
1996–1997	n = 2	n = 20	n = 13	n = 42
Seedling	0	0	0	0.333
Juvenile	1.0	0.8	0	0
Vegetative	0	0.1	0.462	0.024
Reproductive	0	0	0.462	0.976
1997–1998	n = 14	n = 18	n = 9	n = 47
Seedling	0	0	0	0.191
Juvenile	0.857	0.778	0	0
Vegetative	0	0.056	0.667	0.277
Reproductive	0	0	0.222	0.702

Appendix 2

Transition probability matrices for the two populations of *Geum rivale*.

Table tablec. Population C

Stageat time*t*+1	Stage at time *t*				
	Seedling	Juvenile	Small vegetative	Large Vegetative	Reproductive
1993–1994	n = 2	n = 15	n = 22	n = 13	n = 15
Seedling	0	0	0	0	0.533
Juvenile	0	0.333	0	0	0
Small vegetative	0	0.467	0.182	0.154	0.067
Large vegetative	0	0	0.500	0.385	0.267
Reproductive	0	0	0.318	0.462	0.667
1994–1995	n = 8	n = 3	n = 21	n = 21	n = 23
Seedling	0	0	0	0	0.261
Juvenile	0	0.667	0	0	0
Small vegetative	0	0	0.524	0.095	0.087
Large vegetative	0	0.333	0.238	0.429	0.130
Reproductive	0	0	0.238	0.429	0.783
1995–1996	n = 6	n = 2	n = 16	n = 17	n = 33
Seedling	0	0	0	0	0.333
Juvenile	0	1.0	0	0	0
Small vegetative	0	0	0.375	0.235	0.152
Large vegetative	0	0	0.125	0.353	0.152
Reproductive	0	0	0.250	0.353	0.667

Table tabled. Population D

Stage at time *t*+1	Stage at time *t*				
	Seedling	Juvenile	Small vegetative	Large vegetative	Reproductive
1993–1994	n = 10	n = 19	n = 78	n = 48	n = 5
Seedling	0	0	0	0	3.0
Juvenile	0.6	0.526	0	0	0
Small vegetative	0	0.421	0.821	0.271	0.200
Large vegetative	0	0	0.128	0.667	0.400
Reproductive	0	0	0.013	0.063	0.200
1994–1995	n = 15	n = 17	n = 115	n = 57	n = 14
Seedling	0	0	0	0	2.786
Juvenile	0.600	0.294	0	0	0
Small vegetative	0	0.471	0.557	0.298	0.143
Large vegetative	0	0	0.461	0.614	0.429
Reproductive	0	0	0	0.053	0.429
1995–1996	n = 39	n = 14	n = 94	n = 88	n = 9
Seedling	0	0	0	0	1.444
Juvenile	0.308	0.286	0	0	0
Small vegetative	0	0.214	0.436	0.102	0
Large vegetative	0	0.143	0.447	0.739	0.778
Reproductive	0	0	0	0.091	0.111

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